Ecology and Conservation of the Indochinese tiger (*Panthera tigris corbetti*) in the Dong Phayayen-Khao Yai Forest Complex in Eastern Thailand

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DECLARATION

I declare that this thesis was composed by myself and that the work contained herein is my own except where explicitly stated in the text. The work has not been submitted for any degree or professional qualification except as specified.

ABSTRACT

Catastrophic population declines threaten the under-studied and Endangered Indochinese tiger (*Panthera tigris corbetti*) with extinction. Thailand now plays a critical role in the conservation of the Indochinese subspecies, given few known breeding populations in other range countries. Thailand's Dong Phayayen-Khao Yai forest complex (DPKY) is recognised as a tiger landscape of national importance, though it has been largely understudied. A lack of information on the status, ecology, and conservation of tigers in this landscape undermines effective management and renders an incomplete picture of its role in the conservation of tigers in the region.

The goal of this thesis is to assess the ecology and conservation status of tigers in the Dong Phayayen-Khao Yai Forest Complex. Specifically, through this thesis, I aim to: 1) Assess tiger presence, persistence, breeding, and population density; 2) Explore important associations with habitat, prey, and threats that influence the population; 3) Investigate long-term habitat connectivity and population viability; and (4) Conduct novel assessments on methods commonly used in ecological research.

In ***Chapter 1***, I contextualize the research conducted in this thesis by providing an overview of the conservation history and status of tigers in Southeast Asia and Thailand. This chapter also highlights prevailing methodological trends involved in such research.

Chapter 2 of this thesis represents the first dedicated, long-term study on tigers across DPKY. Here, I describe heterogeneity in the distribution of tigers across the landscape, identify potential prey species, and document long-term persistence of individuals. Importantly, results confirm breeding at the site, establishing DPKY as one of the few remaining breeding populations of Indochinese tigers globally and a tiger landscape of global conservation significance.

In ***Chapter 3***, I investigate the degree to which scale- and functional form (shape)-optimization affect

performance of habitat selection models for tigers and conduct a first-of-its-kind assessment of optimization approaches in modelling species-habitat relationships. Importantly, results confirm the importance of optimizing such models for spatial scale while optimizing for functional form did not improve model performance. These results reinforce the importance of broad-scale protection of core tiger habitat in DPKY as part of a landscape-scale management strategy.

In ***Chapter 4***, I evaluate the degree to which prey, human presence, and environmental factors explain tiger presence in DPKY both independently and collectively. I found that tiger presence had strong, positive associations with wild boar (*Sus scrofa*) presence and prey richness, and strong negative associations with human settlements, public roads, and poacher presence. However, environmental characteristics, particularly confounded with human factors, best explained variance in tiger presence, suggesting these factors could aid in modelling potential tiger occurrence where other data may be lacking.

Chapter 5 of this thesis represents the first dedicated peer-reviewed study to estimate tiger population density in DPKY. Importantly, I utilize simulations to aid in the development, validation, and implementation of an effective survey design, an approach which may be beneficial for similar studies of low-density carnivore populations. While estimated density (0.63 ± SE0.22 [0.32–1.21] tigers per 100km^2) and population (20 [14–33]) were relatively low, these key metrics provide a crucial, reliable baseline for evaluating population changes over time.

In ***Chapter 6***, I simultaneously evaluate the potential for DPKY’s tiger population to disperse to other potential habitat and assess the sensitivity of connectivity models to changes in key parameters. Here, I demonstrate that landscape connectivity models can be highly sensitive to parameter values with significant interactions and relative strength of effects varying by timestep. Dispersal ability, mortality risk, and their interaction dominated predictions, underscoring the importance of incorporating these factors in a spatially- and temporally-dynamic framework. Results from this study suggest reasonable dispersal potential of tigers to Khao Yai National Park in DPKY though dispersal and persistence within and beyond the landscape could be drastically undermined by increased mortality.

In ***Chapter 7***, I utilize an individual-based, spatially-explicit population modelling approach to evaluate the effects of landscape change scenarios and mortality risk on the probability of tiger persistence in DPKY as well as model sensitivity to mortality risk, resistance surface transformation, and population density. Mortality risk dominated predictions of population persistence with results indicating strong negative effects resulting from road expansion and construction of dams. The high sensitivity of models to mortality risk and high variability in population trajectories suggest this population is extremely vulnerable to extinction.

Lastly, in ***Chapter 8***, I summarize and synthesize findings from previous chapters. Here, I discuss the implications of this research for the management and conservation of tigers in this landscape, offer perspectives on methods of research in this field, and contextualize results within the broader realms of conservation in Thailand and Southeast Asia.

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PUBLICATIONS AND CONTRIBUTIONS

This thesis has been approved to be submitted as an integrated thesis/collection of papers. The publication status of Chapter 2 through Chapter 7 are noted in the title pages of these chapters. As primary author on all chapters and publications, I substantially led conceptual development, analytical implementation, interpretation, and writing of these works, supported appropriately by my supervisors and collaborators. Data included in the thesis originated from field work conducted in Thailand in collaboration with Freeland Foundation, and the Department of National Parks, Wildlife and Plant Conservation. Those that played key roles in data collection and support are acknowledged as co-authors in resulting publications. I acted as the primary driver behind the management, design, and execution of studies in this thesis and was involved in all facets of implementation. My contribution represents a substantial majority of work in these studies. Additional, related published works to which I contributed are also highlighted in the Appendix of this thesis.

CONTENTS

Chapter 1

Introduction

Introduction

Few species have inspired human imagination, fear, and reverence like the tiger (*Panthera tigris, Linnaeus 1758*). Across a history spanning two to three million years (Luo et al. 2004; Davis et al. 2010), the tiger has become entrenched in the consciousness and culture of people living with the species (Paddle 2003; Thapar 2004). The tiger is pervasive in human culture, becoming arguably the most recognizable, admired, and charismatic species in the world (Macdonald et al. 2015; Courchamp et al. 2018; Albert et al. 2018).

Apex predators, such as tigers, are believed to exert an important top-down influence on the ecological systems in which they are embedded (Paine 1980; Luo et al. 2010; Terborgh and Estes 2010). While there is a paucity of tiger-specific studies relating to trophic cascades resulting from their removal from an ecosystem, available studies of other apex predators, such as wolves (*Canis lupus*), document far-reaching, complex, and potentially unforeseen ecosystem impacts following extirpation (Ripple and Beschta 2004; Ripple et al. 2014).

In threatened ecosystems, tigers can effectively serve as flagship species to attract funding for conservation efforts (Sergio et al. 2006). Due to the large home range size of the tiger (Sunquist 2010), such efforts may result in benefits to a wide variety of other species within the local ecosystem. For species that lack scientific research, recognition, or perceived charisma, the tiger may serve as an effective ecological and conservation umbrella or ambassador species (Sergio et al. 2006; Wikramanayake et al. 2010; Dickman et al. 2015; Macdonald et al. 2017) .

While protection of tigers for their own sake is arguably convincing in its own right, the role of tigers in an ecosystem can also have significant and far-reaching economic benefits. A single protected area with tigers may generate substantial local benefits through tourism, forest products, and community forestry (Heinen and Mehta 2000; Wikramanayake et al. 2010; Badola et al. 2010). Indirectly, these ecosystems have larger-scale benefits such as carbon sequestration and maintenance of watersheds (Cutter and Hean 2010; Bhagabati et al. 2014) which underpin economic security for millions of people in tiger range countries, with potential income-generation opportunities via payment for ecosystem services initiatives (Dinerstein et al. 2013).

1. The Global Decline of Tigers

Despite the role of tigers in culture, ecosystems, and economies and its pervasiveness in humanity's collective consciousness, the species is no longer pervasive within the forests of Asia. Historically, tigers once ranged throughout Asia (Luo et al. 2004). However, both the tiger's range and population have been subject to catastrophic declines, particularly over the past century (Walston et al. 2010b). This has been driven by significant human pressure, including direct killing, loss of prey, and loss of habitat, compounded by habitat fragmentation (Dinerstein et al. 2007; Goodrich et al. 2015; Sandom et al. 2017a, b). Such pressures have arisen in part from rapid increases in human population in Asia, which tripled in size from 1950 to 2015 (UN DESA 2015), driving accelerated growth in resource demands and infrastructure. The result has been an estimated 96% loss in the tiger's population and a 93% loss in habitat since the start of the 20th century (Sanderson et al. 2006; Walston et al. 2010b). Habitat loss has been particularly acute in South and Southeast Asia, with a 41% reduction between 1996 and 2006 (Sanderson et al. 2006) and an estimated forest loss of 71,134km^2 in priority tiger conservation landscapes (TCLs) from 2001 to 2014 (Joshi et al. 2016).

Of nine currently described subspecies of tiger (Luo et al. 2004; Goodrich et al. 2015), three are now classified as extinct - the Bali tiger (*Panthera tigris balica*), the Caspian tiger *Panthera tigris virgata*), the Javan tiger (*Panthera tigris sundaica*) - and a fourth, the South China tiger (*Panthera tigris amoyensis*) is likely to be extinct in the wild (Tilson et al. 2004; Goodrich et al. 2015). Remaining described subspecies extant in the wild include the Bengal tiger (*Panthera tigris tigris*), the Sumatran tiger (*Panthera tigris sumatrae*), the Malayan tiger (*Panthera tigris jacksoni*[1]), the Amur tiger (*Panthera tigris altaica*), and the Indochinese tiger (*Panthera tigris corbetti*)[2]. Currently, approximately 2,154-3,159 individuals are believed to occur in the wild across their global range (Goodrich et al. 2015).

[1] Kitchener et al. (2017) assert that *Panthera tigris jacksoni,* "has not been named in accordance with the rules of the ICZN and is a *nomen nudum*".
[2] A task force of the IUCN Cat Specialist Group (Kitchener et al. 2017) proposed a revision of *Panthera tigris* and its subspecies, which included reclassification of tiger taxonomy into two subspecies: a mainland tiger subspecies (*Panthera tigris tigris* Linnaeus, 1758) and a Sunda island tiger subspecies (*Panthera tigris sundaica,* Temminck, 1844). At the time of this writing, the IUCN Red List has not yet formally adopted this reclassification (Goodrich et al. 2015). As such, prevailing IUCN Red List classifications are used in this thesis.

Tigers have been subject to considerable funding, research, and management efforts in order to understand and recover populations (Walston et al. 2010b). Such investments appear to be generating positive results, as evidenced by the recent announcements of a rise in global tiger numbers, though not without debate (Karanth et al. 2016; WWF 2016a, b; Harihar et al. 2017). Caution should be taken in viewing global population increases as indicative of the current state of tiger conservation overall. Walston et al. (2010b) documented only 42 source sites with confirmed breeding throughout the tiger's range, an area covering 90,000km^2, or approximately 5.9% of the tiger's current estimated range (Sanderson et al. 2006). Even marginal population increases in tiger range states that support larger numbers of tigers may obscure catastrophic declines in smaller populations elsewhere. This is most starkly illustrated in Southeast Asia, where recent declines may represent national extirpation of tigers and, consequently, a reduction in the number of current range states with wild tigers, severely constraining global recovery efforts.

2. Tigers in Southeast Asia

The Indochinese tiger (*Panthera tigris corbetti*) was historically distributed throughout most of mainland Southeast Asia (Luo et al. 2004; Fig. 1). Historical range states included Cambodia, Lao PDR, Myanmar, Thailand, Viet Nam and southern China (Lynam 2010). Now classified as Endangered under the IUCN Red List, the subspecies has followed a similarly catastrophic population trajectory as its counterparts (Lynam and Nowell 2011; Goodrich et al. 2015). Obscuring this decline has been a paucity of reliable population data in current range countries, suggesting this may be one of the least understood subspecies of tiger (Lynam and Nowell 2011).

The most recent IUCN Red List assessment of the Indochinese tiger (Lynam and Nowell 2011) is cause for concern. Government estimates cited in the assessment estimate a total wild population of 352 individuals in Cambodia, Lao PDR, Myanmar, Thailand, and Viet Nam, though these figures are noted as being speculative. At the time of the assessment, reviewers expressed particular concern about a lack of confirmed records of tigers in Cambodia and Viet Nam as well as low figures in one site in Myanmar.

More recent information has cast further doubt on the status of tigers in Southeast Asia and further reinforces the suggestion of Lynam and Nowell (2011) that the subspecies could qualify for Critically Endangered status (IUCN 2000). Potentially three range states have lost viable populations. In Lao PDR, Nam Et-Phou Louey National Protected Area was considered the country's only source site, with approximately 17 individuals (Walston et al. 2010a). Despite previous evidence of a viable breeding population (Johnson et al. 2006; Vongkhamheng 2011), it is now believed that tigers have been extirpated from this site (Rasphone et al. 2019). In 2016, the Cambodian government declared tigers extinct in their country and is pursuing reintroduction (AFP 2016; Gray et al. 2017), a decision met with scepticism by some (Connor 2017; Miquelle et al. 2018). Lastly, Viet Nam remains a country without a confirmed tiger record in more than 20 years (Lynam and Nowell 2011).

It is possible that the only remaining source sites for the subspecies are in Myanmar and Thailand. Myanmar's national tiger population estimate is 85 individuals though records supporting this estimate are scarce (Lynam and Nowell 2011). One population estimate for Hukuang Valley Tiger Reserve, the largest of its kind in the world, ranged considerably from 7 to 71 individuals (Lynam et al. 2009). A later study by (Naing et al. 2015) reported low and declining detection rates of tigers in the reserve over nine years, while an interview-based study on community hunting practices in an adjoining protected area reported a likely decline and possible extirpation of tigers (Rao et al. 2010). More recently, a study in the Htamanthi landscape documented seven individuals (Naing et al. 2019) while another in the Tanintharyi landscape near the Thai border documented at least five individuals (Aung et al. 2017). Tigers have also been documented in Karen state, but numbers of individuals have not been publicly disclosed (Moo et al. 2018). In 2016, a tiger from Thailand crossed the border into Myanmar and was killed by villagers, indicating transboundary movement along the shared Tenasserim mountain landscape (Smith and Saunter 2016). Protection of tigers in Myanmar is likely undermined by ongoing civil unrest, mining, infrastructure development, and hunting of tigers and prey (Lynam 2003; Lim et al. 2017) . Furthermore, rampant trade in tigers and other felids in border markets appears to continue unabated, representing a looming threat for tigers that remain (Oswell 2010; Nijman and Shepherd 2015).

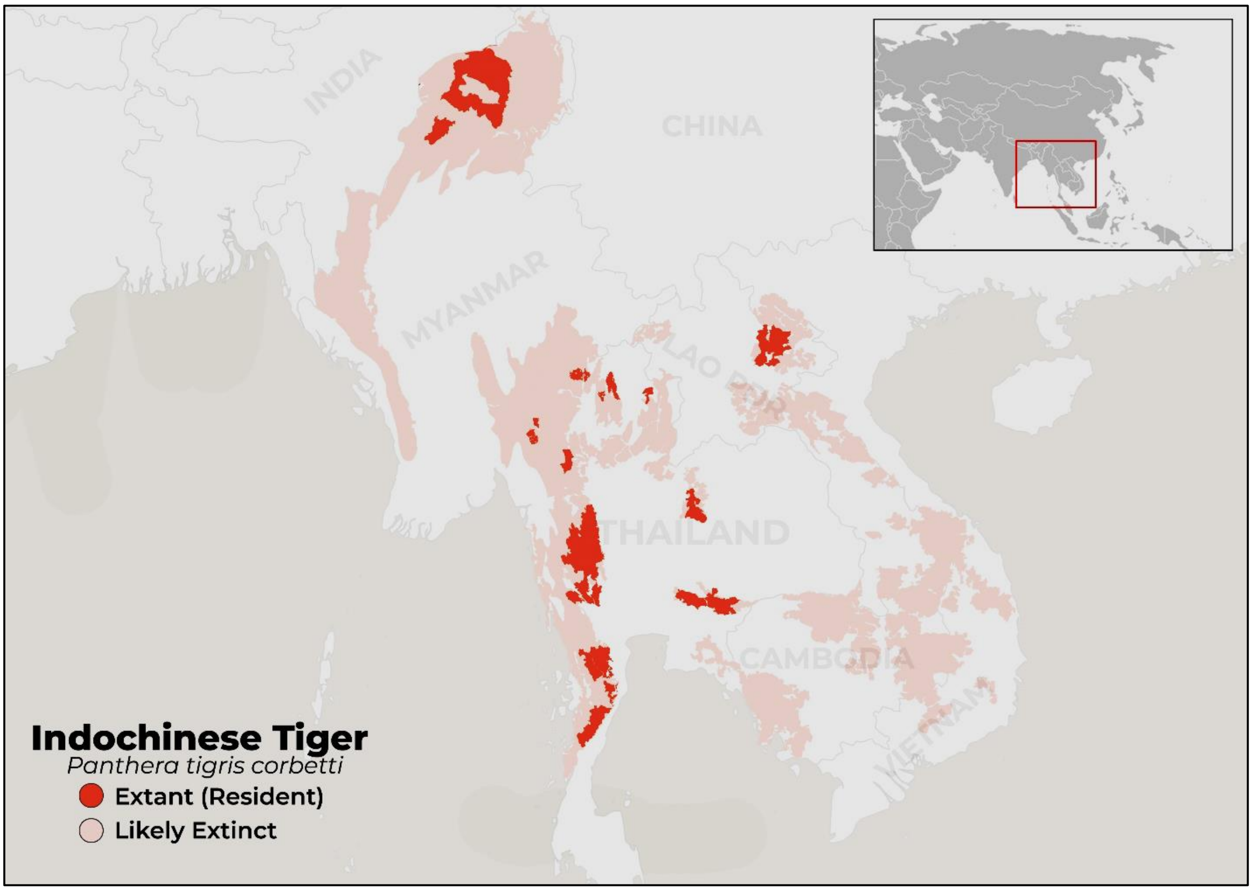

Fig. 1 Estimated extant and likely extirpated range of the Indochinese tiger (Panthera tigris; adapted from Luo et al. 2004; Panthera 2015). Given recent evidence, this range map may overestimate current range in some areas (Lynam and Nowell 2011; DNP 2016; Rasphone et al. 2019).

Severe declines are also observed in another big cat in mainland Southeast Asia, the Indochinese leopard (*Panthera pardus delacouri*). A study by Rostro-García et al. (2016) found the subspecies likely occurs in 6.2% of its historical range with only 2.4% of areas with confirmed presence. It is now likely that only two strongholds remain in the region, Peninsular Malaysia and the Northern Tenasserim Forest Complex. Many of the factors driving the decline in the region's leopards, such as poaching, habitat loss, and prey depletion, are drivers for the decline in tigers (Dinerstein et al. 2007). The likely extirpation of leopards from large parts of the region, including functional extinction in Viet Nam and Lao PDR (Rostro-García et al. 2016; Rasphone et al. 2019), appears consistent with the available evidence for tigers.

3. Tigers in Thailand

3.1 Historical context

Historically, much of Thailand was covered in forest (Mouhot 1864; Johnston 1975). Accounts from Mouhot (1864) suggest that interactions between tigers and communities were relatively common. Phylogenetic data indicates the Indochinese tiger population was historically contiguous (Luo et al. 2004), suggesting that tigers were widespread throughout, what is now, modern day Thailand.

A policy-driven expansion of agriculture, particularly rice cultivation to capitalize on emerging global markets, resulted in the deforestation of lowland areas in and around Thailand's central Chao Praya basin (Molle 2005). Much of the basin had relatively intact forest up until the 1860s (Johnston 1975) when agricultural expansion accelerated. By the 1970s, much of central Thailand had been converted to agriculture or other uses by human activities (Molle 2005).

Combined with human activities in other areas of the country, forest cover is believed to have declined from an estimated 75% in 1913 to 25% in the 1990s (Klinsawat 2016). In the 1980s, Thailand had the highest rate of annual forest loss in the region (Hirsch 1990). A national logging ban in natural forests in 1989, put in place following high-profile natural disasters and public pressure (Hirsch et al. 1989), had mixed effects (Durst et al. 2001; Lang 2002). While forest cover stabilized and increased slightly post-ban (Klinsawat 2016), encroachment into forested areas continued (Durst et al. 2001; Lang 2002).

The conversion of large forested areas in Thailand during the 20th century resulted in a restriction in the tiger's range in Thailand into fragmented forest landscapes (Tunhikorn et al. 2004). Many of these were in protected areas, which were established following the declaration of Khao Yai National Park in the 1960s (Emphandhu and Chettamart 2013). These protected areas were largely gazetted in mountainous areas that were typically unsuitable for traditional farming, prior to improvements in accessibility (Hirsch et al. 1989; Kalyawongsa et al. 1997; Molle 2005). This has resulted in a lack of representation of lowland forest and other forest types in Thailand's protected area system (Trisurat 2007). By the start of the 21st century, it is likely that tigers occurred almost exclusively within these protected area systems (Pisdamkam et al. 2010).

Not only did Thailand's tigers lose habitat during the 20th century, the country also lost two potential prey species. The Schomburgk deer (*Rucervus schomburgki*) likely became extinct in the 1930s (Duckworth et al. 2015) and Eld's Deer (*Rucervus eldii*) is likely extirpated from Thailand, save for a handful of reintroduced individuals (Gray et al. 2015). The loss of these species was likely a result of the conversion of their preferred open lowland habitat (Duckworth et al. 2015; Gray et al. 2015). Rabinowitz (1989) suggests four of six cervid species in Thailand, which typically account for a large proportion of tiger diets range wide (Sunquist et al. 1999), are rare or extinct. Elsewhere in the tiger's range, tiger density appears closely associated with prey density and prey size (Karanth et al. 2004; Sunquist 2010). While tigers are considered habitat generalists, the availability of preferred habitat of prey species is a significant limiting factor (Sunquist 2010). Rabinowitz (1993) cited lowland forest mosaic habitat as optimal habitat for tigers and prey (Sunquist et al. 1999), asserting that the loss of such areas may have been a significant contributor to the loss of tigers in Thailand, now restricted to sub-optimal, mountainous areas.

Exacerbating declines in tigers from range restrictions may have been a potential increase in poaching and trade in tigers in the early 1990s (Day 1995), though poaching statistics specific to Thailand from this period are lacking. The period was marked by an increase in poaching and trafficking globally, primarily for end markets in China which had depleted stockpiles of tiger products for traditional medicines (Mills and Jackson 1994).

3.2 Thailand tiger assessments and action plans

Estimates of Thailand's tiger population in the past several decades have been varied. The first systematic attempt at quantifying Thailand's remaining tiger population was made by Rabinowitz (1993), a survey that ran from 1987 to 1991. At the time, Rabinowitz (1993) estimated the population to number no more than 250 adults, differing substantially from previous rough estimates ranging from 400 to 600 as cited in Lekagul and McNeely (1977), Leng-EE (1979) and Jackson (1990). Later, Smith et al. (1999) estimated that Thailand had a potential national breeding population of approximately 500 tigers in 15 populations, an estimate derived from track and sign surveys.

Thailand's first national tiger action plan (Tunhikorn et al. 2004) did not provide an updated population estimate, but noted that tigers had declined substantially (Fig. 2). Authors of the plan concluded that tigers occurred almost exclusively in protected areas, specifically 15 metapopulations across 50 protected areas.

The status of tigers in the country was again updated in 2010 with the Thailand Tiger Action Plan (2010-2022; Pisdamkam et al. 2010). In addition to updating management goals, the plan provided an estimate of 190-250 tigers in the country (Fig. 3). The number of protected areas in which the tiger was believed to have occurred was also revised, reduced from 50 to 25 protected areas. These protected areas were grouped into ten conservation landscapes and metapopulations.

In 2016, Thailand's Department of National Parks, Wildlife and Plant Conservation (DNP) produced a 20-year plan for tiger management (DNP 2016). While no official population estimate was included in the report, individual population estimates for Thailand's forest complexes as described in the report (Fig. 4) totalled only 101-128+ tigers in four metapopulations (though inclusive of a vague upper bound). If this recent population range is reasonably accurate, this would constitute a much lower estimate than cited in the most recent IUCN Red List Assessment for the subspecies (Lynam and Nowell 2011). Furthermore, the plan also suggested that there may be as few as one or two tigers in two previously established and priority tiger landscapes, Kaeng Krachan Forest Complex (3,002km^2) and Phu Khieo-Nam Nao Forest Complex (2,546km^2; Pisdamkam et al. 2010). Effective extirpation of tigers from these two landscapes would be considerably damaging to the conservation prospects of Thailand's tigers, leaving two remaining potential strongholds, the Western Forest Complex (25,000km^2) and the Dong Phayayen-Khao Yai Forest Complex (6,155km^2).

3.3 Current threats

Tigers that remain in the wild in Thailand continue to be threatened by a number of human activities. Poaching and trade of tigers continues in the country (Oswell 2010; Pinitwong 2015; Pongrai 2015; Stoner et al. 2016); one of the most prolific tiger poachers, Luethai Diawcharoen, has been arrested and released on multiple occasions (*Personal Communication, T. Redford 2017*). In a recent, high-profile case, a poacher was arrested after having travelled from Viet Nam, specifically to poach tigers (Wongruang 2013). This highlights

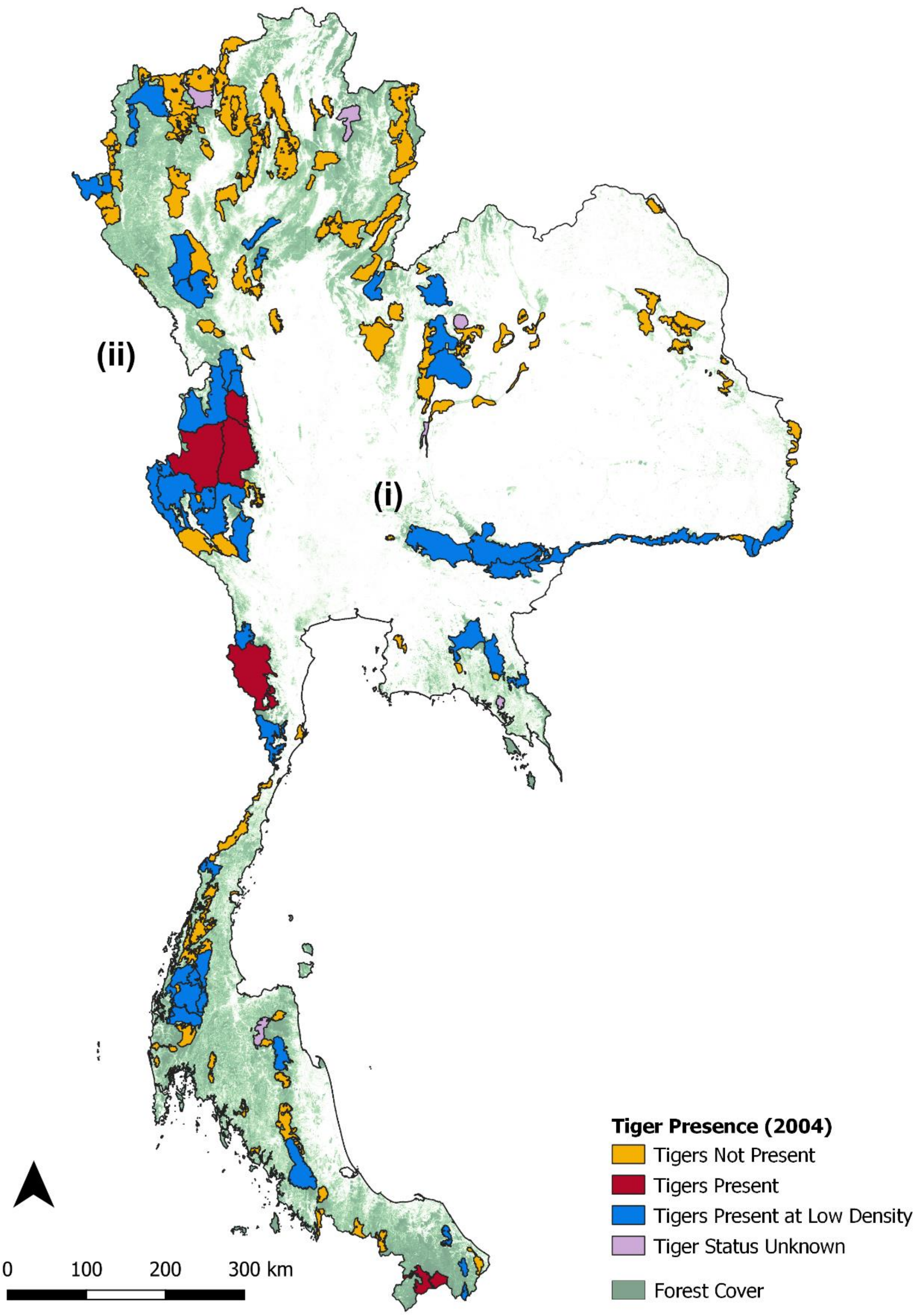

Fig. 2 Estimated range of tigers in Thailand in 2004. In the national tiger action plan in which this range map was featured, no population estimate was given, but tigers were believed to have occurred in 15 metapopulations including: (i) the Dong Phayayen-Khao Yai Forest Complex (DPKY), and (ii) the Western Forest Complex (WEFCOM). Adapted from Tunhikorn et al. (2004) with forest cover from Hansen et al. (2013).

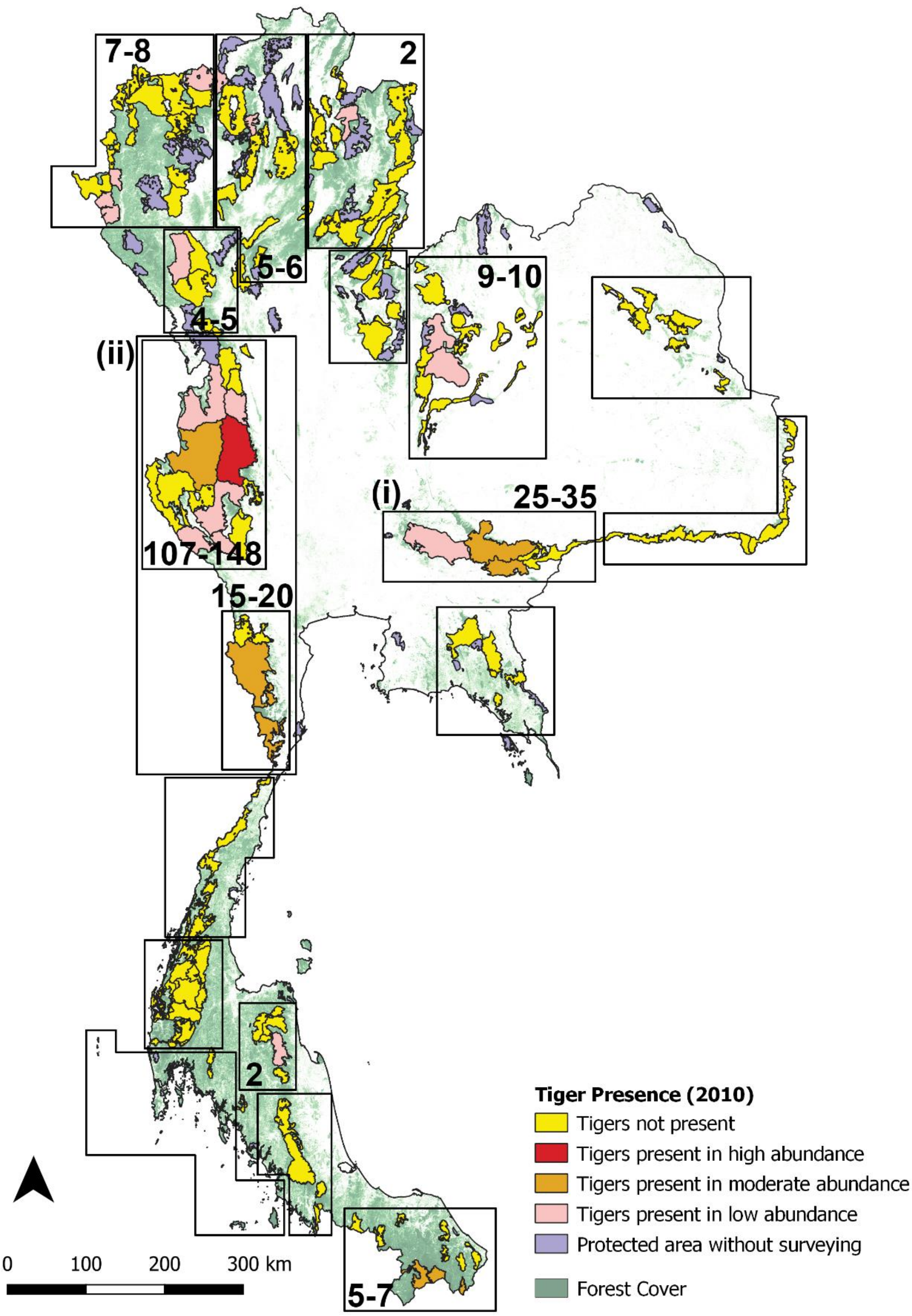

Fig. 3 Estimated range of tigers in Thailand in 2010, with population estimation of 189-252 wild tigers in 10 metapopulations, including (i) the Dong Phayayen-Khao Yai Forest Complex (DPKY), and (ii) the Western Forest Complex (WEFCOM). Adapted from Pisdamkam et al. (2010) with forest cover from Hansen et al. (2013).

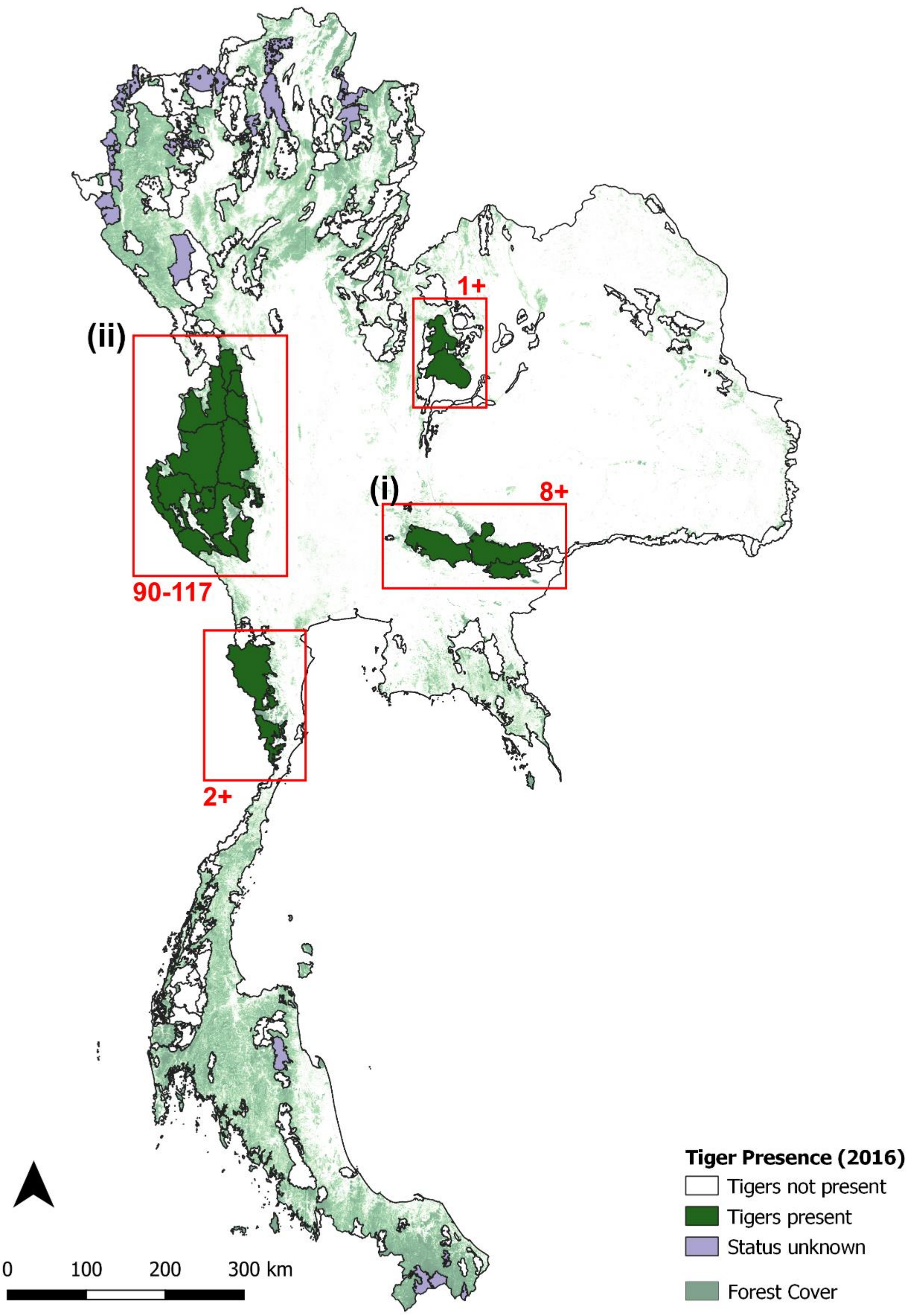

Fig. 4 Estimated range of tigers in Thailand in 2016 with a population estimation of 101-128+ wild tigers in four metapopulations, including (i) the Dong Phayayen-Khao Yai Forest Complex (DPKY), and (ii) the Western Forest Complex (WEFCOM). Adapted from DNP (2016) with forest cover from Hansen et al. (2013).

that some poachers are willing to travel large distances and that the loss of tigers elsewhere in the region may inexorably drive an increase in poaching pressure on remaining Thai populations.

While tigers are believed to occur primarily in protected areas, large scale intensification of human activities, habitat conversion, and large infrastructure projects could threaten the integrity of these landscapes (Pisdamkam et al. 2010). The increasing economic development of Thailand may facilitate additional growth of urban areas and transnational economic corridors in and around tiger habitat (Kobayashi et al. 2017; Wongwuttiwat and Lawanna 2018). In turn, this could facilitate increasing pressure to expand or develop roads in, and in close proximity to, remaining tiger habitat (IUCN World Heritage Outlook 2020). In addition, population growth and climate change is driving concerns over water security as a considerable socio-economic challenge (Marks 2011; Seeboonruang 2016; Manorom 2020). This may prompt increasing pressure for additional dams and reservoirs at major rivers originating in protected areas, projects that could potentially inundate parts of tiger habitat (IUCN 2015; IUCN World Heritage Outlook 2020).

Long-term genetic viability of tiger persistence is also a concern, given the high degree of fragmentation of tiger populations in the country. Only one population in the country may be genetically viable over the next 100 years (Klinsawat 2016). Others may be subject to the effects of inbreeding depression and genetic drift, which may leave them vulnerable to environmental and demographic stochasticity (Kenney et al. 2014).

While population figures remain obscure, it is certain that tigers have declined substantially over the past several decades and are now extremely vulnerable to extinction. If Thailand hosts the majority of remaining Indochinese tigers, as evidence may suggest, this represents a critical juncture in the conservation of tigers in Southeast Asia

4. Tigers in the Dong Phayayen-Khao Yai Forest Complex

4.1 Overview

The Dong Phayayen-Khao Yai Forest Complex (DPKY) is located approximately 160km northeast of

Bangkok between 14° 00′ to 14°33′N and 101° 05′ to 103°14′E. It is a primarily forested landscape of approximately 6,155km^2, extending along an east-west orientation along part of the Phnom Dongrak escarpment for approximately 200km. It is situated within the jurisdiction of six provinces, Saraburi, Nakhon Nayok, Nakhon Ratchasima, Prachinburi, Sa Kaew and Buriram. To the east, it partially borders the international boundary between Thailand and northwest Cambodia. Its terrain is relatively mountainous with elevations ranging from 100m to 1,351m a.s.l..

DPKY consists of five protected areas, four national parks and one wildlife sanctuary (DNP 2004). The first park established was Khao Yai National Park (KYNP; 2,168km^2), the nation's first, in 1962. This was followed by Thap Lan National Park (TLNP; 2,236km^2) in 1981 and Pang Sida National Park (PSNP; 844km^2) in 1982. Ta Phraya National Park (TPNP; 594km^2) and Dong Yai Wildlife Sanctuary (DYWS; 313km^2) were both designated in 1996.

DPKY contains all major forest types in Eastern Thailand, but primarily consists of mixed evergreen and mixed dipterocarp/deciduous primary and secondary forest (DNP 2004). It also contains grassland/scrub areas, some of which are anthropogenic in origin. The climate of DPKY is dictated by Thailand's three major seasons which run from mid-May to mid-October (Rainy or Monsoon Season), mid-October to mid-February (Cool Season), and mid-February to mid-May (Dry or Hot Season; Khedari et al. 2002). Annual rainfall in DPKY ranges from 1,000mm to 2,270mm, mostly occurring during the rainy season (DNP 2004), characterized by almost daily rainfall. This transitions into a relatively dry period with lower temperatures in the cool season. The dry or hot season is characterized by high temperatures and little rainfall; severe droughts and widespread water scarcity are common during this season (Khedari et al. 2002). The average annual temperature for the complex is 23°C (UNEP 2011).

DPKY's ecological significance has been widely recognized. In 2005, it was inscribed on the United Nations Educational, Scientific and Cultural Organization's (UNESCO) World Heritage List under criterion X[3] for its outstanding natural and conservation value (UNESCO 2017). Among the characteristics cited in this

[3] "*Contain[s] the most important and significant natural habitats for in-situ conservation of biological diversity, including those containing threatened species of outstanding universal value from the point of view of science or conservation." (UNESCO - http://whc.unesco.org/en/criteria/)*

decision was DPKY's significant flora and fauna, including 112 mammals, 392 birds, 200 reptiles/amphibians, and 2,500 plant species (DNP 2004).

The landscape also has considerable economic significance. DPKY is a source for a number of major rivers in five watersheds (DNP 2004). This includes the Mun river, which acts as a tributary of the Mekong. These rivers are also the source of a number of reservoirs around the complex. In effect, the complex is a significant source of water for Northeast Thailand, underpinning an agricultural industry which provides the economic foundation for one of Thailand's poorest areas (Bedi et al. 2007).

The complex also supports a substantial tourism industry. Protected areas in Thailand designated as national parks permit tourism activities within their boundaries; however, wildlife sanctuaries are not open to tourists (UNEP 2011). Due to its proximity to Bangkok, parts of the complex attract large numbers of tourists, particularly Khao Yai National Park. From 2003-2007, Khao Yai National Park averaged approximately 904,845 reported tourists per year, increasing during that period at a rate of 6.94% per annum (Phumathan 2010). This represents a significant source of revenue for Thailand's DNP and local businesses (Cohen 2014; Bangkok Post 2015).

DPKY is situated within a primarily human-dominated landscape of human settlements, agriculture, industry, and silviculture. Major crops include cassava, rice, corn, and sugar cane. Large forest plantations primarily consist of eucalyptus, rubber, and, to a lesser degree, oil palm. The area around the complex also supports industrial activities such as sugar processing. There are no recognized indigenous communities living within or around the complex (UNEP 2011).

Management and oversight of the complex falls under the Department of National Parks, Wildlife and Plant Conservation (DNP), part of Thailand's Ministry of Environment and Natural Resources (MoNRE; DNP 2004). Within the DNP, DPKY's national parks are governed by the Office of National Parks while Dong Yai Wildlife Sanctuary is governed under the Office of Wildlife Conservation.

DPKY's protected area rangers have the legal authority to conduct enforcement operations (such as patrolling) and detain individuals suspected of breaking protected area laws. Legal cases are most often transferred and administered by the Royal Thai Police (RTP). Enforcement may be augmented by other units within DNP such as its Protection and Suppression Division, or the Royal Thai Army (RTA), Border Army, and other agencies (Ash 2015). Rangers conduct regular patrols in DPKY's protected areas, though this varies depending on the park and resources available. There are no official buffer zones in DPKY, as defined by Dudley (2013). Some areas of forest along or near park boundaries are directly adjacent to farmland, representing a "hard" boundary. In boundary areas where land has been reclaimed/reforested or areas that are denuded by human incursions into parks, forest land undergoes a more gradual transition.

DPKY, in recent decades, was subject to a number of significant human pressures which may have played a major role in shaping the current state of wildlife conservation in the area. Up until recently, Khao Yai National Park was home to a number of villages in what is currently the park headquarters area (Lynam et al. 2006). In Thap Lan National Park, the area was subject to occupation by a contingent of communist insurgents in the 1970s (Ash 2015; Stokes 2017). The vicinity of DPKY was also home to a large number of Cambodian refugees in the 1970s and early 1980s. This included "Site II", which hosted approximately 140,000 to 150,000 refugees near Ta Phraya National Park (Russell 1987). Site II was renowned for its lawlessness (Normand 1990) and anecdotal evidence suggests that the hunting of large mammals was rampant. The area also supported a training camp for Khmer Rouge soldiers (Lynam et al. 2006). Some parts of the complex also attracted sport hunting in the 1980s and early 1990s (Lynam et al. 2006). Logging concessions were also present in some parts of the complex, particularly Thap Lan National Park (Lynam et al. 2006). National highway route 3462, was constructed in 1988-1989 along a north-south orientation through the middle of TLNP and Pang Sida NP (Ash 2015). The road remained unpaved following its construction in 1988-1989 and was closed to the public in 2002 (IUCN World Heritage Outlook 2020). This history of human presence and infrastructure likely resulted in considerable pressure on local resources and wildlife.

4.2 Potential threats in the Dong Phayayen-Khao Yai Forest Complex

While all protected areas in the complex have shared borders, the complex is only partially contiguous. Major roads split the complex in two areas, along national highway Route 304 between Khao Yai National Park and Thap Lan National Park, and national highway route 348 which splits parts of Ta Phraya National

Park and Dong Yai Wildlife Sanctuary. Both highways are a potentially significant source of anthropogenic disturbance and barrier for effective wildlife migration (Wilcox and Murphy 1985; Forman and Alexander 1998). Route 304 is the main road transportation link between northeast Thailand and a major shipping port in Laem Chabang, resulting in substantial vehicle traffic (Ash 2015). UNESCO has highlighted this as a source of concern and has requested Thailand to mitigate the effects of these highways (UNESCO 2013, 2014). A highway expansion project along Route 304, which includes various structures to allow movement of wildlife, has been completed though its effects are uncertain. No such crossing structures have been planned for Route 348 (IUCN World Heritage Outlook 2020).

Human encroachment into DPKY's protected areas has been noted as a significant concern. Settlements and agricultural land have claimed approximately 21.5% of TLNP (UNEP 2011) with an estimated additional 10% considered denuded or heavily impacted by human activity, such as cattle grazing (Ash 2015). This, along with encroachment in KYNP and DYWS has been subject to a long-running encroachment crackdown by authorities in recent years (Marukatat 2014; Praiwan 2015).

While legally protected, certain infrastructure projects have been permitted inside DPKY. Notably, this includes the construction of tourist facilities, particularly in KYNP (UNEP 2011). The construction of dams have resulted in the inundation of some parts of the complex, most recently the Huay Samong Dam/ Naruebodindrachinta reservoir, which has inundated a small part of Thap Lan and Pang Sida national parks (IUCN World Heritage Outlook 2020).

Border areas of DPKY are subject to human disturbance in the form of villagers collecting NTFPs (non-timber forest products) and wildlife poaching (Ash 2015). Wildlife poaching by local residents is reported to be relatively common near park boundaries that are more accessible to villages. Most poaching is believed to be for subsistence rather than for trade purposes and is often indiscriminate. Rangers report species poached are often smaller species such as muntjac (*Muntiacus vaginalis*), mouse deer (*Tragulus kanchil*), squirrels, civets, and other rodents, but may also include larger species such as wild boar (*Sus scrofa*), bears, sambar deer (*Rusa unicolor*), or serow (*Capricornis milneedwardsii*). Illegal logging has been an ongoing source of concern, particularly for rosewood (*Dalbergia ssp.*). The high value of rosewood has attracted large numbers of armed poachers in recent years and is considered a major threat to both rosewood and wildlife species in DPKY (Ash 2015).

DPKY, as a World Heritage Site, has come under close scrutiny by UNESCO in recent years (UNESCO 2013, 2014). The UN agency has expressed concern over a number of issues, including illegal logging, cattle grazing, roads, dams, and other potential infrastructure projects. This has prompted UNESCO to consider designation of DPKY to its List of World Heritage in Danger, which has been avoided in recent committee sessions (Chanatinart 2013; IUCN World Heritage Outlook 2020).

4.3 Tiger research in the Dong Phayayen-Khao Yai Forest Complex

Prior to the research described in this thesis, knowledge of the status of tigers in DPKY has been incomplete. While there have been a number of tiger studies conducted in other parts of Thailand, including ongoing monitoring of tigers in Thailand's Western Forest Complex (WEFCOM; Simcharoen et al. 2007, 2014; Duangchantrasiri et al. 2016), this is not the case for DPKY. Prior to this thesis, there had been no major publications released, specific to DPKY, in which tigers were the focal species of interest. Insight into tigers in DPKY have primarily been the result of general assessments of faunal communities, other carnivores, or speculation based on interviews or personal communications (Lynam 2001; Kanwatanakid et al. 2002; Lynam et al. 2006; Jenks et al. 2011). Furthermore, these previous studies were focused on Khao Yai National Park which suggested tigers were, at best, present in low numbers.

A personal communication cited in Lynam et al. (2006), claimed four to five tigers were present in Khao Yai National Park's headquarters area in 1997-1998. Lynam (2001) photographed two tigers within 400 camera-trap nights (CTN) in KYNP between 1999 and 2000. The same study estimated low numbers elsewhere in the complex (4.8 tigers were estimated to occur in Thap Lan National Park). No tigers were photographed in a later study in Khao Yai National Park, which was conducted across 6,260 camera-trap nights (CTN) from 2003-2007 (Jenks et al. 2011).

A study of birds and mammals in DPKY by Lynam et al. (2006), combined camera-trap surveys with track/sign data and interviews. Camera-trap surveys were conducted from 1998-2000 in Khao Yai National

Park, Thap Lan National Park, Ta Phraya National Park, and Dong Yai Wildlife Sanctuary, though surveys were notably more geographically expansive in KYNP. Camera-trap relative abundance indices (RAI; detections per 100 trap nights) for tigers in Khao Yai National Park were relatively low. No tigers were photographed in Thap Lan National Park, Ta Phraya National Park, or Dong Yai Wildlife Sanctuary, though tracks were reported in Thap Lan. Pang Sida National Park was not included in these camera-trap surveys and authors speculated that prey densities were insufficient to support tigers in Ta Phraya National Park or Dong Yai Wildlife Sanctuary. These results were also included in a national-scale felid study by Ngoprasert et al. (2012). Lynam (2010), citing these results and personal communications, concluded that tigers in DPKY were "hanging on in ones and twos", much lower than previously suggested (Smith et al. 1999). Evidence from these studies, particularly those in later years, suggest that tigers in Khao Yai National Park were disappearing and may have been extirpated.

5. Methods in Tiger Ecology and Conservation

Given the precarious status of the tiger in Southeast Asia and Thailand, a comprehensive review of the status and ecology of the tiger in DPKY, a population of potential importance, has been overdue. Tools available for studying vulnerable species such as tigers are diverse, enabling quantitative and qualitative assessments of demographic traits, habitat use, and behavioural patterns necessary for developing management strategies (Norris 2004). However, there are a number of aspects of tiger ecology and behaviour that merit careful consideration in conducting research on tigers.

Application of research tools for tigers has been the subject of extensive discussion and revision (Karanth and Chundawat 2002; Karanth and Nichols 2017). At the site-level, the tiger is inherently difficult to monitor. It is notably elusive, ranges over large areas, and may be present in extremely low densities. These factors create logistic and resource constraints and introduce distinct methodological challenges (Karanth and Nichols 2010; Sunquist 2010).

Tools such as camera-traps can be helpful for answering fundamental questions such as where tigers occur (presence/absence), minimum number of individuals, potential prey, threats, and breeding. Placement of cameras may be opportunistic (e.g., ad hoc, lacking broad-scale organization) or targeted (part of broader placement strategy, but limited in resources[4]; Harihar et al. 2007; Stein et al. 2008; Rovero et al. 2013; Johnson et al. 2016; Rockhill et al. 2016), as is the case for many camera-trap based studies (Burton et al. 2015). If conducted over time, this could contribute valuable insight into tigers and other species in understudied landscapes (Stein et al. 2008; Jenks et al. 2011) and provide a foundation for further ecological enquiries.

With application of specific methodological and statistical frameworks in survey planning, researchers can investigate critical traits of a tiger population such as estimates of population size and density. Recently, the use of camera traps combined with a spatially explicit capture-recapture (SECR) framework (Efford 2004; Royle et al. 2014), has become a widely accepted method of estimating tiger densities which can be used to monitor population change over time (Karanth et al. 2017; Royle et al. 2017). However, researchers may face challenges in meeting statistical assumptions and ensuring resources are sufficient to carry out such surveys (Foster and Harmsen 2012), particularly for low density or understudied populations (White et al. 1982; Karanth and Nichols 1998).

Understanding habitat selection is crucial for the conservation and management of tigers and other species. Notably, processes of habitat selection are inherently scale-sensitive (McGarigal et al. 2016) and the relationships between habitat components and their selection by animals may be complex and non-linear (Austin et al. 1990). However, few studies have formally evaluated the effects of scale (McGarigal and Cushman 2002; McGarigal et al. 2016) and functional response shape (Bar-Massada et al. 2011; Fisher et al. 2011; Mateo-Sánchez et al. 2015; Devoe et al. 2015; Shirk et al. 2018) on habitat relationships. This is particularly relevant to tigers and other large mammals which have large home ranges, can disperse large distances (Smith 1993; Sunquist 2010), and can be affected by variation in the environment at broad scales (Krishnamurthy et al. 2016; Reddy et al. 2017; Hearn et al. 2018). Investigations into habitat selection of

[4] Surveys underpinning the work in much of this thesis are described as "opportunistic" though they more accurately meet the description of "targeted" surveys. For consistency with published works, I retain the use of the term "opportunistic", noting here that camera placement in these surveys was conducted as part of a broader strategy to assess tiger presence with limited resources.

tigers may benefit from explicitly accounting for scale and functional form (shape) in modelling relationships with habitat, but, without explicit evaluation on its influence in model performance, empirical evidence remains scarce.

Along with environmental and habitat considerations, the degree to which prey and human activity influence tiger presence in an area is similarly important. Prey has emerged in studies throughout the tiger's range as the strongest, or among the strongest, predictors of tiger presence (Karanth et al. 2011; Harihar and Pandav 2012; Ngoprasert et al. 2012; Barber-Meyer et al. 2013). Conversely, studies also report strong negative associations between tiger presence and anthropogenic disturbance (Kerley et al. 2002; Sunarto et al. 2012). Understanding the degree to which these factors broadly explain tiger presence independently and confounded could provide critical information for the development of protection strategies.

Lastly, tigers are naturally wide-ranging, occur within metapopulations shaped considerably through dispersal and landscape configuration. The constriction of the tiger's range to largely isolated pockets of forest across their range threatens to undermine evolutionary processes such as the maintenance of genetic diversity (Kenney et al. 1995; Vasudev et al. 2017; Thatte et al. 2018). Further isolation may likely prevent restoration of extirpated populations through natural colonization (Linkie et al. 2006; Banerjee et al. 2010; Thatte et al. 2018). This is of notable relevance to DPKY which is embedded, and potentially isolated, in a human-dominated landscape. Understanding population dynamics, degrees of connectivity with other potential habitat, and how these factors change over time with potential changes to the landscape are critical for developing long-term management and conservation strategies. However, development of such models may be challenging, undermined by uncertainty of parameters, such as population density, landscape resistance to movement, dispersal ability, and spatial variation of mortality risk. Models may be particularly sensitive to these factors and their interactions over time, necessitating careful consideration and sensitivity analysis.

6. Research Aims

Following the suspected extirpation of tigers in Khao Yai National Park, targeted camera-trap surveys were initiated by Freeland Foundation, in partnership with Thailand's Department of National Parks, Wildlife and Plant Conservation, with the purpose of detecting tigers in other areas of the complex. These surveys, which began in 2008, included five protected areas (PAs) in DPKY. Initial surveys documented notable tiger and prey presence, which provided justification for increased survey effort across DPKY. Evidence from these surveys suggested the tiger population in DPKY was larger than previously suggested (Lynam 2010) and, potentially, of considerable conservation significance. These surveys have generated valuable data on tiger presence, prey, threats and other important information, and represent the first dedicated camera-trap survey of tigers over the entirety of the DPKY landscape. This has provided a potential foundation for investigating the status and ecology of tigers throughout DPKY, which is critical for understanding its conservation importance and developing appropriate management strategies.

Given catastrophic population and range declines elsewhere in Thailand and Southeast Asia, understanding the tiger population in DPKY is of national, regional, and potentially global importance. Specifically, I recognize three focal problem statements that guide my research in this thesis:

1. The importance of the Dong Phayayen-Khao Yai forest complex (DPKY) within national and regional conservation paradigms has been unclear - tiger distribution and density, habitat use, prey species, threats, and long-term viability are not yet fully understood;
2. A lack of information on tigers, habitat, prey, threats, and other factors undermines management effectiveness; and
3. Previous tiger population surveys by Freeland/DNP have generated significant and valuable information on tigers, prey, human activity and other areas of conservation importance, but data is under-utilized and findings are unavailable to the greater scientific community.

To address these problem statements, through this thesis, I aim to: (1) analyse and describe results from these extensive camera-trap surveys, assessing the distribution and population of tigers in DPKY; (2) conduct investigations of the tiger population in DPKY, along with habitat, prey, and threats that influence tiger distribution in the landscape; (3) evaluate broad-scale landscape connectivity, long-term population viability, and key factors affecting the tiger population's future; and, (4) concurrently, conduct novel assessments on methods commonly used in ecological research.

7. Research Questions

To guide the research in this thesis, each chapter has been developed to answer a specific research question pertaining to tigers in DPKY:

1. What does opportunistic, long-term monitoring of tigers reveal about the presence of tigers and conservation significance in DPKY?;
2. How does habitat selection of tigers explain heterogeneity in tiger distribution in DPKY?;
3. How do environment, prey, and human factors explain heterogeneity in tiger distribution within DPKY?;
4. What is the population density of tigers in DPKY?;
5. To what extent is DPKY's source population connected to other potential habitat within DPKY, elsewhere in Thailand, and in Cambodia/Lao PDR?; and
6. What is the potential long-term viability of the tiger population in DPKY and what factors affect this viability?

In addition, some thesis chapters also explore research questions pertaining to methods used in ecological research, including:

7. To what degree is the explanatory power of habitat selection models affected by spatial scale- and functional form (shape) optimization?;
8. To what extent can simulations be used to guide study design for population density surveys?; and
9. How sensitive are population connectivity and viability models to parametric variation and to what degree do model parameters interact to affect model predictions?

8. Thesis Overview

I explore the research questions outlined above in six distinct studies (***Chapter 2*** – ***Chapter 7***) and provide a summary and synthesis of important findings in a concluding Discussion chapter (***Chapter 8***). I briefly describe these chapters below:

Chapter 2 - Opportunity for Thailand's forgotten tigers: Assessment of the Indochinese tiger **Panthera tigris corbetti** ***and its prey with camera-trap surveys***

This chapter presents and summarizes results from the first camera-trap study focused on tigers across all protected areas in DPKY from 2008-2017. The goal of this chapter was to assess tiger and prey populations across all five protected areas of this forest complex, reviewing discernible patterns in rates of detection, as well as individual persistence, evidence of breeding, and presence of other species of interest.

Chapter 3 - Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: A case study of tigers (**Panthera tigris*****) in Thailand.***

The third chapter of this thesis concurrently evaluates patterns of habitat selection of tigers in DPKY while providing the first formal assessment of the relative impacts of scale-optimization and functional form (shape) optimization on model performance and habitat suitability predictions. This chapter also explores how the optimization of models influences conclusions regarding tiger habitat selection and spatial variation of the probability of occurrence across DPKY.

Chapter 4 – Environmental factors, human presence, and prey interact to explain patterns of tiger presence in Eastern Thailand

This chapter examines which factors, among prey, human presence, and environmental characteristics, best explain tiger presence in the Dong Phayayen-Khao Yai Forest Complex (DPKY). Using survey data described in ***Chapter 2***, this chapter evaluates the relationship between tiger presence and a suite of prey, human presence, and environmental variables, using variance partitioning to discern the degree to which variance in tiger detections are explained by these factors independently and confounded.

Chapter 5 - Estimating the density of a globally important tiger (*Panthera tigris*) population: Using simulations to evaluate survey design in Eastern Thailand

This study highlights the challenges associated with developing a robust study design capable of generating a population density estimate for a low-density population. The goal of this chapter is to (1) use simulations to investigate and evaluate spatially-explicit capture-recapture study design, and (2) generate a reliable estimate of density for a population of tigers in DPKY. Simulations were conducted on different camera-trapping arrays with variations of model parameters. Simulation predictions were then compared with real-world performance to validate this approach. Importantly, this chapter also generates a baseline estimate of tiger density and population for future evaluation.

Chapter 6 - How Important Are Resistance, Dispersal Ability, Population Density and Mortality in Temporally Dynamic Simulations of Population Connectivity? A Case Study of Tigers in Southeast Asia

Using spatially- and temporally-explicit simulations, this chapter provides an evaluation of the sensitivity of population distribution, abundance and connectivity of tigers in DPKY and beyond, to variations of resistance surface, dispersal ability, population density, and mortality. Specifically, this study tests the effects and interactions of these factors on predicted population size, distribution and connectivity, as well as displacement and divergence in scenarios across timesteps. This chapter provides insight into how conclusions on landscape connectivity and persistence of species - in this case, tigers in DPKY - are affected by the variation and interaction of these factors.

Chapter 7 - Tigers on the edge: Mortality and landscape change dominate individual-based spatially-explicit simulations of a small tiger population

This chapter utilizes an individual-based, spatially-explicit population modelling approach to evaluate the relative effects of potential landscape change scenarios and mortality risk on the probability of tiger persistence in DPKY. Concurrently, this chapter includes an evaluation of the relative effect of, and sensitivity of predictions to, spatially-differential mortality risk, landscape resistance transformation, and maximum potential population density. Ultimately, this study aims to generate insight on the factors likely to affect tiger persistence for the development of conservation and management strategies in DPKY while highlighting key considerations for spatially-explicit population modelling for other threatened species.

Chapter 8 - Discussion

The final chapter of this thesis provides a broad summary and synthesis of the results from the previous chapters and explores the implications of these results on the conservation of tigers in DPKY and for methods in large carnivore research. Importantly, this chapter aims to highlight notable findings for the development of management strategies and further research, and contextualizes results within the broader realm of conservation in Thailand and Southeast Asia.

References

AFP (2016) Tigers declared extinct in Cambodia. In: Guard. 6 April 2016. https://www.theguardian.com/environment/2016/apr/06/tigers-declared-extinct-in-cambodia. Accessed 27 Mar 2021

Albert C, Luque GM, Courchamp F (2018) The twenty most charismatic species. PLoS One 13:e0199149. https://doi.org/10.1371/journal.pone.0199149

Ash E (2015) Thap Lan National Park - Threat and Needs Assessment (Unpublished). Freeland Foundation, Bangkok

Aung SS, Shwe NM, Frechette J, et al (2017) Surveys in southern Myanmar indicate global importance for tigers and biodiversity. Oryx 51:13–13. https://doi.org/10.1017/s0030605316001393

Austin MP, Nicholls AO, Margules CR (1990) Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. Ecol Monogr 60:161–177. https://doi.org/doi:10.2307/1943043

Badola R, Hussain SA, Mishra BK, et al (2010) An assessment of ecosystem services of Corbett Tiger Reserve, India. Environmentalist 30:320–329. https://doi.org/10.1007/s10669-010-9278-5

Banerjee K, Jhala Y V, Pathak B (2010) Demographic structure and abundance of Asiatic lions Panthera leo persica in Girnar Wildlife Sanctuary, Gujarat, India. Oryx 44:248–251. https://doi.org/10.1017/S0030605309990949

Bangkok Post (2015) Park authorities promote less crowded parks. In: Bangkok Post, 1 Nov 2015. https://www.bangkokpost.com/print/750440/. Accessed 27 Mar 2021

Bar-Massada A, Wood EM, Pidgeon AM, Radeloff VC (2011) Complex effects of scale on the relationships of landscape pattern versus avian species richness and community structure in a woodland savanna mosaic. Ecography (Cop) 35:393–411. https://doi.org/10.1111/j.1600-0587.2011.07097.x

Barber-Meyer SM, Jnawali SR, Karki JB, et al (2013) Influence of prey depletion and human disturbance on tiger occupancy in Nepal.

J Zool 289:10–18. https://doi.org/10.1111/j.1469-7998.2012.00956.x

Bedi T, Coudouel A, Simler K (2007) More than a pretty picture: using poverty maps to design better policies and interventions. World Bank, Washington D.C.

Bhagabati NK, Ricketts T, Sulistyawan TBS, et al (2014) Ecosystem services reinforce Sumatran tiger conservation in land use plans. Biol Conserv 169:147156. https://doi.org/10.1016/j.biocon.2013.11.010

Burton AC, Neilson E, Moreira D, et al (2015) Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. J Appl Ecol 52:675–685. https://doi.org/10.1111/1365-2664.12432

Chanatinart K (2013) Khao Yai park “not being ejected as heritage site.” In: Bangkok Post, 15 June 2013. http://www.nationmultimedia.com/national/Khao-Yai-park-not-being-ejected-as-heritage-site-30208371.html. Accessed 27 Mar 2021

Cohen E (2014) Tourism encroachment on reserved forest areas: A case study from Thailand. Tour Recreat Res 39:185–202. https://doi.org/10.1080/02508281.2014.11081766

Connor L (2017) Is Cambodia’s plan to reintroduce tigers doomed to fail? In: Mongabay, 1 Nov 2017. https://news.mongabay.com/2017/11/is-cambodias-plan-to-reintroduce-tigers-doomed-to-fail/. Accessed 27 Mar 2021

Courchamp F, Jaric I, Albert C, et al (2018) The paradoxical extinction of the most charismatic animals. PLOS Biol 16:e2003997. https://doi.org/10.1371/journal.pbio.2003997

Cutter P, Hean S (2010) Costs and Benefits of Sustaining Wild Tigers in Cambodia: A Strategic Economic Perspective. In: Tilson R, Nyhus P (eds) Tigers of the World, Second Edition. Elsevier, New York, pp 357–365

Davis BW, Li G, Murphy WJ (2010) Supermatrix and species tree methods resolve phylogenetic relationships within the big cats, Panthera (Carnivora: Felidae). Mol Phylogenet Evol 56:64–76. https://doi.org/10.1016/j.ympev.2010.01.036

Day M (1995) Fight for the Tiger: One Man’s Fight to Save the Wild Tiger from Extinction. Trafalgar Square, London

Devoe JD, Garrott RA, Rotella JJ, et al (2015) Summer range occupancy modeling of non-native mountain goats in the greater Yellowstone area. Ecosphere 6:1–20. https://doi.org/10.1890/ES15-00273.1

Dickman AJ, Hinks AE, Macdonald EA, et al (2015) Priorities for Global Felid Conservation. Conserv Biol 29:854–864. https://doi.org/doi:10.1111/cobi.12494

Dinerstein E, Loucks C, Wikramanayake E, et al (2007) The Fate of Wild Tigers. Bioscience 57:508–514. https://doi.org/10.1641/B570608

Dinerstein E, Varma K, Wikramanayake E, et al (2013) Enhancing Conservation, Ecosystem Services, and Local Livelihoods through a Wildlife Premium Mechanism. Conserv Biol 27:14–23. https://doi.org/10.1111/j.1523-1739.2012.01959.x

DNP (2016) Practical Plan to Improve Tiger Population 2015-2035 (20 Years). Department of National Parks, Wildlife and Plant Conservation (DNP), Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

DNP (2004) Submission for Nomination of the Dong Phayayen- Khao Yai Forest Complex. Department of National Parks, Wildlife and Plant Conservation, The Royal Thai Government, Bangkok

Duangchantrasiri S, Umponjan M, Simcharoen S, et al (2016) Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. Conserv Biol 30:639–648. https://doi.org/10.1111/cobi.12655

Duckworth JW, Robichaud WG, Timmins RJ (2015) Rucervus schomburgki. IUCN Red List Threat. Species 2015 e.T4288A79818502

Dudley N (2013) Guidelines for Applying Protected Area Management Categories. International Union for the Conservation of Nature (IUCN), Gland

Durst PB, Waggener TR, Enters T, Cheng TL (2001) Forests out of bounds: Impacts and effectiveness of logging bans in natural forests in Asia-Pacific. Asia-Pacific Forestry Commission, Food and Agricultural Organization of the United Nations, Regional Office for Asia and the Pacific, Bangkok

Efford M (2004) Density estimation in live-trapping studies. Oikos 106:598–610. https://doi.org/10.1111/j.0030-1299.2004.13043.x

Emphandhu D, Chettamart S (2013) Thailand Experience in Protected Area Management. In: IUCN World Parks Congress, Durban, South Africa, 8-17 September 2003

Fisher TJ, Anholt B, Volpe JP (2011) Body mass explains characteristic scales of habitat selection in terrestrial mammals. Ecol Evol 1:517–528. https://doi.org/10.1002/ece3.45

Forman RTT, Alexander LE (1998) Roads and Their Major Ecological Effects. Annu Rev Ecol Syst 29:207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Foster RJ, Harmsen BJ (2012) A critique of density estimation from camera-trap data. J Wildl Manage 76:224–236. https://doi.org/10.1002/jwmg.275

Goodrich JM, Lynam A, Miquelle DG, et al (2015) Panthera tigris. IUCN Red List Threat. Species 2015 e.T15955A50659951

Gray TNE, Brook SM, McShea WJ, et al (2015) Rucervus eldii. The IUCN Red List of Threatened Species 2015: e.T4265A22166803

Gray TNE, Crouthers R, Ramesh K, et al (2017) A framework for assessing readiness for tiger Panthera tigris reintroduction: a case study from eastern Cambodia. Biodivers Conserv 26:2383–2399. https://doi.org/10.1007/s10531-017-1365-1

Hansen MC, Potapov P V., Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science (80-) 342:850–853. https://doi.org/10.1126/science.1244693

Harihar A, Chanchani P, Pariwakam M, et al (2017) Defensible Inference: Questioning Global Trends in Tiger Populations. Conserv Lett 10:502–505. https://doi.org/10.1111/conl.12406

Harihar A, Pandav B (2012) Influence of connectivity, wild prey and disturbance on occupancy of tigers in the human-dominated western Terai Arc landscape. PLoS One 7:e40105. https://doi.org/10.1371/journal.pone.0040105

Harihar A, Prasad DL, Ri C, et al (2007) Status of tiger and its prey species in Rajaji National Park. In: Harihar A, Kurien AJ, Pandev B, Goyal S. (eds) Response of tiger population to habitat, wild ungulate prey and human disturbance in Rajaji National Park, Uttarakhand. Wildlife Institute of India, Dehradun, pp 87–110

Hearn AJ, Cushman SA, Ross J, et al (2018) Spatio-temporal ecology of sympatric felids on Borneo. Evidence for resource partitioning? PLoS One 13:e0200828. https://doi.org/10.1371/journal.pone.0200828

Heinen JT, Mehta JN (2000) Emerging Issues in Legal and Procedural Aspects of Buffer Zone Management with Case Studies from Nepal. J Environ Dev 9:45–67. https://doi.org/10.1177/107049650000900103

Hirsch P (1990) Forests, Forest Reserve, and Forest Land in Thailand. Geogr J 156:166–174. https://doi.org/10.2307/635324

Hirsch P, Lohmann L, Hirsch L. P and L (1989) Contemporary Politics of Environment in Thailand. Asian Surv 29:439–451. https://doi.org/10.2307/2644886

IUCN (2000) IUCN Red List Categories and Criteria: Version 3.1. Second edition. IUCN, Gland, Switzerland, and Cambridge, UK

IUCN (2015) A Review of Thailand’s Proposed Mae Wong Dam. International Union for Conservation of Nature (IUCN), Bangkok

IUCN World Heritage Outlook (2020) Dong Phayayen-Khao Yai Forest Complex: 2020 Conservation Outlook Assessment. IUCN World Heritage Programme & IUCN World Commission on Protected Areas (WCPA), Gland

Jackson P (1990) Tigers. Apple Press, London

Jenks K, Chanteap P, Damrongchainarony K, et al (2011) Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses - an example from Khao Yai National Park, Thailand. Trop Conserv Sci 4:113–131. https://doi.org/10.1177/194008291100400203

Johnson A, Goodrich J, Hansel T, et al (2016) To protect or neglect? Design, monitoring, and evaluation of a law enforcement strategy to recover small populations of wild tigers and their prey. Biol Conserv 202:99–109. https://doi.org/10.1016/j.biocon.2016.08.018

Johnson A, Vongkhamheng C, Hedemark M, Saithongdam T (2006) Effects of human-carnivore conflict on tiger (Panthera tigris) and prey populations in Lao PDR. Anim Conserv 9:421–430. https://doi.org/10.1111/j.1469-1795.2006.00049.x

Johnston DB (1975) Rural society and the rice economy in Thailand, 1880-1930. Yale University, New Haven, Conn

Joshi AR, Dinerstein E, Wikramanayake E, et al (2016) Tracking changes and preventing loss in critical tiger habitat. Sci Adv 2:e1501675–e1501675. https://doi.org/10.1126/sciadv.1501675

Kalyawongsa S, Amano M, Pragtong K, et al (1997) Historical Changes of Forest Area in Thailand : A Case Study of Mae Klong Watershed Research Station-Lintin, Kanchanaburi. J For Plan 3:65–72. https://doi.org/10.20659/JFP.3.2_65

Kanwatanakid C, Lynam T, Galster S, et al (2002) Ecological monitoring of large mammals and birds at Khao Yai National Park, Thailand [Thai]. J Wildl Thail 10:97–105

Karanth K., Nichols JD (2010) Non-invasive Survey Methods for Assessing Tiger Populations. In: Tilson R, Nyhus PJ (eds) Tigers of the World, Second Edition. Elsevier Inc., New York, pp 241–261

Karanth KU, Chundawat RS (2002) Ecology of the Tiger: Implications for Population Monitoring. In: Karanth KU, Nichols JD (eds) Monitoring tigers and their prey : a manual for researchers, managers, and conservationists in tropical Asia. Centre for Wildlife Studies, Bangalore, pp 9–22

Karanth KU, Gopalaswamy AM, Kumar NS, et al (2011) Monitoring carnivore populations at the landscape scale: Occupancy modelling of tigers from sign surveys. J Appl Ecol 48:1048–1056. https://doi.org/10.1111/j.1365-2664.2011.02002.x

Karanth KU, Miquelle D, Goodrich J, Gopalaswamy A (2016) Statement of Concern by Tiger Biologists. In: WCS Newsroom, 15 Apr 2016. https://newsroom.wcs.org/News-Releases/articleType/ArticleView/articleId/8872/Statement-of-Concern-by-Tiger-Biologists.aspx. Accessed 27 Mar 2021

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862. https://doi.org/10.2307/176521

Karanth KU, Nichols JD (eds) (2017) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore

Karanth KU, Nichols JD, Harihar A, et al (2017) Field practices: Assessing tiger population dynamics using photographic captures. In: Karanth KU, Nichols JD (eds) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore, pp 191–224

Karanth KU, Nichols JD, Kumar NS, et al (2004) Tigers and their prey: Predicting carnivore densities from prey abundance. Proc Natl Acad Sci U S A 101:4854–4858. https://doi.org/10.1073/pnas.0306210101

Kenney J, Allendorf FW, McDougal C, Smith JLD (2014) How much gene flow is needed to avoid inbreeding depression in wild tiger populations? Proc R Soc B Biol Sci 281:20133337–20133337. https://doi.org/10.1098/rspb.2013.3337

Kenney JS, Smith JLD, Starfield AM, McDougal CW (1995) The Long-Term Effects of Tiger Poaching on Population Viability. Conserv Biol 9:1127–1133. https://doi.org/10.1046/j.1523-1739.1995.9051116.x-i1

Kerley LI, Goodrich JM, Miquelle DG, et al (2002) Effects of Roads and Human Disturbance on Amur Tigers. Conserv Biol 16:97–108. https://doi.org/10.1046/j.1523-1739.2002.99290.x

Khedari J, Sangprajak A, Hirunlabh J (2002) Thailand climatic zones. Renew Energy 25:267–280. https://doi.org/10.1016/S0960-1481(01)00005-2

Kitchener A, Breitenmoser-Würsten C, Eizirik E, et al (2017) A revised taxonomy of the Felidae. Final Rep. Cat Classif. Task Force IUCN/SSC Cat Spec. Group, Cat News Spec. Issue 11 80pp

Klinsawat W (2016) Phylogeography and landscape genetics of tigers (Panthera tigris) and Asian elephants (Elephas maximus) in Thailand. University of Minnesota. PhD Thesis.

Kobayashi K, Rashid KA, Furuichi M, Anderson WP (2017) Economic integration and regional development: the ASEAN economic community. Routledge, Abingdon, United Kingdom

Krishnamurthy R, Cushman SA, Sarkar MS, et al (2016) Multi-scale prediction of landscape resistance for tiger dispersal in central

India. Landsc Ecol 31:1355–1368. https://doi.org/10.1007/s10980-016-0363-0

Lang G (2002) Deforestation, floods, and state reactions in China and Thailand. In: The Environmental State Under Pressure. Emerald Group Publishing Limited, Bingley, pp 195–220

Lekagul B, McNeely JA (1977) Mammals of Thailand. Association for the Conservation of Wildlife, Bangkok

Leng-EE P (1979) Status of the tiger in Thailand. Tiger-paper 6:21

Lim CL, Prescott GW, De Alban JDT, et al (2017) Untangling the proximate causes and underlying drivers of deforestation and forest degradation in Myanmar. Conserv Biol 31:1362–1372. https://doi.org/10.1111/cobi.12984

Linkie M, Chapron G, Martyr DJ, et al (2006) Assessing the viability of tiger subpopulations in a fragmented landscape. J Appl Ecol 43:576–586. https://doi.org/10.1111/j.1365-2664.2006.01153.x

Luo S-J, Johnson WE, Smith JLD, O'Brien SJ (2010) What Is a Tiger? Genetics and Phylogeography. In: Tilson R, Nyhus PJ (eds) Tigers of the World. Elsevier, New York, pp 35–51

Luo SJ, Kim JH, Johnson WE, et al (2004) Phylogeography and genetic ancestry of tigers (Panthera tigris). PLoS Biol 2:e442. https://doi.org/10.1371/journal.pbio.0020442

Lynam A (2001) Status, Ecology, and Conservation of Tigers in their Critical Habitats in Thailand, September 2001. Wildlife Conservation Society, Bangkok

Lynam A, Nowell K (2011) Panthera tigris ssp. corbetti. IUCN Red List Threat. Species 2011 e.T136853A4346984

Lynam A, Round P, Brockelman W (2006) Status of Birds and Large Mammals in Thailand's Dong Phayayen - Khao Yai Forest Complex. Wildlife Conservation Society and Biodiversity Research Training (BRT) Programme, Bangkok

Lynam AJ (2003) A National Tiger Action Plan for the Union of Myanmar. Myanmar Forest Department, Ministry of Forestry, Government of Myanmar, Yangon

Lynam AJ (2010) Securing a future for wild Indochinese tigers: Transforming tiger vacuums into tiger source sites. Integr Zool 5:324–334. https://doi.org/10.1111/j.1749-4877.2010.00220.x

Lynam AJ, Rabinowitz A, Myint T, et al (2009) Estimating abundance with sparse data: Tigers in northern Myanmar. Popul Ecol 51:115–121. https://doi.org/10.1007/s10144-008-0093-5

Macdonald EA, Burnham D, Hinks AE, et al (2015) Conservation inequality and the charismatic cat: Felis felicis . Glob Ecol Conserv 3:851–866. https://doi.org/10.1016/j.gecco.2015.04.006

Macdonald EA, Hinks A, Weiss DJ, et al (2017) Identifying ambassador species for conservation marketing. Glob Ecol Conserv 12:204–214. https://doi.org/10.1016/j.gecco.2017.11.006

Manorom K (2020) Thailand's Big Water Challenge. In: Dipl. 23 March 2020. https://thediplomat.com/2020/03/thailands-big-water-challenge/. Accessed 8 Mar 2021

Marks D (2011) Climate Change and Thailand: Impact and Response. Contemp Southeast Asia 33:229–258. https://doi.org/10.1355/cs33-2d

Marukatat S (2014) It's a jungle out there for park officials. Bangkok Post, 1 Dec 2014

Mateo-Sánchez MC, Balkenhol N, Cushman S, et al (2015) A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow? Landsc Ecol 30:1405–1420. https://doi.org/10.1007/s10980-015-0194-4

McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12:335–345. https://doi.org/10.1890/1051-0761(2002)012[0335:CEOEAT]2.0.CO;2

McGarigal K, Wan HY, Zeller KA, et al (2016) Multi-scale habitat selection modeling: introduction to the special issue. Landsc Ecol 31:1157–1160. https://doi.org/10.1007/s10980-016-0388-4

Mills JA, Jackson P (1994) Killed for a cure: a review of the worldwide trade in tiger bone. Traffic International, Cambridge

Miquelle DG, Poole CM, Mahood SP, et al (2018) Comments on “a framework for assessing readiness for tiger reintroductions.” Biodivers Conserv 27:3287–3293. https://doi.org/10.1007/s10531-018-1591-1

Molle F (2005) Elements for a political ecology of river basins development: The case of the Chao Phraya River Basin, Thailand. International Water Management Institute, Paris

Moo SSB, Froese GZL, Gray TNE (2018) First structured camera-trap surveys in Karen State, Myanmar, reveal high diversity of globally threatened mammals. Oryx 52:537–543. https://doi.org/10.1017/S0030605316001113

Mouhot H (1864) Travels in the central parts of Indo-China (Siam), Cambodia, and Laos : during the years 1858, 1859, and 1860. John Murray, London

Naing H, Fuller TK, Sievert PR, et al (2015) Assessing large mammal and bird richness from camera-trap records in the Hukaung valley of Northern Myanmar. Raffles Bull Zool 63:376–388. https://doi.org/10.1007/s12595-011-0009-9

Naing H, Ross J, Burnham D, et al (2019) Population density estimates and conservation concern for clouded leopards Neofelis nebulosa, marbled cats Pardofelis marmorata and tigers Panthera tigris in Htamanthi Wildlife Sanctuary, Sagaing, Myanmar. Oryx 53:654–662. https://doi.org/10.1017/S0030605317001260

Ngoprasert D, Lynam AJ, Sukmasuang R, et al (2012) Occurrence of Three Felids across a Network of Protected Areas in Thailand: Prey, Intraguild, and Habitat Associations. Biotropica 44:810–817. https://doi.org/10.1111/j.1744-7429.2012.00878.x

Nijman V, Shepherd CR (2015) Trade in tigers and other wild cats in Mong La and Tachilek, Myanmar - A tale of two border towns. Biol Conserv 182:1–7. https://doi.org/10.1016/j.biocon.2014.10.031

Normand R (1990) Inside Site 2. J Refug Stud 3:155–162

Norris K (2004) Managing threatened species: The ecological toolbox, evolutionary theory and declining-population paradigm. J Appl Ecol 41:413–426. https://doi.org/10.1111/j.0021-8901.2004.00910.x

Oswell AH (2010) The Big Cat Trade in Myanmar and Thailand. TRAFFIC Southeast Asia, Petaling Jaya, Malaysia

Paddle R (2003) Frontiers of Fear: Tigers and People in the Malay World, 1600–1950. Yale University Press, Anne Arbor

Paine RT (1980) Food Webs: Linkage, Interaction Strength and Community Infrastructure. J Anim Ecol 49:666–685. https://doi.org/10.2307/4220

Phumathan S (2010) Environmental Impacts of Tourism in Khao Yai National Park, Thailand. PhD Thesis. Texas A&M University, College Station

Pinitwong A (2015) Two arrested with dead tiger bound for restaurant. Bangkok Post, 12 Nov 2015

Pisdamkam C, Prayurasiddhi T, Kanchanasaka B, et al (2010) Thailand Tiger Action Plan - 2010-2012. Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

Pongrai J (2015) Two forest rangers killed in gun battle with tiger hunters. Nation, 14 Sep 2015

Praiwan P (2015) Taking the forest fight to court. In: Bangkok Post, 1 Feb 2015. https://www.bangkokpost.com/print/463076/

Rabinowitz A (1989) The density and behaviour of large cats in a dry tropical forest mosaic in Huai Kha Khaeng Wildlife Sanctuary, Thailand. Nat Hist Bull Siam Soc 37:235–251

Rabinowitz A (1993) Estimating the Indochinese tiger (Panthera tigris corbetti) population in Thailand. Biol Conserv 65:213–217. https://doi.org/10.1016/0006-3207(93)90055-6

Rao M, Htun S, Zaw T, Myint T (2010) Hunting, livelihoods and declining wildlife in the Hponkanrazi wildlife sanctuary, North Myanmar. Environ Manage 46:143–153. https://doi.org/10.1007/s00267-010-9519-x

Rasphone A, Kéry M, Kamler JF, Macdonald DW (2019) Documenting the demise of tiger and leopard, and the status of other carnivores and prey, in Lao PDR's most prized protected area: Nam Et - Phou Louey. Glob Ecol Conserv 20:e00766. https://doi.org/10.1016/j.gecco.2019.e00766

Reddy PA, Cushman SA, Srivastava A, et al (2017) Tiger abundance and gene flow in Central India are driven by disparate combinations of topography and land cover. Divers Distrib 23:863–874. https://doi.org/10.1111/ddi.12580

Ripple WJ, Beschta RL (2004) Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? Bioscience 54:755. https://doi.org/10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2

Ripple WJ, Estes JA, Beschta RL, et al (2014) Status and ecological effects of the world's largest carnivores. Science (80-) 343:. https://doi.org/10.1126/science.1241484

Rockhill AP, Sollman R, Powell RA, DePerno CS (2016) A Comparison of Survey Techniques for Medium- to Large-Sized Mammals in Forested Wetlands. Southeast Nat 15:175–187. https://doi.org/10.1656/058.015.0112

Rostro-García S, Kamler JF, Ash E, et al (2016) Endangered leopards: Range collapse of the Indochinese leopard (Panthera pardus delacouri) in Southeast Asia. Biol Conserv 201:293–300. https://doi.org/10.1016/j.biocon.2016.07.001

Rovero F, Zimmermann F, Berzi D, Meek P (2013) "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. Hystrix 24:148–156. https://doi.org/10.4404/hystrix-24.2-8789

Royle J, Chandler RB, Sollmann R, Gardner B (2014) Spatial Capture-Recapture. Elsevier, Oxford

Royle JA, Gopalaswamy AM, Dorazio RM, et al (2017) Concepts: Assessing Tiger Population Dynamics Using Capture–Recapture Sampling. In: Karanth KU, Nichols JD (eds) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore, pp 163–189

Russell R (1987) Cambodia: A Country Study. GPO for the Library of Congress, Washington

Sanderson E, Forrest J, Loucks C, et al (2006) Setting Priorities for the Conservation and Recovery of Wild Tigers: 2005-2015 - The Technical Assessment. WCS, WWF, Smithsonian, and NFWF-STF, New York - Washington, DC

Sandom CJ, Faurby S, Svenning JC, et al (2017a) Learning from the past to prepare for the future: felids face continued threat from declining prey. Ecography (Cop) 41:140–152. https://doi.org/10.1111/ecog.03303

Sandom CJ, Williams J, Burnham D, et al (2017b) Deconstructed cat communities: Quantifying the threat to felids from prey defaunation. Divers Distrib 23:667–679. https://doi.org/10.1111/ddi.12558

Seeboonruang U (2016) Impact assessment of climate change on groundwater and vulnerability to drought of areas in Eastern Thailand. Environ Earth Sci 75:42. https://doi.org/10.1007/s12665-015-4896-3

Sergio F, Newton I, Marchesi L, Pedrini P (2006) Ecologically justified charisma: Preservation of top predators delivers biodiversity conservation. J Appl Ecol 43:1049–1055. https://doi.org/10.1111/j.1365-2664.2006.01218.x

Shirk AJ, Cushman SA, Waring KM, et al (2018) Southwestern white pine (Pinus strobiformis) species distribution models project a large range shift and contraction due to regional climatic changes. For Ecol Manage 411:176–186. https://doi.org/10.1016/j.foreco.2018.01.025

Simcharoen A, Savini T, Gale GA, et al (2014) Female tiger Panthera tigris home range size and prey abundance: important metrics for management. Oryx 48:370–377. https://doi.org/10.1017/S0030605312001408

Simcharoen S, Pattanavibool A, Karanth KU, et al (2007) How many tigers Panthera tigris are there in Huai Kha Khaeng Wildlife Sanctuary, Thailand? An estimate using photographic capture-recapture sampling. Oryx 41:447–453. https://doi.org/10.1017/S0030605307414107

Smith JLD (1993) The Role of Dispersal in Structuring the Chitwan Tiger Population. Behaviour 124:165–195. https://doi.org/10.1163/156853993X00560

Smith JLD, Tunhikorn S, Tanhan S, et al (1999) Metapopulation structure of tigers in Thailand. In: Seidensticker J, Christie S, Jackson P (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge

Smith S, Saunter S (2016) Endangered Tiger Killed in Myanmar Came from Thailand. WCS Newsroom

Stein AB, Fuller TK, Marker LL (2008) Opportunistic use of camera traps to assess habitat-specific mammal and bird diversity in northcentral Namibia. Biodivers Conserv 17:3579–3587. https://doi.org/10.1007/s10531-008-9442-0

Stokes D (2017) Thap Lan: Thailand’s unsung forest gem under threat, but still abrim with life. In: Mongabay, 31 January 2017. https://news.mongabay.com/2017/01/thap-lan-thailands-unsung-forest-gem-under-threat-but-still-abrim-with-life/. Accessed 27 Mar 2021

Stoner S, Krishnasamy K, Wittmann T, et al (2016) Reduced to Skin and Bones Re-examined: Full Analysis. TRAFFIC, Southeast Asia Regional Office, Petaling Jaya, Malaysia

Sunarto S, Kelly MJ, Parakkasi K, et al (2012) Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS One 7:e30859. https://doi.org/10.1371/journal.pone.0030859

Sunquist M (2010) What Is a Tiger? Ecology and Behavior. In: Tilson R, Nyhus PJ (eds) Tigers of the World, Second Edition. Elsevier, New York, pp 19–33

Sunquist M, Karanth UK, Sunquist F (1999) Ecology, behaviour and resilience of the tiger and its conservation needs. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 5–18

Terborgh J, Estes JA (2010) Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island Press, Washington DC

Thapar V (2004) Tiger: The Ultimate Guide. Two Brothers Press, New York

Thatte P, Joshi A, Vaidyanathan S, et al (2018) Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations. Biol Conserv 218:181–191. https://doi.org/10.1016/j.biocon.2017.12.022

Tilson R, Defu H, Muntifering J, Nyhus PJ (2004) Dramatic decline of wild South China tigers Panthera tigris amoyensis: field survey of priority tiger reserves. Oryx 38:40–47. https://doi.org/10.1017/S0030605304000079

Trisurat Y (2007) Applying gap analysis and a comparison index to evaluate protected areas in Thailand. Environ Manage 39:235–245. https://doi.org/10.1007/s00267-005-0355-3

Tunhikorn S, Smith JLD, Prayurasiddhi T, et al (2004) Saving Thailand’s Tigers: An Action Plan. Department of National Parks, Wildlife and Plant Conservation, The Royal Thai Government

UN DESA (2015) World Population Prospects, the 2015 revision. In: Eur. Environ. Agency, United Nations Dep. Econ. Soc. Aff. (UN DESA). https://www.eea.europa.eu/data-and-maps/indicators/total-population-outlook-from-unstat-3/assessment-1. Accessed 12 Sep 2018

UNEP (2011) Dong Phayayen-Khao Yai Forest Complex, Thailand. United Nations Environment Program (UNEP), Cambridge

UNESCO (2017) Dong Phayayen-Khao Yai Forest Complex. In: UNESCO World Herit. Cent. http://whc.unesco.org/en/list/590. Accessed 27 Nov 2017

UNESCO (2013) Decisions adopted by the World Heritage Committee at its 37th session (Phnom Penh, 2013). Phnom Penh, Cambodia, 16-27 June 2013

UNESCO (2014) Decisions Adopted by the World Heritage Committee at its 38th Session (Doha, 2014). United Nations Educational, Scientific and Cultural Organization, Doha, Qatar 15-15 June 2014

Vasudev D, Nichols JD, Ramakrishnan U, et al (2017) Assessing Landscape Connectivity for Tigers and Prey Species: Concepts and Practice. In: Karanth KU, Nichols JD (eds) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore, pp 255–288

Vongkhamheng C (2011) Abundance and Distribution of Tiger and Prey in Montane Tropical Forest in Northern Lao People Democratic Republic. PhD Thesis, University of Florida, Gainesville, FL, USA

Walston J, Karanth U, Stokes E (2010a) Avoiding the unthinkable : What will it cost to prevent Tigers becoming extinct in the wild ? Wildlife Conservation Society, New York

Walston J, Robinson JG, Bennett EL, et al (2010b) Bringing the tiger back from the brink-the six percent solution. PLoS Biol 8:6–9. https://doi.org/10.1371/journal.pbio.1000485

White GC, Anderson DR, Burnham KP, Otis DL (1982) Capture-Recapture and Removal Methods for Sampling Closed Populations. Los Alamos National Laboratory, LA 8787-NERP, Los Alamos

Wikramanayake E, Manandhar A, Bajimaya S, et al (2010) The Terai Arc Landscape: A Tiger Conservation Success Story in a Human-dominated Landscape. In: Tilson R, Nyhus PJ (eds) Tigers of the World. Elsevier, New York, pp 163–173

Wilcox BA, Murphy DD (1985) Conservation Strategy: The Effects of Fragmentation on Extinction. Am Nat 125:879–887. https://doi.org/10.1086/284386

Wongruang P (2013) A different killer lurking in the forest. In: Bangkok Post, 29 Sep 2013. http://www.bangkokpost.com/print/372044/

Wongwuttiwat J, Lawanna A (2018) The digital Thailand strategy and the ASEAN community. Electron J Inf Syst Dev Ctries 84:e12024. https://doi.org/10.1002/isd2.12024

WWF (2016a) Global wild tiger population increases, but still a long way to go. In: World Wildl. Fund, 10 Apr 2016. http://wwf.panda.org/wwf_news/?uNewsID=265197. Accessed 27 Mar 2021

WWF (2016b) WWF Response to Statement of Concern by Tiger Biologists. World Wildlife Fund for Nature

Chapter 2

Opportunity for Thailand's forgotten tigers: Assessment of the Indochinese tiger *Panthera tigris corbetti* and its prey with camera-trap surveys

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Title

Opportunity for Thailand's Forgotten Tigers: Assessment of Indochinese tiger *Panthera tigris corbetti* and prey from camera-trap surveys in Eastern Thailand

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Abstract

Dramatic population declines threaten the Endangered Indochinese tiger *Panthera tigris corbetti* with extinction. Thailand now plays a critical role in its conservation, as there are few known breeding populations in other range countries. Thailand's Dong Phayayen-Khao Yai Forest Complex is recognized as an important tiger recovery site, but it remains poorly studied. Here, we present results from the first camera-trap study focused on tigers and implemented across all protected areas in this landscape. Our goal was to assess tiger and prey populations across the five protected areas of this forest complex, reviewing discernible patterns in rates of detection. We conducted camera-trap surveys opportunistically during 2008-2017. We recorded 1,726 detections of tigers in 79,909 camera-trap nights. Among these were at least 16 adults and six cubs/juveniles from four breeding females. Detection rates of both tigers and potential prey species varied considerably between protected areas over the study period. Our findings suggest heterogeneity in tiger distribution across this relatively continuous landscape, potentially influenced by distribution of key prey species. This study indicates that the Dong Phayayen-Khao Yai Forest Complex is one of the few remaining breeding locations of the Indochinese tiger. Despite limitations posed by our study design, our findings have catalysed increased research and conservation interest in this globally important population at a critical time for tiger conservation in South-east Asia.

Keywords *Bos gaurus*; distribution; Dong Phayayen-Khao Yai Forest Complex; Indochinese tiger; *Panthera tigris corbetti*; prey abundance; *Rusa unicolor*; *Sus scrofa*

1. Introduction

The tiger *Panthera tigris* has suffered catastrophic declines in its population (96%) and habitat (95%) over the past century (Nowell and Jackson 1996; Goodrich et al. 2015; Wolf and Ripple 2017). Evidence suggests only 42 source sites (i.e., sites with breeding populations that have the potential to support future recovery of the tiger over a larger area) remain across the species' range, totalling 90,000km^2 (5.9% of current range; Walston et al. 2010). Habitat loss has been particularly acute in South and South-east Asia, with a 41% reduction from 1996 and 2006 (Sanderson et al. 2006) and an estimated forest loss of 71,134km^2 in priority tiger conservation landscapes from 2001 to 2014 (Joshi et al. 2016).

The Indochinese tiger *Panthera tigris corbetti* is one of six extant tiger subspecies and is categorized as Endangered on the IUCN Red List (Lynam and Nowell 2011; Goodrich et al. 2015). It was historically distributed throughout most of mainland South-east Asia (Luo et al. 2004, 2019) across Cambodia, Lao, Myanmar, southern China, Thailand, and Viet Nam (Lynam 2010). Evidence suggests three range countries (Cambodia, Lao and Viet Nam) have lost viable populations, and the Indochinese subspecies may qualify for Critically Endangered status (Lynam and Nowell 2011). Despite previous evidence of a viable breeding population in Nam Et Phou Louey National Protected Area in Lao (Johnson et al. 2006; Vongkhamheng 2011), recent evidence suggests tigers may have been extirpated from the country (Rasphone et al. 2019). Tigers are probably extinct in Cambodia, prompting plans for reintroduction (Gray et al. 2017) and, in Viet Nam there have been no confirmed tiger records in > 20 years (Lynam and Nowell 2011). A paucity of reliable population data in current range countries has obscured these declines (Lynam and Nowell 2011) and information on remaining populations is needed urgently.

It is possible that the only remaining source sites for the Indochinese tiger are in Myanmar and Thailand. However, studies in key landscapes in Myanmar have documented low and potentially declining numbers (Lynam et al. 2009; Rao et al. 2010; Moo et al. 2018; Naing et al. 2019) reinforcing the importance of Thailand as the tiger's last stronghold in the region. In Thailand's 2010 action plan, the national tiger population was estimated to be 190–250 individuals (Pisdamkam et al. 2010). A recent, updated government report included landscape-specific population estimates of at least 101-128 individuals (DNP 2016), with potentially only two viable populations of tigers, in the Western Forest Complex (25,000km^2) and the Dong Phayayen-Khao Yai Forest Complex (6,155km^2) in Eastern Thailand.

Although a number of tiger-focused studies have been conducted in other parts of Thailand, including ongoing monitoring in the Western Forest Complex (Duangchantrasiri et al. 2016), data from the Dong Phayayen-Khao Yai Forest Complex are limited. Information on tigers there has originated primarily from general assessments of faunal communities or other carnivores, or from interviews and personal communications (Lynam 2001; Kanwatanakid et al. 2002; Lynam et al. 2006; Jenks et al. 2011). Evidence suggests that tigers may have been extirpated in Khao Yai National Park, but almost no information is available from other areas in this forest complex. To our knowledge, there have been no studies focusing on tigers across this forest complex in its entirety. Comprehensive studies on prey species, an important factor for tiger distribution and persistence (Karanth and Stith 1999; Karanth et al. 2004), are also lacking.

Given catastrophic population and range declines elsewhere in Thailand and South-east Asia, knowledge of the tiger population of the Dong Phayayen-Khao Yai Forest Complex is of national, regional and global importance. Here, we describe results from the first camera-trap study focused on tigers and implemented across all protected areas in this landscape, conducted during 2008–2017. We aimed to assess

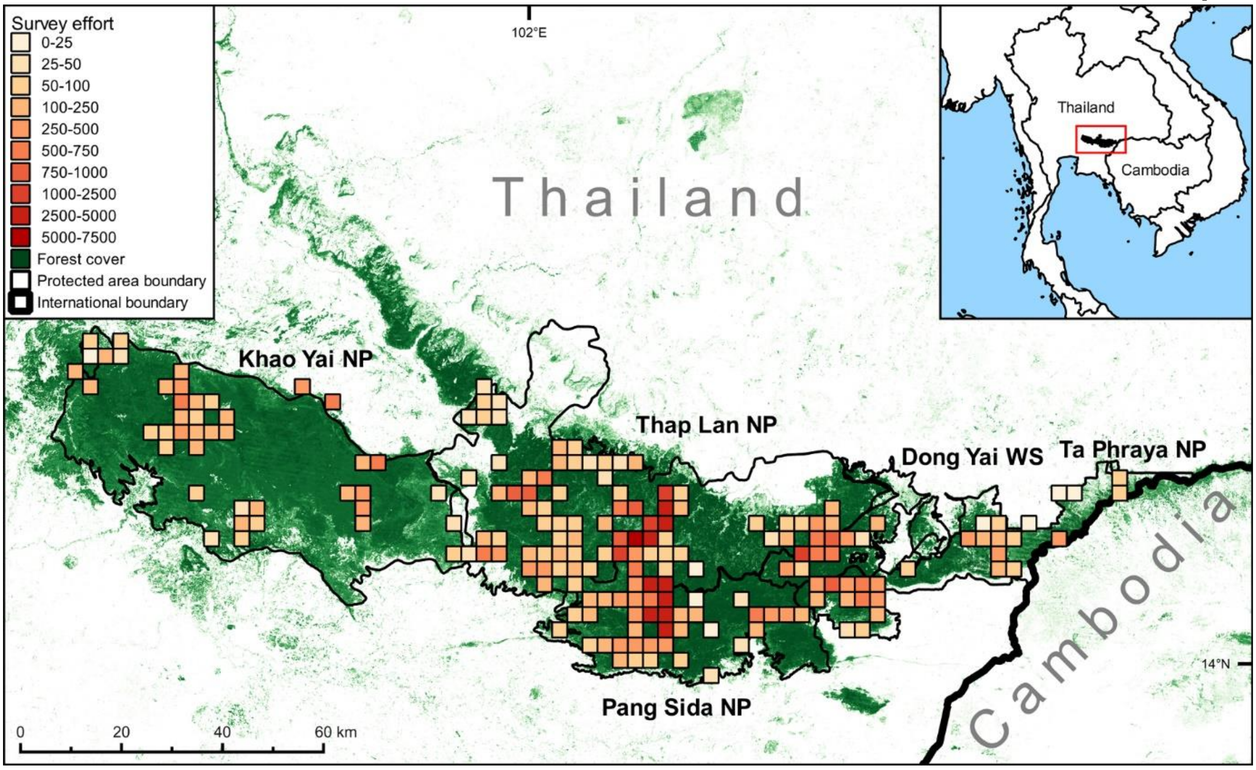

Fig. 1 Survey locations in the Dong Phayayen-Khao Yai Forest Complex, which includes five protected areas: Dong Yai Wildlife Sanctuary, Khao Yai National Park, Pang Sida National Park, Thap Lan National Park and Ta Phraya National Park. Survey locations are depicted as 3 × 3km grids and shaded according to total survey effort (number of camera-trap nights) from 2008-2017. Forest cover adapted from Hansen et al. (2013).

tiger and prey populations and to identify any patterns in detection frequencies of tigers and prey species amongst protected areas. Our findings provide baseline information for tigers and their prey, and also document potentially important information on other mammal species of research and conservation interest.

2. Methods

2.1 Study area

The Dong Phayayen-Khao Yai Forest Complex (DPKY) lies c.160km north-east of Bangkok (Fig. 1). To the east it partially borders the international boundary between Thailand and north-west Cambodia. The terrain is hilly, with altitudes ranging from 100m to 1,351m a.s.l.. The forest complex consists of five protected areas: Dong Yai Wildlife Sanctuary, Khao Yai National Park, Pang Sida National Park, Thap Lan National Park and Ta Phraya National Park (DNP 2004). These parks are collectively inscribed on the UNESCO

Table 1 Survey effort across protected areas in Thailand's Dong Phayayen-Khao Yai Forest Complex during 2008–2017, showing camera-trap nights and total number of camera stations (stations with paired camera traps in brackets).

	No. of camera-trap nights / camera stations (paired stations)				
Year	**Dong Yai WS[1]**	**Khao Yai NP[1]**	**Pang Sida NP[1]**	**Thap Lan NP[1]**	**Ta Phraya NP[1]**
2008				525 / 22 (3)	
2009				2,886 / 89 (5)	
2010		126 / 3 (1)	399 / 26 (0)	4,965 / 151 (9)	
2011			6,727 / 149 (6)	2,172 / 36 (7)	
2012	1,574 / 57 (0)	2,402 / 38 (0)	5,092 / 94 (11)	1,804 / 16 (7)	
2013	1,564 / 38 (0)		3,802 / 56 (32)	2,260 / 14 (4)	844 / 30 (0)
2014		2,357 / 24 (0)	2,294 / 23 (1)	3,062 / 18 (4)	4,230 / 66 (2)
2015	210 / 6 (0)	2,539 / 26 (0)	4,242 / 22 (3)	3,636 / 15 (5)	690 / 6 (1)
2016	1,455 / 12 (0)	197 / 3 (0)	5,765 / 27 (10)	10,784 / 75 (71)	
2017[2]	68 / 4 (0)		437 / 15 (5)	851 / 28 (26)	
Total camera-trap nights (%)	4,871 (6.10)	7,621 (9.54)	28,698 (35.91)	32,955 (41.24)	5,764 (7.21)

[1]WS, Wildlife Sanctuary; NP, National Park

[2] January-February only.

World Heritage List (UNESCO 2017).

The complex contains all major forest types characteristic of eastern Thailand, but is primarily covered by mixed evergreen and mixed dipterocarp/deciduous primary and secondary forest. It also contains grassland/scrub areas, some of which are anthropogenic. These forests have been influenced to varying degrees by a complex history of human presence and exploitation, including logging, settlements, agriculture and other activities (Lynam et al. 2006). Currently, the complex is surrounded almost completely by a human-dominated matrix of villages, farmland and infrastructure.

We conducted camera-trap surveys during March 2008–February 2017. The study design was opportunistic because of limited resources, and data collection for the five protected areas varied in spatial and temporal extent (Supplementary Fig. 1, Supplementary Material 1), precluding analysis within an occupancy framework. We placed camera traps in locations suitable for tigers, to maximize detections. Such locations included geographical or topographic features (e.g., ridges, river valleys) and access roads or trails likely to be used regularly by tigers (Karanth 1995; Karanth and Nichols 1998). We also used tiger track and sign (e.g., pugmarks, scats), and presence of prey species, to identify prospective camera locations.

We considered consecutive detections of a species at one camera station to be independent if they occurred after > 30 minutes (O'Brien et al. 2003). Individual tigers were given an alphanumeric identifier to compile detection histories. Tigers not conclusively identified were marked as unknown. We calculated detection rates of tigers and prey as the number of detections per 100 camera-trap nights, with cumulative rates reported for each protected area across survey years. Although such indices do not reliably indicate abundance (Jennelle et al. 2002; Sollmann et al. 2013), we also carried out a comparative analysis of photographic capture rates for tigers and prey for all five protected areas (Supplementary Material 1).

3. Results

Camera traps were active for a total of 79,909 camera-trap nights (CTN) at 914 locations. Survey effort varied significantly across protected areas. Thap Lan National Park (32,955 CTN) and Pang Sida National Park (28,698 CTN) accounted for approximately 77.15% (61,653) of total camera-trap nights and c.74.18% (*n*=678) of stations. Survey effort by protected area and year is summarized in Table 1.

Surveys recorded 1,726 independent detections of tigers during the study period (Table 2). Tigers were documented in three of the five protected areas (Thap Lan National Park, Pang Sida National Park and Dong Yai Wildlife Sanctuary), with Thap Lan National Park and Pang Sida National Park accounting for > 99% of detections (1,203 and 516 detections, respectively). Tigers were detected in Dong Yai Wildlife Sanctuary only in 2016 (seven detections). Tigers were not detected in Khao Yai National Park and Ta Phraya National Park. Detection rates in Thap Lan National Park were higher than in Pang Sida National Park with cumulative means of 3.65 (range 0.54-7.18) and 1.80 (range 0.41-3.40) detections per 100 camera-trap nights, respectively.

In total, at least 16 adults were documented: seven females, seven males and 2–3 partially identified adults whose sex could not be confirmed (Table 3). A minimum of 12 individuals were documented in Thap Lan National Park, nine in Pang Sida National Park and two in Dong Yai Wildlife Sanctuary, with six being detected across multiple protected areas. The number of individual tigers detected was highly correlated with survey effort. Five individuals were recorded over a period of ≥ 8 years and six individuals over 3-5 years

Table 2 Cumulative tiger *Panthera tigris* detections and detection rates (detections per 100 camera-trap nights) for protected areas in the Dong Phayayen-Khao Yai Forest Complex during 2008-2017).

Year	Dong Yai WS[1]	Khao Yai NP[1]	Pang Sida NP[1]	Thap Lan NP[1]	Ta Phraya NP[1]
2008				15 (2.80)	
2009				30 (1.04)	
2010		0 (0)	2 (0.59)	27 (0.54)	
2011			229 (3.40)	78 (3.59)	
2012	0 (0)	0 (0)	21 (0.41)	58 (3.22)	
2013	0 (0)		47 (1.24)	90 (3.98)	0 (0)
2014		0 (0)	38 (1.66)	220 (7.18)	0 (0)
2015	0 (0)	0 (0)	82 (1.93)	131 (3.60)	0 (0)
2016	7 (0.48)	0 (0)	92 (1.60)	493 (4.57)	
2017[2]	0 (0)		5 (1.14)	61 (7.17)	

[1]*WS, Wildlife Sanctuary; NP, National Park*

[2] *January-February only.*

(Supplementary Fig. 2, Supplementary Material 1).

Surveys documented successful breeding in 2015 and 2016, with six cubs/juveniles from four adult females. One litter of two juveniles were photographed without their mother (who could thus not be identified). One cub (C1), first documented in 2015, appeared to be independent from its mother by 2017.

We documented six potential prey species: gaur *Bos gaurus*, banteng *Bos javanicus*, Chinese serow *Capricornis milneedwardsii*, northern red muntjac *Muntiacus vaginalis*, sambar *Rusa unicolor* and wild boar *Sus scrofa*. We considered these species potential tiger prey based on information from Thailand and elsewhere within the tiger's range (Karanth et al. 2004; Sunquist 2010; Steinmetz et al. 2013). All but one potential prey species (banteng) were documented in all five protected areas.

Mean cumulative detection rates of sambar (Supplementary Table 1, Supplementary Material 1) were considerably higher in Thap Lan National Park (14.70 detections per 100 camera-trap nights) than in other protected areas (0.02-8.67), whereas detection rates of other prey species were comparatively lower in this park. Mean cumulative detection rates for wild boar were highest in Dong Yai Wildlife Sanctuary (6.67 detections per 100 camera-trap nights) and Pang Sida National Park (6.66). Sambar and wild boar were generally detected more frequently than other prey species.

Although tigers were the primary focus of surveys, we also documented a number of other species (Supplementary Table 1, Supplementary Material 1), with 947 detections of other felids, including the Asiatic golden cat *Catopuma temminckii* (35 detections), mainland clouded leopard *Neofelis nebulosa* (158), marbled cat *Pardofelis marmorata* (30) and leopard cat *Prionailurus bengalensis* (724). We did not detect leopards *Panthera pardus*. We documented 37 mammal species in total, including one Critically Endangered, five Endangered, 10 Vulnerable, three Near Threatened and 18 categorized as Least Concern.

4. Discussion

This study provides insights into tigers and their prey in the understudied Dong Phayayen-Khao Yai Forest Complex. Most of our detections of tigers were in Thap Lan and Pang Sida national parks, potentially a result of larger survey effort (32,955 and 28,698 camera-trap nights, respectively, of a total of 79,909). This was the result of our opportunistic study design, which prioritized survey areas based on potential or confirmed tiger presence. Nonetheless, the absence of detections of tigers or their sign from two of the five protected areas, despite reasonable survey effort, suggests higher tiger abundance in these two parks than elsewhere in this forest complex. Tiger presence across the complex appears to be heterogeneous, but to an unknown degree. Our records from Dong Yai Wildlife Sanctuary are from an area just outside the formerly known extant range of *P. tigris* (Goodrich et al. 2015). The lack of tiger detections from Khao Yai National Park is consistent with speculation that tigers have been extirpated from this protected area (Lynam et al. 2006; Jenks et al. 2011), although our survey effort and coverage in this park was relatively low (7,622 CTN).

Although the number of tigers we documented in the complex is not a population estimate, our results suggest the population may be larger than previously assumed (Lynam 2010), and also document the long-term persistence of a number of individuals in this area (Supplementary Fig. 2, Supplementary Material 1). To our knowledge, the photographs of tiger cubs we obtained are the first confirmed records of successful breeding in the forest complex since at least 1999 (Lynam et al. 2003, 2006; Jenks et al. 2011) and confirm that the site supports a breeding population. Breeding and subsequent dispersal could potentially result in expansion into Khao Yai National Park, and contribute to overall population recovery.

The presence of prey is an important factor for tiger distribution, density, and persistence (Karanth and Stith 1999; Karanth et al. 2004), as noted by studies elsewhere in Thailand (Steinmetz et al. 2013; Simcharoen et al. 2014). Thap Lan and Pang Sida national parks both had relatively higher rates of detection of sambar and wild boar, respectively, two species with which tigers have strong associations (Ngoprasert et al. 2012) and that are important prey elsewhere in the tiger's range (Sunquist et al. 1999; Biswas and Sankar 2002; Hayward et al. 2012). However, a dedicated prey study is required to determine the extent to which tigers in these parks rely on these species. Low prey detection rates in Ta Phraya National Park and Dong Yai Wildlife Sanctuary could explain the absence of tiger detections in these two areas.

We did not detect leopards, which, given that they have similar behavioural patterns to tigers and can tolerate some degree of spatial overlap (Karanth and Sunquist 1995; Andheria et al. 2007), suggests they may be absent from the forest complex. The Indochinese leopard *Panthera pardus delacouri* has not been detected recently in other parts of Southeast Asia, suggesting a decline in its population and range (Rostro-García et al. 2016). Abundance and diversity of suitable prey are important for the co-existence of tigers and leopards (Karanth and Sunquist 1995; Andheria et al. 2007). Historical overhunting of prey in the forest complex could have driven competitive exclusion of leopards by tigers or other carnivores (Harihar et al. 2011; Volmer et al. 2017). Direct hunting by humans may have also driven population declines. However, given the paucity of reliable historical data, the reasons for the absence of the leopard in the Dong Phayayen-Khao Yai Forest Complex remain unconfirmed.

Our data could not be used to estimate tiger occupancy or population size because the study design would violate key assumptions of the appropriate methods (Harmsen et al. 2010; Welsh et al. 2013). Methodologically-rigorous study designs should be employed wherever possible in monitoring wildlife populations, but if resources are constrained an opportunistic study design may be appropriate (Harihar et al. 2007; Stein et al. 2008; Johnson et al. 2016). Although conclusions that can be drawn from such studies are limited, they can contribute important insights into species presence in poorly studied areas (Stein et al. 2008; Jenks et al. 2011).

At the start of this study, tigers were believed to have disappeared from Khao Yai National Park

Table 3 Individual tiger detections during the study period. Cubs are placed under their mother with the exception of C5 and C6 whose mother was not confirmed. Blank cells indicate no detections.

		2008	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017***
Adult ID	Cub ID										
M1		2									
M2		8	14	11	110	36	81	98	84	181	14
M3					2	3	1				
M4								26	24	61	11
M5		3	5	6	122	2	18	41	4	2	
M6										17	
M7							1			9	
F1		1	8	6	2		1			1	
F2							4	7	35	29	3
	C1 (M)								3	13	
F3			1	1	44	33	18	49	51	154	16
	C2 (F)									36	9
	C3 (F)									33	5
F4			1	1	2	1				7	
F6							1		3	9	5
	C4 (M)									1	1
F7							2	33	2	19	
F8										1	
**											
	C5 (M)									5	
	C6 (F)									3	
UL1						1					
UR1						1					
UR2									1		
U		1	1	4	25	2	10	4	6	11	2
Detections		15	30	29	307	79	137	258	213	592	66
Stations		19	89	173	169	196	138	128	76	116	48
CTN		535	2,886	5,430	8,899	10,872	8,470	11,943	11,317	18,201	1.356
Detection Rate		2.80	1.04	0.53	3.45	0.73	1.62	2.16	1.88	3.25	4.87

[1]*M indicates male and F female individuals; U is used for individuals for which only one side was photographed, with L and R denoting whether the left or right flank of the individual was captured (sex could not be determined for these individuals and it is unknown whether UL1 is the same tiger as UR1 or UR2); U without L or R denotes detections of unidentified individuals (poor image quality or partial photographs).*

[2] *January–February only.*

(Lynam 2001; Lynam et al. 2006; Jenks et al. 2011), information was lacking for other areas and resources were limited. In these circumstances, an opportunistic study design was suitable to address our fundamental research question, specifically, to confirm tiger presence. Early findings suggested tigers were present in the area, which enabled us to secure further funding and improved access to resources such as camera traps that were later used for tiger density and population estimates. Additional funding also enabled investments in law enforcement, patrol-based monitoring and community outreach programmes. To build on this work, we recommend additional analyses to model relationships between tigers, prey, threats and habitat required for spatial prioritization of protection and recovery interventions.

Our study provides insight into what is probably one of the most important extant tiger populations remaining in mainland South-east Asia. A comprehensive investigation of the tiger in other understudied sites in the region is urgently needed to generate a more accurate picture of their status. In order to recover and double the population of wild tigers (Global Tiger Initiative 2011; Harihar et al. 2018), additional resources will need to be allocated to implement robust monitoring in sites where tigers remain.

To our knowledge, our work is the first to assess the tiger population across the Dong Phayayen-Khao Yai Forest Complex and suggests this region is important for the Indochinese tiger, which has lost most of its range in South-east Asia. Our findings establish this forest complex as home to one of the few remaining breeding populations of Indochinese tigers, demonstrate the long-term persistence of some individuals, and suggest heterogeneous tiger presence across the five protected areas, potentially influenced by distribution of prey species. Our initial results have catalysed increased research and conservation investment in this landscape at a critical time for tiger conservation in South-east Asia.

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Author contributions Study design and data collection: EA, TR; support in project planning and logistics: AN, PC, BJ, SR, KS; data analysis: EA, with support of ZK, DWM; writing: EA, TR, CH, ZK, DWM

Conflicts of interest None

Ethical standards This study abided by the Oryx guidelines on ethical standards. All research was conducted non-invasively.

References

Andheria AP, Karanth KU, Kumar NS (2007) Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. J Zool 273:169–175. https://doi.org/10.1111/j.1469-7998.2007.00310.x

Biswas S, Sankar K (2002) Prey abundance and food habit of tigers (Panthera tigris tigris) in Pench National Park, Madhya Pradesh, India. J Zool 256:411–420. https://doi.org/10.1017/S0952836902000456

DNP (2016) Practical Plan to Improve Tiger Population 2015-2035 (20 Years). Department of National Parks, Wildlife and Plant Conservation (DNP), Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

DNP (2004) Submission for Nomination of the Dong Phayayen- Khao Yai Forest Complex. Department of National Parks, Wildlife and Plant Conservation, The Royal Thai Government, Bangkok

Duangchantrasiri S, Umponjan M, Simcharoen S, et al (2016) Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. Conserv Biol 30:639–648. https://doi.org/10.1111/cobi.12655

Global Tiger Initiative (2011) Global Tiger Recovery Program 2010–2022. The World Bank, Washington D.C.

Goodrich JM, Lynam A, Miquelle DG, et al (2015) Panthera tigris. IUCN Red List Threat. Species 2015 e.T15955A50659951

Gray TNE, Crouthers R, Ramesh K, et al (2017) A framework for assessing readiness for tiger Panthera tigris reintroduction: a case study from eastern Cambodia. Biodivers Conserv 26:2383–2399. https://doi.org/10.1007/s10531-017-1365-1

Hansen MC, Potapov P V., Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science (80-) 342:850–853. https://doi.org/10.1126/science.1244693

Harihar A, Chanchani P, Borah J, et al (2018) Recovery planning towards doubling wild tiger Panthera tigris numbers: Detailing 18 recovery sites from across the range. PLoS One 13:e0207114. https://doi.org/10.1371/journal.pone.0207114

Harihar A, Pandav B, Goyal SP (2011) Responses of leopard Panthera pardus to the recovery of a tiger Panthera tigris population. J Appl Ecol 48:806–814. https://doi.org/10.1111/j.1365-2664.2011.01981.x

Harihar A, Prasad DL, Ri C, et al (2007) Status of tiger and its prey species in Rajaji National Park. In: Harihar A, Kurien AJ, Pandev B, Goyal S. (eds) Response of tiger population to habitat, wild ungulate prey and human disturbance in Rajaji National Park, Uttarakhand. Wildlife Institute of India, Dehradun, pp 87–110

Harmsen BJ, Foster RJ, Silver S, et al (2010) Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. Biotropica 42:126–133. https://doi.org/10.1111/j.1744-7429.2009.00544.x

Hayward MW, Jedrzejewski W, Jedrzewska B (2012) Prey preferences of the tiger Panthera tigris. J Zool 286:221–231. https://doi.org/10.1111/j.1469-7998.2011.00871.x

Jenks K, Chanteap P, Damrongchainarony K, et al (2011) Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses - an example from Khao Yai National Park, Thailand. Trop Conserv Sci 4:113–131. https://doi.org/10.1177/194008291100400203

Jennelle CS, Runge MC, MacKenzie DI (2002) The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. Anim Conserv 5:119–120. https://doi.org/10.1017/S1367943002002160

Johnson A, Goodrich J, Hansel T, et al (2016) To protect or neglect? Design, monitoring, and evaluation of a law enforcement strategy to recover small populations of wild tigers and their prey. Biol Conserv 202:99–109. https://doi.org/10.1016/j.biocon.2016.08.018

Johnson A, Vongkhamheng C, Hedemark M, Saithongdam T (2006) Effects of human-carnivore conflict on tiger (Panthera tigris) and prey populations in Lao PDR. Anim Conserv 9:421–430. https://doi.org/10.1111/j.1469-1795.2006.00049.x

Joshi AR, Dinerstein E, Wikramanayake E, et al (2016) Tracking changes and preventing loss in critical tiger habitat. Sci Adv 2:e1501675–e1501675. https://doi.org/10.1126/sciadv.1501675

Kanwatanakid C, Lynam T, Galster S, et al (2002) Ecological monitoring of large mammals and birds at Khao Yai National Park, Thailand [Thai]. J Wildl Thail 10:97–105

Karanth KU (1995) Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture models. Biol Conserv 71:333–338. https://doi.org/10.1016/0006-3207(94)00057-W

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862. https://doi.org/10.2307/176521

Karanth KU, Nichols JD, Kumar NS, et al (2004) Tigers and their prey: Predicting carnivore densities from prey abundance. Proc Natl Acad Sci U S A 101:4854–4858. https://doi.org/10.1073/pnas.0306210101

Karanth KU, Stith BM (1999) Prey depletion as a critical determinant of tiger population viability. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 100–113

Karanth KU, Sunquist ME (1995) Prey Selection By Tiger, Leopard and Dhole in Tropical Forests. J Anim Ecol 64:439–450. https://doi.org/10.2307/5647

Luo S-J, Liu Y-C, Xu X (2019) Tigers of the World: Genomics and Conservation. Annu Rev Anim Biosci 7:521–548. https://doi.org/10.1146/annurev-animal-020518-115106

Luo SJ, Kim JH, Johnson WE, et al (2004) Phylogeography and genetic ancestry of tigers (Panthera tigris). PLoS Biol 2:e442. https://doi.org/10.1371/journal.pbio.0020442

Lynam A (2001) Status, Ecology, and Conservation of Tigers in their Critical Habitats in Thailand, September 2001. Wildlife Conservation Society, Bangkok

Lynam A, Nowell K (2011) Panthera tigris ssp. corbetti. IUCN Red List Threat. Species 2011 e.T136853A4346984

Lynam A, Round P, Brockelman W (2006) Status of Birds and Large Mammals in Thailand’s Dong Phayayen - Khao Yai Forest Complex. Wildlife Conservation Society and Biodiversity Research Training (BRT) Programme, Bangkok

Lynam AJ (2010) Securing a future for wild Indochinese tigers: Transforming tiger vacuums into tiger source sites. Integr Zool 5:324–334. https://doi.org/10.1111/j.1749-4877.2010.00220.x

Lynam AJ, Kanwatanakid C, Suckaseam C (2003) Ecological monitoring of wildlife at Khao Yai National Park, Thailand. Final Report submitted to Department of National Parks, Wildlife and Plants and Khao Yai Conservation Project, Bangkok

Lynam AJ, Rabinowitz A, Myint T, et al (2009) Estimating abundance with sparse data: Tigers in northern Myanmar. Popul Ecol 51:115–121. https://doi.org/10.1007/s10144-008-0093-5

Moo SSB, Froese GZL, Gray TNE (2018) First structured camera-trap surveys in Karen State, Myanmar, reveal high diversity of globally threatened mammals. Oryx 52:537–543. https://doi.org/10.1017/S0030605316001113

Naing H, Ross J, Burnham D, et al (2019) Population density estimates of clouded leopard and tigers in Htamanthi Wildlife Sanctuary, Sagaing, Myanmar. Oryx 53:654–662. https://doi.org/10.1017/S0030605317001260

Ngoprasert D, Lynam AJ, Sukmasuang R, et al (2012) Occurrence of Three Felids across a Network of Protected Areas in Thailand:

Prey, Intraguild, and Habitat Associations. Biotropica 44:810–817. https://doi.org/10.1111/j.1744-7429.2012.00878.x

Nowell K, Jackson P (1996) Wild Cats : Status Survey and Conservation Action Plan. IUCN/SSC Cat Specialist Group, International Union for the Conservation of Nature, Gland, Switzerland

O'Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim Conserv 6:131–139. https://doi.org/10.1017/S1367943003003172

Pisdamkam C, Prayurasiddhi T, Kanchanasaka B, et al (2010) Thailand Tiger Action Plan - 2010-2012. Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

Rao M, Htun S, Zaw T, Myint T (2010) Hunting, livelihoods and declining wildlife in the Hponkanrazi wildlife sanctuary, North Myanmar. Environ Manage 46:143–153. https://doi.org/10.1007/s00267-010-9519-x

Rasphone A, Kéry M, Kamler JF, Macdonald DW (2019) Documenting the demise of tiger and leopard, and the status of other carnivores and prey, in Lao PDR's most prized protected area: Nam Et - Phou Louey. Glob Ecol Conserv 20:e00766. https://doi.org/10.1016/j.gecco.2019.e00766

Rostro-García S, Kamler JF, Ash E, et al (2016) Endangered leopards: Range collapse of the Indochinese leopard (Panthera pardus delacouri) in Southeast Asia. Biol Conserv 201:293–300. https://doi.org/10.1016/j.biocon.2016.07.001

Sanderson E, Forrest J, Loucks C, et al (2006) Setting Priorities for the Conservation and Recovery of Wild Tigers: 2005-2015 - The Technical Assessment. WCS, WWF, Smithsonian, and NFWF-STF, New York - Washington, DC

Simcharoen A, Savini T, Gale GA, et al (2014) Female tiger Panthera tigris home range size and prey abundance: important metrics for management. Oryx 48:370–377. https://doi.org/10.1017/S0030605312001408

Sollmann R, Mohamed A, Samejima H, Wilting A (2013) Risky business or simple solution–Relative abundance indices from camera-trapping. Biol Conserv 159:405–412. https://doi.org/10.1016/j.biocon.2012.12.025

Stein AB, Fuller TK, Marker LL (2008) Opportunistic use of camera traps to assess habitat-specific mammal and bird diversity in northcentral Namibia. Biodivers Conserv 17:3579–3587. https://doi.org/10.1007/s10531-008-9442-0

Steinmetz R, Seuaturien N, Chutipong W (2013) Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. Biol Conserv 163:68–78. https://doi.org/10.1016/j.biocon.2012.12.016

Sunquist M (2010) What is a Tiger? Ecology and Behavior. In: Tilson R, Nyhus P (eds) Tigers of the World, Second Edition. Elsevier, New York, pp 19–34

Sunquist M, Karanth UK, Sunquist F (1999) Ecology, behaviour and resilience of the tiger and its conservation needs. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 5–18

UNESCO (2017) Dong Phayayen-Khao Yai Forest Complex. In: UNESCO World Herit. Cent. http://whc.unesco.org/en/list/590. Accessed 27 Nov 2017

Volmer R, Hölzchen E, Wurster A, et al (2017) Did Panthera pardus (Linnaeus, 1758) become extinct in Sumatra because of competition for prey? Modeling interspecific competition within the Late Pleistocene carnivore guild of the Padang Highlands, Sumatra. Palaeogeogr Palaeoclimatol Palaeoecol. https://doi.org/10.1016/j.palaeo.2017.08.032

Vongkhamheng C (2011) Abundance and Distribution of Tiger and Prey in Montane Tropical Forest in Northern Lao People Democratic Republic. PhD Thesis, University of Florida, Gainesville, FL, USA

Walston J, Robinson JG, Bennett EL, et al (2010) Bringing the tiger back from the brink-the six percent solution. PLoS Biol 8:6–9. https://doi.org/10.1371/journal.pbio.1000485

Welsh AH, Lindenmayer DB, Donnelly CF (2013) Fitting and Interpreting Occupancy Models. PLoS One 8:e52015. https://doi.org/10.1371/journal.pone.0052015

Wolf C, Ripple WJ (2017) Range contractions of the world's large carnivores. R Soc Open Sci 4:170052. https://doi.org/10.1098/rsos.170052

Supplementary Material 1

Opportunity for Thailand's forgotten tigers: assessment of the Indochinese tiger *Panthera tigris corbetti* and its prey with camera-trap surveys

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Supplementary Material 1 Comprehensive analysis of the photographic capture rate index for tigers and prey for all five parks.

1. Introduction

The use of photographic capture rates (photographic capture rate index, PCRI; or relative abundance index, RAI) as a correlate with abundance is controversial (Carbone et al. 2001; Jennelle et al. 2002; Harmsen et al. 2010), notably because it fails to account for detection probabilities. Jenks et al. (2011) highlighted that such rates, while not a true metric of abundance and limited in applications, may be useful for opportunistic camera-trap studies, which have been common across Asia. This includes identifying areas for conservation interventions and potential trends to merit further research (Carbone et al. 2001; Jenks et al. 2011). This method was employed previously in Khao Yai National Park to document species declines and identify species hotspots to focus further research or management inquiries (Jenks et al. 2011). If used with additional analysis, such indices can be useful for comparing detection rates between areas of interest (Rayan and Linkie 2015, 2016). In addition to the methods described in the main text, we conducted additional analysis on PCRI to compare rates across protected areas and survey years. However, as such indices are not a true measure of abundance, results should not be assumed to reflect actual differences in abundance. We feel results may nonetheless be of interest and have therefore included this supplementary information.

2. Methods

We define PCRI as the number of species detections per 100 camera-trap nights (O'Brien et al. 2003; O'Brien 2011) and calculated this separately per year for each camera station by dividing the sum of detections for a species by the total number of camera-trap nights divided by 100. PCRI values for prey species were calculated separately for each species as well as for all species combined, calculated as the sum of PCRI values for each individual prey species (Ngoprasert et al. 2007).

We conducted individual comparisons among PCRI for tiger, individual prey species, and combined prey across parks and years using analysis of variance (ANOVA; Sokal and Rohlf 1981). To determine significance of differences in mean PCRI between protected areas and years, we applied a post-hoc Tukey honest significance difference test (Tukey 1949), examining differences in PCRI between parks, years, and the interaction between parks and years. We considered differences significant when $P < 0.01$, very significant when $P < 0.001$, and highly significant when $P < 0.0001$.

3. Results

Tiger PCRI was generally higher in Thap Lan National Park than Pang Sida National Park (Fig. 1). Results of ANOVA and Tukey honest significance difference test for tigers in Thap Lan NP and Pang Sida NP indicated highly significant ($P < 0.0001$) differences in mean PCRI (Table 1), with Thap Lan NP characterized by a much higher mean PCRI compared to Pang Sida NP. We also found highly significant differences in PCRI between certain years and for several interactions of park and year. Particularly, mean PCRI for Thap Lan NP in 2014 were higher than almost all years in Pang Sida NP. In general, mean PCRI in the latter years of the study (2013–2016) were significantly higher in comparison to early years (2010, 2012; Table 2), which are mostly attributable to Thap Lan NP.

Differences between combined prey species mean PCRI (Fig. 2) among all variables were highly significant. Thap Lan NP had significantly higher mean PCRI for prey compared to Pang Sida NP, Ta Phraya NP, and Dong Yai WS (Table 3). Mean PCRI for Thap Lan NP in 2015 were higher than most years for Pang Sida NP. Mean PCRI for Khao Yai NP, particularly for 2014 and 2015, were also significantly higher compared to those of Pang Sida NP, Ta Phraya NP, and Dong Yai WS. Similar to tigers, prey PCRI was generally higher in the later years of the study (2013–2016) compared to earlier years (2009, 2010, 2012; Table 2).

A number of notable significant relationships are evident among prey species (Table 3, Fig. 3). For sambar, mean PCRI for Thap Lan NP was higher to a significant or highly significant degree compared to Pang Sida NP, Ta Phraya NP, and Dong Yai WS across a number of years. Furthermore, wild boar mean PCRI in Pang Sida NP was significantly higher than in Thap Lan NP, particularly in 2016. For gaur, differences in mean PCRI were significant for all variables with Khao Yai NP and Pang Sida NP having higher mean PCRI values compared with Thap Lan NP to a highly significant degree.

4. Discussion

The significant differences in PCRI between the studied parks over time provide insight into this previously understudied tiger population. Large and highly significant differences in mean PCRI occur between Thap Lan NP and Pang Sida NP, particularly with substantial survey effort. These differences occur despite contiguous forest cover between Thap Lan NP, Pang Sida NP, Ta Phraya NP, and Dong Yai WS. This may imply a heterogeneity in suitability of this landscape for tigers, which merits further investigation.

We documented significantly higher PCRI values overall in later years of study compared to earlier years for tigers, particularly for Thap Lan NP. Higher overall PCRI values over time may have resulted from population changes during the study period, however, this cannot be confidently concluded because of limitations in the study design. It is possible that detection probabilities increased over time as a result of increased knowledge of the tigers' use of the landscape and/or improvements in camera-trap performance. Despite the limitations mentioned, we can conclude that conditions in at least some areas of DPKY support breeding and dispersal of tigers, which could provide a foundation for population recovery and expansion into areas such as Khao Yai NP.

Given that prey is an important factor for tiger distribution, density and persistence (Karanth and Stith 1999; Karanth et al. 2004; Chapron et al. 2008), significant differences in PCRI of prey between Thap Lan NP and Pang Sida NP could be linked to differences in tiger PCRI between these parks. We found that mean PCRI for sambar in Thap Lan NP was significantly higher than in Pang Sida NP, whereas Pang Sida NP had significantly higher mean PCRI for gaur and wild boar than Thap Lan NP. Elsewhere in Thailand, studies indicate that sambar, gaur, banteng (Petdee 2000; Prommakul 2003) and wild boar (Ngoprasert et al. 2012) are important prey species for tigers, which is corroborated by studies elsewhere in the tiger's range (Andheria et al. 2007; Sunquist 2010; Hayward et al. 2012). Mean PCRI for combined prey were generally higher in the latter part of the study period. Although this could reflect increases in prey populations, it could also be a result of increased detection probabilities.

Given limitations imposed by the study design, we feel analysis of PCRI, although not ideal, was useful for examining differences in detections in our study overall and to illuminate potential trends for more targeted investigation. Our assessments are conservative, given that our study design precludes calibration of PCRI with independent estimates of density or detection probability (Nichols et al. 2010). Further, we do not make comparisons across species or studies nor do we recommend this approach over occupancy or mark–recapture based methods. Methodologically-rigorous study designs should be employed wherever possible in monitoring tiger populations.

References

Andheria AP, Karanth KU, Kumar NS (2007) Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. J Zool 273:169–175. https://doi.org/10.1111/j.1469-7998.2007.00310.x

Carbone C, Christie S, Conforti K, et al (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. Anim Conserv 4:75–79. https://doi.org/10.1017/S1367943001001081

Chapron G, Miquelle DG, Lambert A, et al (2008) The impact on tigers of poaching versus prey depletion. J Appl Ecol 45:1667–1674. https://doi.org/10.1111/j.1365-2664.2008.01538.x

Harmsen BJ, Foster RJ, Silver S, et al (2010) Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. Biotropica 42:126–133. https://doi.org/10.1111/j.1744-7429.2009.00544.x

Hayward MW, Jedrzejewski W, Jedrzewska B (2012) Prey preferences of the tiger Panthera tigris. J Zool 286:221–231. https://doi.org/10.1111/j.1469-7998.2011.00871.x

Jenks K, Chanteap P, Damrongchainarony K, et al (2011) Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses - an example from Khao Yai National Park, Thailand. Trop Conserv Sci 4:113–131. https://doi.org/10.1177/194008291100400203

Jennelle CS, Runge MC, MacKenzie DI (2002) The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. Anim Conserv 5:119–120. https://doi.org/10.1017/S1367943002002160

Karanth KU, Nichols JD, Kumar NS, et al (2004) Tigers and their prey: Predicting carnivore densities from prey abundance. Proc Natl

Acad Sci U S A 101:4854–4858. https://doi.org/10.1073/pnas.0306210101

Karanth KU, Stith BM (1999) Prey depletion as a critical determinant of tiger population viability. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 100–113

Ngoprasert D, Lynam AJ, Gale GA (2007) Human disturbance affects habitat use and behaviour of Asiatic leopard Panthera pardus in Kaeng Krachan National Park, Thailand. Oryx 41:343–351. https://doi.org/10.1017/S0030605307001102

Ngoprasert D, Lynam AJ, Sukmasuang R, et al (2012) Occurrence of Three Felids across a Network of Protected Areas in Thailand: Prey, Intraguild, and Habitat Associations. Biotropica 44:810–817. https://doi.org/10.1111/j.1744-7429.2012.00878.x

Nichols JD, Karanth KU, O'Connell AF (2010) Science, Conservation, and Camera Traps. In: O'Connell AF, Nichols JD, Karanth KU (eds) Camera Traps in Animal Ecology: Methods and Analyses. Springer, London, pp 45–56

O'Brien TG (2011) Abundance, density and relative abundance: a conceptual framework. In: O'Connell AF, Nichols JD, Karanth KU (eds) Camera Traps in Animal Ecology: Methods and Analyses. Springer, London, pp 71–96

O'Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim Conserv 6:131–139. https://doi.org/10.1017/S1367943003003172

Petdee A (2000) Feeding habits of the tiger Panthera tigris (Linnaeus) in Huai Kha Khaeng Wildlife Sanctuary by fecal analysis. MSc Thesis, Kasetsart University, Bangkok, Thailand

Prommakul P (2003) Habitat utilization and prey of the tiger Panthera tigris (Linnaeus) in eastern ThungYai Naresuan Wildlife Sanctuary [Thai]. MSc Thesis. Kasetsart University, Bangkok

Rayan DM, Linkie M (2015) Conserving tigers in Malaysia: A science-driven approach for eliciting conservation policy change. Biol Conserv 184:18–26. https://doi.org/10.1016/j.biocon.2014.12.024

Rayan DM, Linkie M (2016) Managing conservation flagship species in competition: Tiger, leopard and dhole in Malaysia. Biol Conserv 204:360–366. https://doi.org/10.1016/j.biocon.2016.11.009

Sokal RR, Rohlf FJ (1981) Biometry: The Principles and Practice of Statistics in Biological Research. W.H. Freeman, San Francisco

Sunquist M (2010) What is a Tiger? Ecology and Behavior. In: Tilson R, Nyhus P (eds) Tigers of the World, Second Edition. Elsevier, New York, pp 19–34

Tukey JW (1949) One degree of freedom for non-additivity. Biometrics 5:232–242

Table 1 Cumulative species detections and detection rates (detections per 100 camera-trap nights) for protected areas in DPKY.

Scientific Name	Common Name	IUCN Red List Status[1]	DYWS[2]	KYNP[2]	PSNP[2]	TLNP[2]	TPNP[2]
Panthera tigris	Indochinese tiger	EN	7 (0.14)		516 (1.8)	1203 (3.65)	
Manis javanica	Sunda pangolin	CR	2 (0.04)	2 (0.03)	7 (0.02)	9 (0.03)	
Bos javanicus	Banteng	EN			7 (0.02)		11 (0.19)
Cuon alpinus	Dhole	EN	11 (0.23)	109 (1.43)	147 (0.51)	366 (1.11)	3 (0.05)
Elephas maximus	Asian elephant	EN	309 (6.34)	128 (1.68)	1047 (3.65)	1500 (4.55)	5 (0.09)
Viverra megaspila	Large-spotted civet	EN	3 (0.06)	8 (0.1)	7 (0.02)	53 (0.16)	10 (0.17)
Arctictis binturong	Binturong	VU	1 (0.02)	2 (0.03)	11 (0.04)	9 (0.03)	
Arctonyx collaris	Hog badger	VU	5 (0.1)	16 (0.21)	186 (0.65)	84 (0.25)	
Bos gaurus	Gaur	VU	119 (2.44)	292 (3.83)	815 (2.84)	422 (1.28)	173 (3)
Helarctos malayanus	Malayan sun bear	VU	33 (0.68)	21 (0.28)	467 (1.63)	144 (0.44)	17 (0.29)
Lutrogale perspicillata	Smooth-coated otter	VU		5 (0.07)	1 (0.003)		
Macaca leonina	Pig-tailed macaque	VU	60 (1.23)	275 (3.61)	292 (1.02)	641 (1.95)	86 (1.49)
Neofelis nebulosa	Clouded leopard	VU	3 (0.06)	19 (0.25)	83 (0.29)	46 (0.14)	7 (0.12)
Nycticebus bengalensis	Bengal slow loris	VU			1 (0.003)		
Rusa unicolor	Sambar	VU	81 (1.66)	661 (8.67)	56 (0.2)	4844 (14.7)	1 (0.02)
Ursus thibetanus	Asiatic black bear	VU	21 (0.43)	35 (0.46)	152 (0.53)	104 (0.32)	10 (0.17)
Capricornis milneedwardsii	Chinese serow	NT	2 (0.04)	9 (0.12)	93 (0.32)	47 (0.14)	12 (0.21)
Catopuma temminckii	Asiatic golden cat	NT		2 (0.03)	11 (0.04)	22 (0.07)	
Pardofelis marmorata	Marbled cat	NT		2 (0.03)	10 (0.03)	17 (0.05)	1 (0.02)
Arctogalidia trivirgata	Three-striped palm	LC				1 (0.003)	
Atherurus macrourus	Asiatic brush-tailed	LC	6 (0.12)	3 (0.04)	144 (0.5)	12 (0.04)	28 (0.49)
Canis aureus	Golden jackal	LC		10 (0.13)	16 (0.06)	34 (0.1)	10 (0.17)
Herpestes javanicus	Small Asian mongoose	LC	1 (0.02)	16 (0.21)	9 (0.03)	12 (0.04)	6 (0.1)
Herpestes urva	Crab-eating mongoose	LC	7 (0.14)	15 (0.2)	152 (0.53)	144 (0.44)	1 (0.02)
Hystrix brachyura	Malayan porcupine	LC	97 (1.99)	181 (2.38)	770 (2.68)	804 (2.44)	22 (0.38)
Lepus peguensis	Siamese hare	LC		5 (0.07)	1 (0.003)	25 (0.08)	1 (0.02)
Macaca fascicularis	Long-tailed macaque	LC	1 (0.02)				
Martes flavigula	Yellow-throated	LC	7 (0.14)	4 (0.05)	62 (0.22)	182 (0.55)	3 (0.05)
Muntiacus vaginalis	Northern red muntjac	LC	177 (3.63)	461 (6.05)	691 (2.41)	724 (2.2)	160 (2.78)

TABLE 1 continued.

Scientific Name	**Common Name**	**IUCN Red List Status[1]**	**DYWS[2]**	**KYNP[2]**	**PSNP[2]**	**TLNP[2]**	**TPNP[2]**
Paradoxurus hermaphroditus	Common palm civet	LC	11 (0.23)	74 (0.97)	261 (0.91)	224 (0.68)	25 (0.43)
Prionailurus bengalensis	Leopard cat	LC	20 (0.41)	51 (0.67)	271 (0.94)	369 (1.22)	13 (0.23)
Prionodon pardicolor	Spotted linsang	LC			4 (0.01)	9 (0.03)	
Rhizomys pruinosus	Hoary bamboo rat	LC			7 (0.02)	7 (0.02)	
Sus scrofa	Wild boar	LC	325 (6.67)	398 (5.22)	1911 (6.66)	1522 (4.62)	199 (3.45)
Tragulus kanchil	Lesser mouse-deer	LC	49 (1.01)	28 (0.37)	287 (0.1)	40 (0.12)	10 (0.17)
Viverra zibetha	Large Indian civet	LC	16 (0.33)	114 (1.5)	424 (1.48)	584 (1.77)	9 (0.16)
Viverricula indica	Small Indian civet	LC	4 (0.08)	14 (0.18)	43 (0.15)	198 (0.6)	2 (0.03)
Camera-trap nights			4,871	7,621	28,698	32,955	5,764
Number of Species			27	30	35	33	26

[1]CR, Critically Endangered; EN, Endangered; VU Vulnerable; NT, Near Threatened; LC, Least Concern.

[2]DYWS, Dong Yai Wildlife Sanctuary; KYNP, Khao Yai National Park; PSNP, Pang Sida National Park; TLNP, Thap Lan National Park; TPNP, Ta Phraya National Park.

Table 2 Summary of Tukey honest significance difference test results comparing differences in mean tiger PCRI values for and their significance among the interaction between protected areas and years. Only Thap Lan NP and Pang Sida NP were included because of low or no detections of tigers in other protected areas.

	TL10	TL11	TL12	TL13	TL14	TL15	TL16	TL17	PS10	PS11	PS12	PS13	PS14	PS15	PS16	PS17
TL10		-2.5	-1.9	-4.5	-6.3	-3.9	-4.0	-3.2	-0.2	-2.7	0.4	-0.4	-1.2	-1.6	-1.1	-0.3
TL11	2.5		0.6	-1.9	-3.8	-1.4	-1.5	-0.6	2.4	-0.1	2.9	2.1	1.3	0.9	1.5	2.2
TL12	1.9	-0.6		-2.5	-4.4	-2.0	-2.1	-1.2	1.8	-0.7	2.3	1.5	0.7	0.3	0.9	1.6
TL13	4.5	1.9	2.5		-1.8	0.5	0.4	1.3	4.3	1.8	4.9	4.1	3.3	2.8	3.4	4.2
TL14	6.3	3.8	4.4	1.8		2.3	2.2	3.1	6.1	3.6	6.7	5.9	5.1	4.7	5.2	6.0
TL15	3.9	1.4	2.0	-0.5	-2.3		-0.1	0.8	3.8	1.3	4.3	3.5	2.7	4.7	2.9	3.7
TL16	4.0	1.5	2.1	-0.4	-2.2	0.1		0.9	3.9	1.4	4.5	3.7	2.9	2.4	3.0	3.8
TL17	3.2	0.6	1.2	-1.3	-3.1	-0.8	-0.9		3.0	0.5	3.6	2.8	2.0	1.5	2.1	2.9
PS10	0.2	-2.4	-1.8	-4.3	-6.1	-3.8	-3.9	-3.0		-2.5	0.6	-0.2	-1.0	-1.5	-0.9	-0.1
PS11	2.7	0.1	0.7	-1.8	-3.6	-1.3	-1.4	-0.5	2.5		3.1	2.3	1.5	1.0	1.6	2.4
PS12	-0.4	-2.9	-2.3	-4.9	-6.7	-4.3	-4.5	-3.6	-0.6	-3.1		-0.8	-1.6	-2.0	-1.5	-0.7
PS13	0.4	-2.1	-1.5	-4.1	-5.9	-3.5	-3.7	-2.8	0.2	-2.3	0.8		-0.8	-1.2	-0.7	0.1
PS14	1.2	-1.3	-0.7	-3.3	-5.1	-2.7	-2.9	-2.0	1.0	-1.5	1.6	0.8		-0.4	0.1	0.9
PS15	1.6	-0.9	-0.3	-2.8	-4.7	-4.7	-2.4	-1.5	1.5	-1.0	2.0	1.2	0.4		0.6	1.3
PS16	1.1	-1.5	-0.9	-3.4	-5.2	-2.9	-3.0	-2.1	0.9	-1.6	1.5	0.7	-0.1	-0.6		0.8
PS17	0.3	-2.2	-1.6	-4.2	-6.0	-3.7	-3.8	-2.9	0.1	-2.4	0.7	-0.1	-0.9	-1.3	-0.8	

P < 0.0001　　0.0001 ≤ P < 0.001　　0.001 ≤ P < 0.01　　0.01 ≤ P ≤0.05

Table 3 Summary of Tukey honest significance difference test results comparing differences in mean PCRI values and their significance across years for tigers and combined prey species. For tigers, only Thap Lan NP and Pang Sida NP were included because of low or no detections of tigers in other protected areas.

Tiger

	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
2008		-	-	-	-	-	-	-	-	-
2009			-	-	-	-	-	-	-	-
2010		-		-4.0	-1.5	-3.0	-4.8	-3.6	-3.5	-2.7
2011		-	4.0		2.5	1.0	-0.9	0.4	0.5	1.3
2012		-	1.5	-2.5		-1.5	-3.4	-2.1	-2.0	-1.2
2013		-	3.0	-1.0	1.5		-1.8	-0.6	-0.5	0.4
2014		-	4.8	0.9	3.4	1.8		1.3	1.4	2.2
2015		-	3.6	-0.4	2.1	0.6	-1.3		0.1	0.9
2016		-	3.5	-0.5	2.0	0.5	-1.4	-0.1		0.8
2017		-	2.7	-1.3	1.2	-0.4	-2.2	-0.9	-0.8	

Combined prey

	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
2008		13.2	16.0	4.1	5.7	-2.3	-0.3	-7.5	-4.0	5.7
2009	-13.2		2.8	-9.1	-7.5	-15.5	-13.5	-20.7	-17.2	-7.4
2010	-16.0	-2.8		-11.9	-10.2	-18.3	-16.2	-23.5	-20.0	-10.2
2011	-4.1	9.1	11.9		1.7	-6.4	-4.3	-11.6	-8.1	1.7
2012	-5.7	7.5	10.2	-1.7		-8.0	-6.0	-13.2	-9.7	0.0
2013	2.3	15.5	18.3	6.4	8.0		2.0	-5.2	-1.7	8.1
2014	0.3	13.5	16.2	4.3	6.0	-2.0		-7.2	-3.7	6.0
2015	7.5	20.7	23.5	11.6	13.2	5.2	7.2		3.5	13.2
2016	4.0	17.2	20.0	8.1	9.7	1.7	3.7	-3.5		9.8
2017	-5.7	7.4	10.2	-1.7	0.0	-8.1	-6.0	-13.2	-9.8	

P < 0.0001　　0.0001 ≤ P < 0.001　　0.001 ≤ P < 0.01　　0.01 ≤ P ≤ 0.05

Table 4 Summary of Tukey honest significance difference test results comparing differences in mean PCRI values amongst protected areas for combined prey, gaur *Bos gaurus*, sambar *Rusa unicolor* and wild boar *Sus scrofa*.

Combined prey

	DYWS	KYNP	PSNP	TLNP	TPNP
DYWS		-12.3	0.3	-11.7	3.8
KYNP	12.3		12.5	0.6	16.1
PSNP	-0.3	-12.5		-11.9	3.6
TLNP	11.7	-0.6	11.9		15.5
TPNP	-3.8	-16.1	-3.6	-15.5	

Gaur

	DYWS	KYNP	PSNP	TLNP	TPNP
DYWS		-1.3	-0.6	0.8	-0.5
KYNP	1.3		0.8	2.1	0.8
PSNP	0.6	-0.8		1.3	0.1
TLNP	-0.8	-2.1	-1.3		-1.3
TPNP	0.5	-0.8	-0.1	1.3	

Sambar

	DYWS	KYNP	PSNP	TLNP	TPNP
DYWS		-7.6	1.2	-14.2	1.3
KYNP	7.6		8.8	-6.6	8.9
PSNP	-1.2	-8.8		-15.4	0.2
TLNP	14.2	6.6	15.4		15.5
TPNP	-1.3	-8.9	-0.2	-15.5	

Wild boar

	DYWS	KYNP	PSNP	TLNP	TPNP
DYWS		-0.3	-0.9	0.8	2.4
KYNP	0.3		-0.7	1.1	2.6
PSNP	0.9	0.7		1.8	3.3
TLNP	-0.8	-1.1	-1.8		1.5
TPNP	-2.4	-2.6	-3.3	-1.5	

$P < 0.0001$ $0.0001 \leq P < 0.001$ $0.001 \leq P < 0.01$ $0.01 \leq P \leq 0.05$

Table 5 Summary of ANOVA test results comparing differences in mean PCRI values and their significance among protected areas (PARK), years (YEAR), and the interaction between protected areas and years (PARK:YEAR). Only Thap Lan NP and Pang Sida NP were included because of low or no detections of tigers in other protected areas.

		Sum of squares	**Mean square**	**F-value**	***p***	**Significance**
Tiger	PARK	637.83	637.83	28.12	1.45E-07	***
	YEAR	1973.38	219.26	9.67	3.69E-14	***
	PARK:YEAR	408.28	58.33	2.57	1.26E-02	
	Residuals	19598.57	22.68			
Combined prey	PARK	95200.16	23800.04	21.38	2.45E-17	***
	YEAR	114570.51	12730.06	11.44	1.06E-17	***
	PARK:YEAR	55125.62	3242.68	2.91	5.69E-05	***
	Residuals	2554308.87	1112.99			
Sambar	PARK	122714.90	30678.73	33.43	3.85E-27	***
	YEAR	57491.87	6387.99	6.96	5.76E-10	***
	PARK:YEAR	28359.21	1668.19	1.82	2.11E-02	
	Residuals	2106122.78	917.70			
Gaur	PARK	1267.02	316.75	11.75	1.90E-09	***
	YEAR	652.39	72.49	2.69	4.14E-03	*
	PARK:YEAR	2333.33	137.25	5.09	4.46E-11	***
	Residuals	61876.47	26.96			
Wild boar	PARK	2471.56	617.89	5.58	1.80E-04	**
	YEAR	5347.12	594.12	5.37	2.69E-07	***
	PARK:YEAR	4470.12	262.95	2.38	1.23E-03	*
	Residuals	254016.40	110.68			
Muntjac	PARK	2992.86	748.21	21.47	2.10E-17	***
	YEAR	4174.74	463.86	13.31	5.68E-21	***
	PARK:YEAR	2182.20	128.36	3.68	4.96E-07	***
	Residuals	79994.68	34.86			
Banteng	PARK	4.56	1.14	4.26	1.94E-03	*
	YEAR	3.91	0.43	1.62	1.03E-01	
	PARK:YEAR	6.38	0.38	1.40	1.25E-01	
	Residuals	613.90	0.27			
Serow	PARK	18.74	4.69	3.05	1.601E-02	
	YEAR	20.73	2.30	1.50	1.415E-01	
	PARK:YEAR	17.41	1.02	0.67	8.375E-01	
	Residuals	3521.12	1.53			

* $p < 0.01$.
**$p < 0.001$
***$p < 0.0001$

Table 6 Summary of Tukey honest significance difference test results comparing differences in observed mean PCRI for combined prey, confidence intervals, adjusted p-values (p), and their significance among the interaction between specific protected areas and years (PARK:YEAR).

Variables	Difference in Means	Lower Confidence Interval	Upper Confidence Interval	*P*	Significance
TL:2015-PS:2012	41.08	22.55	59.60	3.06E-11	***
TL:2015-TP:2014	41.51	22.85	60.17	3.06E-11	***
TL:2015-PS:2011	41.54	23.60	59.49	3.07E-11	***
TL:2015-TL:2010	41.75	23.40	60.11	3.07E-11	***
TL:2015-PS:2015	40.03	20.10	59.97	3.27E-11	***
TL:2015-TL:2009	38.55	18.62	58.48	4.98E-11	***
TL:2015-KY:2012	41.22	18.78	63.67	3.81E-10	***
TL:2015-PS:2013	37.62	17.04	58.20	4.79E-10	***
TL:2015-DY:2012	41.18	17.69	64.67	3.89E-09	***
PS:2016-TL:2015	-32.35	-51.02	-13.67	6.98E-09	***
TL:2016-PS:2011	20.01	7.71	32.30	1.15E-07	***
TL:2015-TP:2013	46.52	17.76	75.28	1.48E-07	***
TL:2016-TL:2010	20.22	7.34	33.10	5.05E-07	***
TL:2015-PS:2014	34.88	11.95	57.81	1.67E-06	***
TL:2016-TP:2014	19.97	6.67	33.28	2.74E-06	***
TL:2015-DY:2013	37.85	12.58	63.12	2.93E-06	***
TL:2016-PS:2012	19.54	6.42	32.66	3.65E-06	***
TL:2013-PS:2011	29.09	9.36	48.83	5.21E-06	***
TL:2015-PS:2010	48.44	15.55	81.32	5.33E-06	***
TL:2013-TL:2010	29.30	9.20	49.41	7.71E-06	***
TL:2015-TL:2014	29.69	8.91	50.47	1.50E-05	***
TP:2014-TL:2013	-29.06	-49.45	-8.68	1.61E-05	***
TL:2013-PS:2012	28.63	8.36	48.89	2.16E-05	***
PS:2015-TL:2013	-27.58	-49.14	-6.02	3.79E-04	**
DY:2016-TL:2015	-34.76	-62.00	-7.51	4.10E-04	**
TL:2015-TL:2011	28.87	5.95	51.80	5.69E-04	**
KY:2014-PS:2011	23.12	4.62	41.62	6.85E-04	**
TL:2016-TL:2015	-21.54	-38.78	-4.30	6.94E-04	**
KY:2015-PS:2011	23.37	4.46	42.28	9.03E-04	**
KY:2014-TL:2010	23.33	4.44	42.23	9.19E-04	**
TL:2016-PS:2015	18.49	3.45	33.54	1.03E-03	*
KY:2015-TL:2010	23.58	4.29	42.88	1.18E-03	*
TL:2013-TL:2009	26.10	4.54	47.66	1.47E-03	*
TL:2013-KY:2012	28.77	4.88	52.67	1.67E-03	*
TP:2014-KY:2014	-23.09	-42.28	-3.90	1.69E-03	*
TP:2015-TL:2015	-41.67	-76.64	-6.71	2.10E-03	*
KY:2015-TP:2014	23.34	3.75	42.93	2.10E-03	*
KY:2014-PS:2012	22.66	3.60	41.72	2.22E-03	*
KY:2015-PS:2012	22.91	3.45	42.37	2.76E-03	*
TL:2013-DY:2012	28.73	3.84	53.61	4.15E-03	*
TL:2017-TL:2015	-33.63	-63.12	-4.15	5.30E-03	*
TP:2013-TL:2013	-34.07	-63.98	-4.16	5.45E-03	*
TL:2013-PS:2013	25.17	3.02	47.33	5.74E-03	*
TL:2016-TL:2009	17.01	1.97	32.05	6.31E-03	*

* Significant ($P < 0.01$).
**Very Significant ($P < 0.001$).
*** Highly Significant ($P < 0.0001$).

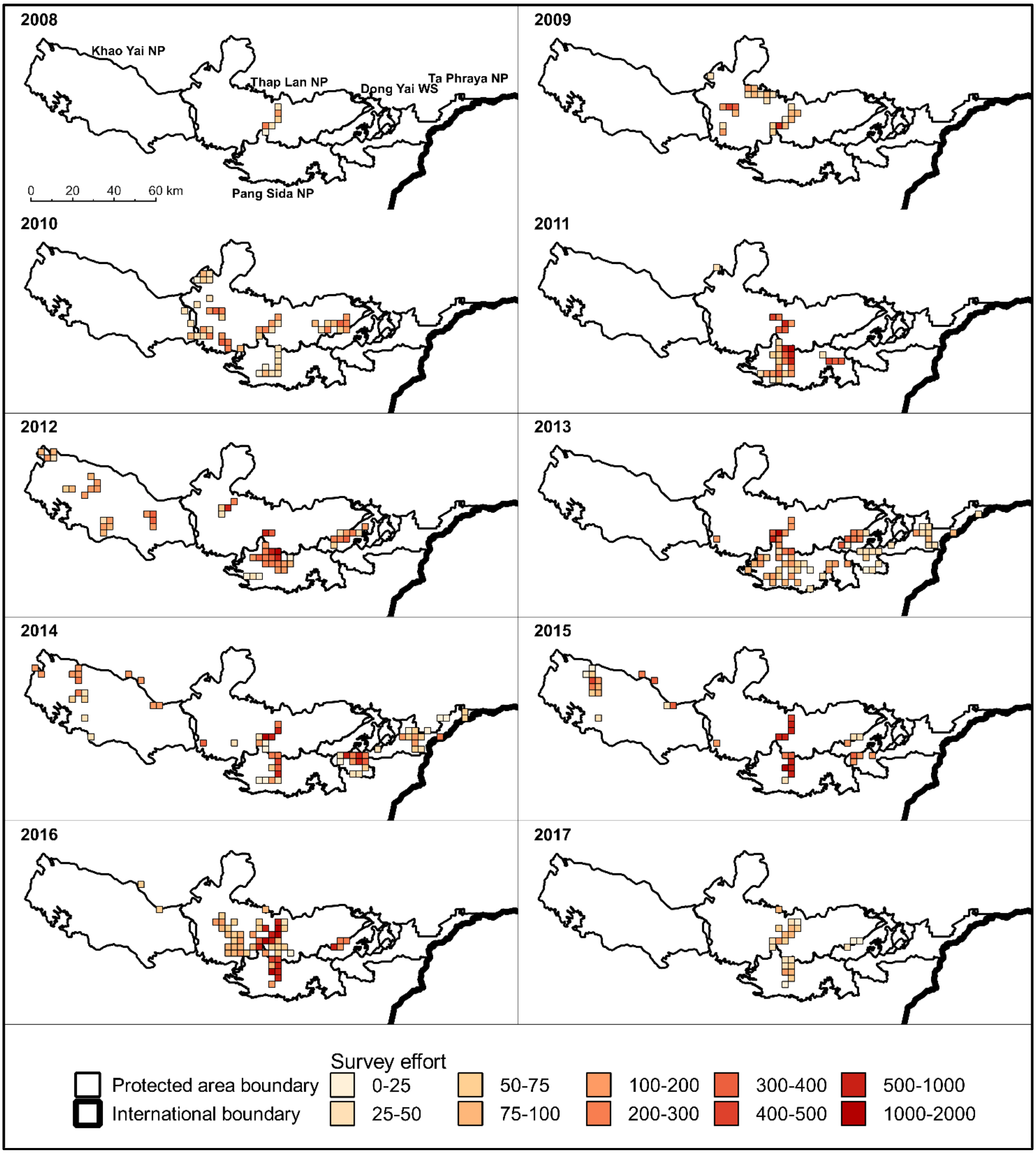

Fig. 1 Spatial extent of surveys in 2008–2017, shaded according to total survey effort (number of camera-trap nights).

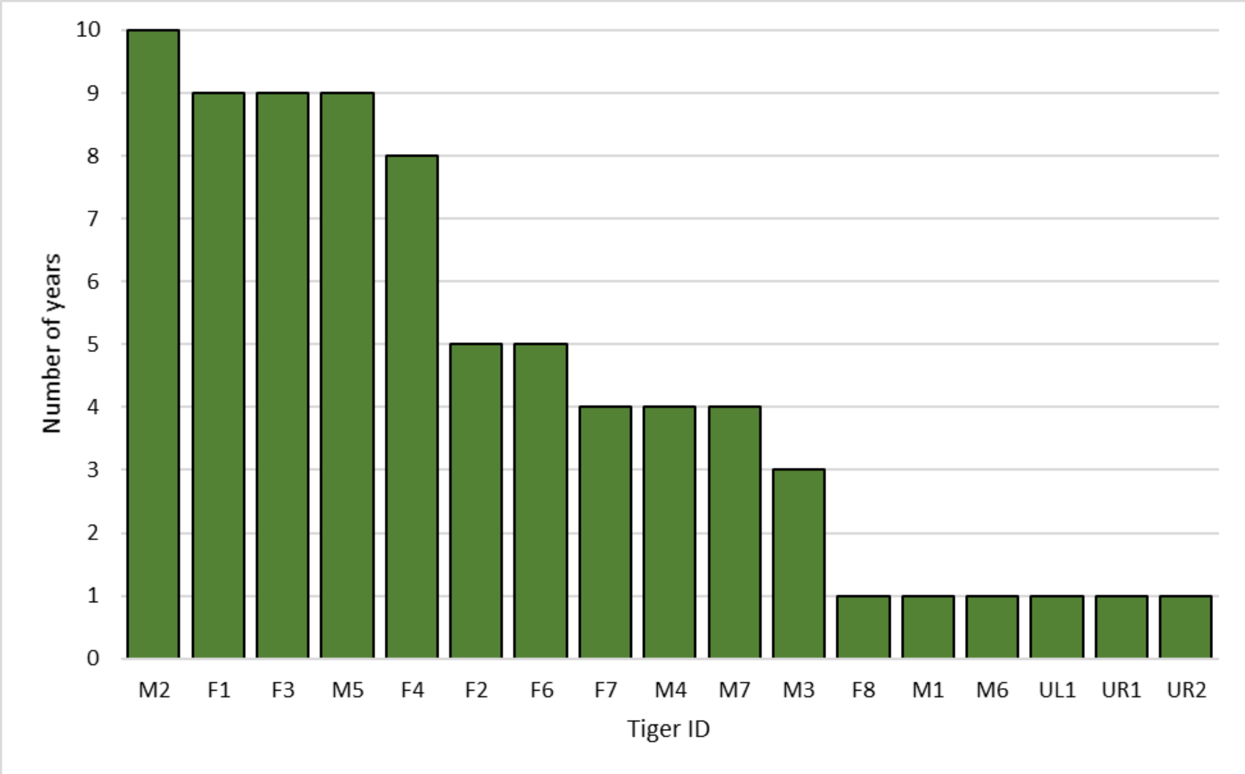

Fig. 2 Number of years between first and last confirmed detections of individual adult tigers, indicating the minimum length of persistence within the study site since first detection. Five individuals were detected over a period of 8–10 years, six individuals were detected over 3–5 years, and another six were documented in 1 year during the study.

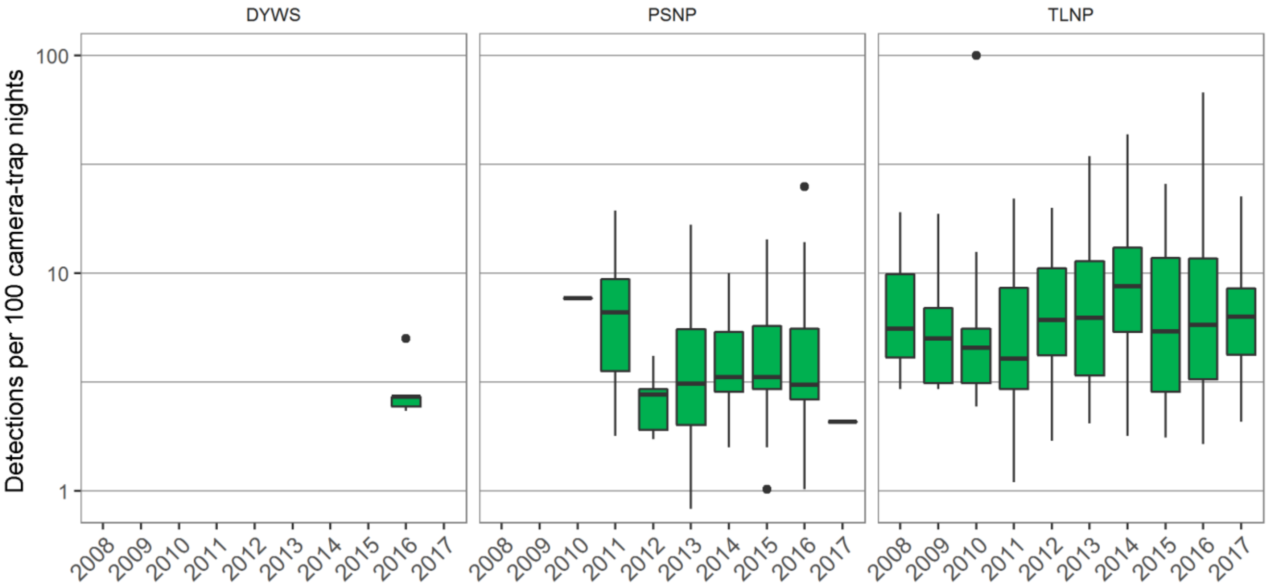

Fig. 3 Boxplot of photographic capture rate indices (PCRI) of tigers for Dong Yai WS, Pang Sida NP, and Thap Lan NP over the study period (2008–2017). Boxes indicate the range between 25th and 75th percentiles, with an internal line designating the median. Whiskers indicate the range between minimum and maximum values, with dots representing outliers.

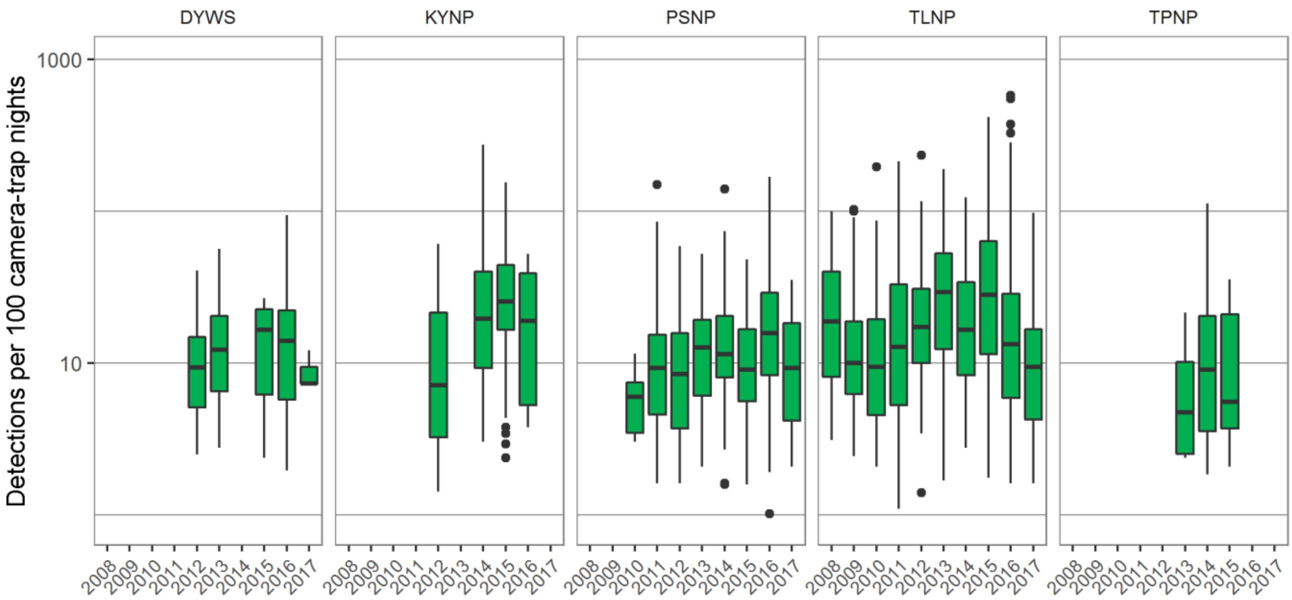

Fig. 4 Boxplot of photographic capture rate indices (PCRI) of combined prey (sambar *Rusa unicolor*, wild boar *Sus scrofa*, gaur *Bos gaurus*, northern red muntjac *Muntiacus vaginalis*, banteng *Bos javanicus* and Chinese serow *Capricornis milneedwardsii*) for each park in DPKY over the study period (2008–2017).

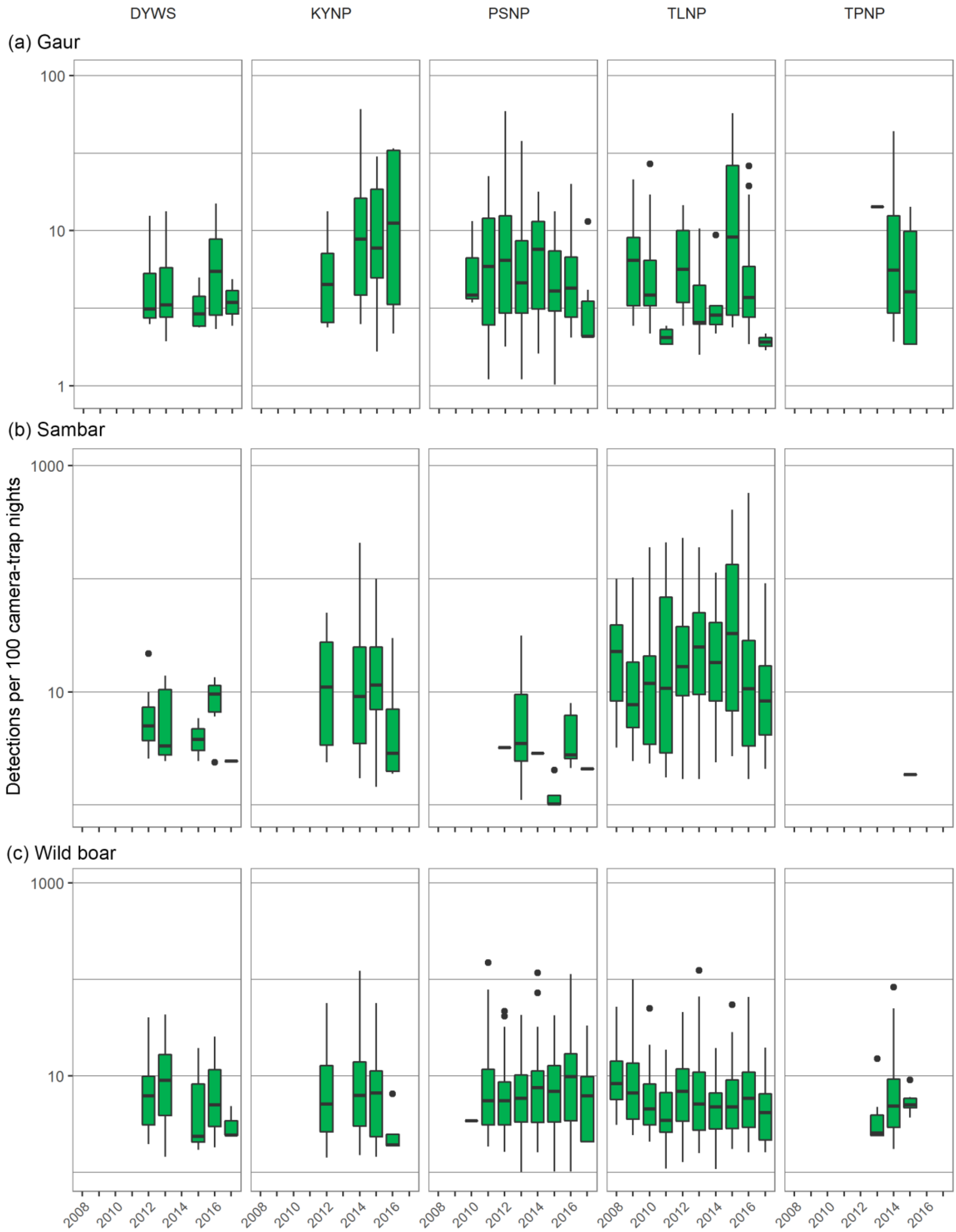

Fig. 5 Boxplot of photographic capture rate indices (PCRI; detections per 100 camera-trap nights) of prey species (a) gaur, (b) sambar and (c) wild boar, for each park in DPKY over the study period (2008–2017).

Chapter 3

Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: A case study of tigers (*Panthera tigris*) in Thailand

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Title

Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: a case study of tigers (*Panthera tigris*) in Thailand

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Abstract

Context Species habitat suitability models rarely incorporate multiple spatial scales or functional shapes of a species' response to covariates. Optimizing models for these factors may produce more robust, reliable, and informative habitat suitability models, which can be beneficial for the conservation of rare and endangered species, such as tigers (*Panthera tigris*).

Objectives We provide the first formal assessment of the relative impacts of scale-optimization and shape-optimization on model performance and habitat suitability predictions. We explored how optimization influences conclusions regarding habitat selection and mapped probability of occurrence.

Methods We collated environmental variables expected to affect tiger occurrence, calculating focal statistics and landscape metrics at spatial scales ranging from 250m to 16km. We then constructed a set of presence–absence generalized linear models including: (1) single-scale optimized models (SSO); (2) a multi-scale optimized model (MSO); (3) single-scale shape-optimized models (SSSO); and (4) a multi-scale- and shape-optimized model (MSSO). We compared performance and resulting prediction maps for top performing models.

Results The SSO (16km), SSSO (16km), MSO, and MSSO models performed equally well (AUC [0.9). However, these differed substantially in prediction and mapped habitat suitability, leading to different ecological understanding and potentially divergent conservation recommendations. Habitat selection was highly scale-dependent and the strongest relationships with environmental variables were at the broadest scales analysed. Modelling approach had a substantial influence in variable importance among top models.

Conclusions Our results suggest that optimization of the scale of resource selection is crucial in modelling tiger habitat selection. However, in this analysis, shape-optimization did not improve model performance.

Keywords functional form; habitat selection; *Panthera tigris*; scale-optimization; shape-optimization; Dong Phayayen-Khao Yai Forest Complex

1. Introduction

Much of modern ecological analysis is underpinned by ecological niche theory (Hutchinson 1957). At the center of ecological inquiries is the organism, with its distribution, abundance, and survival dictated by its niche, defined as a function of limited resources within an *n*-dimensional hypervolume of continuous space (Hegel et al. 2010; Blonder 2018). The proliferation of modern analytical tools (Elith et al. 2006; Blonder 2018) and increased computational power to quantify these fundamental and realized niches has advanced the field of landscape ecology and enabled more powerful habitat selection modelling (Hegel et al. 2010). However, such assessments, even for well-studied species, are rarely straightforward (Mayor et al. 2009).

Gradients of factors along niche hypervolume axes can exhibit complex patterns across a continuum of spatial scales (Cushman 2007; Hegel et al. 2010), with organism responses to its environment simultaneously influenced by both fine- and broad-scale environmental attributes (Wiens 1976; Johnson et al. 1992; Levin 1992). No single spatial scale is typically sufficient to elucidate organism-habitat relationships.

Thus, investigations into habitat selection should be conducted at multiple, ecologically-relevant spatial scales (Wiens 1989; Goodwin and Fahrig 1998; McGarigal et al. 2016). In addition, organism responses to environmental and other factors, may not necessarily be linear. Austin et al. (1990) provide evidence of complex, non-linear organism responses in habitat studies, a result reflected in a number of other studies on species-habitat relationships (Wasserman et al. 2012; Hebblewhite et al. 2014; Timm et al. 2016; Bosco et al. 2019; Macdonald et al. 2019). However, related assumptions pertaining to these relationships have largely been untested.

The importance of incorporating spatial scale into modelling of species–habitat relationships is well-established (McGarigal and Cushman 2002; McGarigal et al. 2016). Failing to do so can undermine the performance of habitat selection models and their interpretation (e.g., Wasserman et al. 2012; Mateo-Sanchez et al. 2014; Shirk et al. 2014), potentially leading to errors of inference and application (McGarigal and Cushman 2002; Wasserman et al. 2012). Optimized multiple-scale approaches (see definitions by McGarigal et al. [2016]) have been used to model habitat selection, limiting factors, and threats for a number of species (Thompson and McGarigal 2002; Toews 2011; Gonthier et al. 2014; Wan et al. 2017), and typically out-perform single-scale models in predictive or explanatory power (Kanagaraj et al. 2011; Wasserman et al. 2012; Mateo-Sanchez et al. 2014; Timm et al. 2016; McGarigal et al. 2016). It is notable, that despite the increased consideration of scale in habitat suitability studies since the publication of the influential McGarigal et al. (2016) review paper, few studies have formally applied scale-optimization to evaluate the effects of landscape components on species habitat suitability at multiple scales.

Conversely, the extent to which the functional shape of a species' response to covariates (i.e., functional form) affects model performance has largely been overlooked. Assuming a single response type for data being modelled may fail to account for different forms of relationship, an assumption that may not be appropriate even for modelling simple ecological associations (Oksanen and Minchin 2002). Indeed, the functional form of species–habitat relationships can vary across habitat characteristics (Redfern et al. 2006) and scales (Wan et al. 2017). Inclusion of variable-specific, non-linear functional relationships may strengthen the relationship between dependent and independent variables, improving representation of covariates in top models that may otherwise be obscured and, potentially, improving explanatory power (Carle 2006).

Generalized linear models (GLMs) have been the most widely-used approach in habitat modelling studies, given their intuitiveness and flexibility (McGarigal et al. 2016). GLMs assume a linear relationship between link function-transformed predictor variables and explanatory variables (Nelder and Wedderburn 1972). However, variables may have unique, non-linear response shapes. The vast majority of habitat relationships studies have assumed linear relationships. In the relatively few cases in which different functional forms have been explicitly investigated, they have typically been restricted to quadratic relationships (Mateo-Sanchez et al. 2014; Mashintonio et al. 2014; Dzialak et al. 2015; Bosco et al. 2019; Macdonald et al. 2019). A few studies have examined other, more complex relationships (Bar-Massada et al. 2011; Fisher et al. 2011; Mateo-Sánchez et al. 2015; Devoe et al. 2015; Shirk et al. 2018), although this appears not to have widespread application. Importantly, no published study, to our knowledge, has formally compared the performance and interpretation of models with and without functional shape-optimization.

The effect of scale- and shape-optimization in quantifying species niches and, by extension, species-habitat relationships merits investigation. Our goal in this paper is to explicitly evaluate the effects of scale- and shape-optimization on modelling habitat selection, using a globally important and understudied tiger population in Thailand as a case study. Tigers are an ideal species in which to investigate this, given large home ranges (Smith 1993; Sunquist 2010), potential influence of broad-scale environmental variation (Krishnamurthy et al. 2016; Reddy et al. 2017), and high conservation priority (Lynam and Nowell 2011; Goodrich et al. 2015). Using long-term camera-trap studies, we evaluate how shape- and scale-optimization affect predictive power and interpretation of models in comparison with non-optimized models. In doing so, we also evaluate how covariates influence habitat selection of tigers and the degree of scale- and shape-dependency. We test four central hypotheses. First, we expect that habitat selection is highly scale-dependent, with clear patterns of relationship between the scale of analysis and strength of relationship between occurrence and environmental variables. Second, we expect that, for most variables, the relationship with tiger occurrence will be strongest at broad spatial scales, reflecting large home range sizes and high sensitivity to human influences. Third, we expect the multi scale-optimized model to outperform any of the single-scale optimized models, given evidence from previous studies. Lastly, we expect that shape-optimized models will outperform non-optimized models, given each variable is included with its independent shape of functional relationship with species occurrence.

2. Methods

2.1 Study site

The Dong Phayayen–Khao Yai Forest Complex (DPKY) covers 6,155km^2 in eastern Thailand (Fig. 1). It consists of five protected areas—Khao Yai National Park (KYNP), Thap Lan National Park (TLNP), Pang Sida National Park (PSNP), Ta Phraya National Park (TPNP), and Dong Yai Wildlife Sanctuary (DYWS). The complex is relatively mountainous with elevations ranging from 100m to 1,351 m a.s.l. It contains a number of forest types, but primarily consists of mixed evergreen (77%) and mixed dipterocarp/deciduous primary and secondary forest (6%). The complex is biologically diverse, supporting 112 mammalian species, 392 birds, 200 reptiles/amphibians, and 2,500 plant species (DNP 2004), and is on the UNESCO World Heritage List in recognition of its outstanding natural and conservation value (UNESCO 2017). Currently, DPKY is almost completely surrounded by villages and human infrastructure.

2.2 Camera-trap surveys and data processing

From 2008 to 2017, we conducted camera-trap surveys throughout DPKY to investigate tiger presence in each of its five protected areas (Ash et al. 2020). Survey coverage and intensity increased during this period as funding, camera-traps, and related resources increased, covering diverse habitats across DPKY. Within these areas, cameras were placed to maximize detection of tigers by prioritizing camera placement in areas with previous tiger or prey records and identifying topographic (e.g., ridges, river valleys) or other features (e.g., roads, trails) likely used by tigers (Karanth and Chundawat 2002; Sunarto et al. 2012; Barber-Meyer et al. 2013). To reduce spatial autocorrelation, if more than one camera was present within a 300m radius, we selected the camera with the highest number of tiger detections or, if no tigers were detected, by

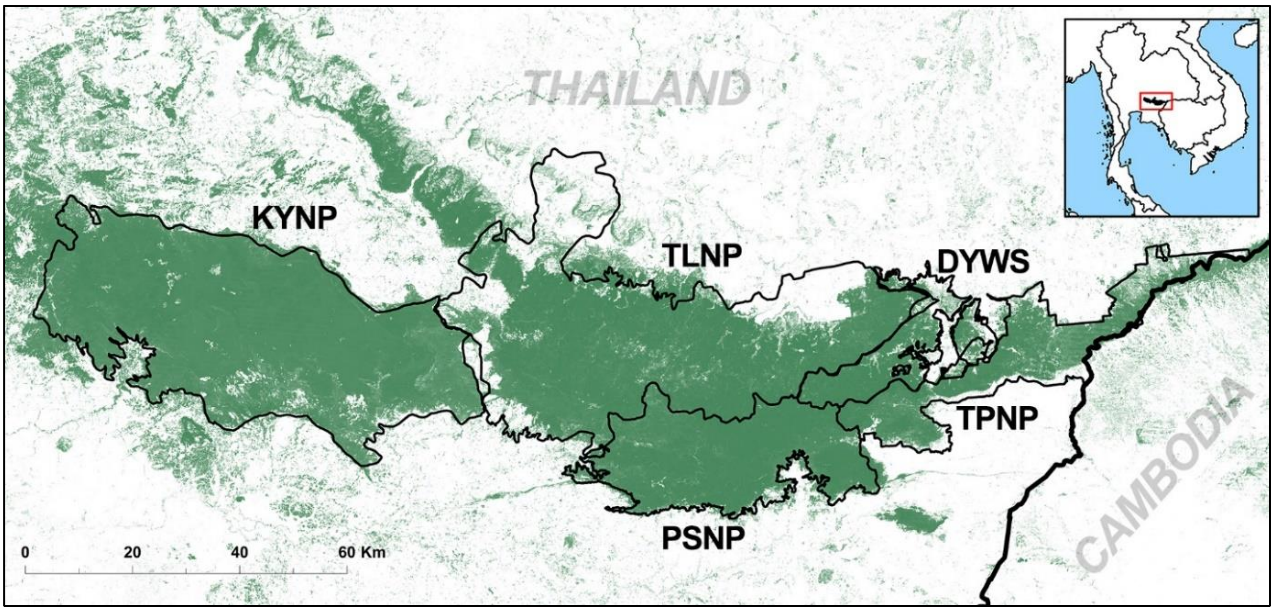

Fig. 1 Map of the Dong Phayayen–Khao Yai forest complex (DPKY) and its five protected areas (~ 14° 00′ to 14° 33′ N and ~ 101° 05′ to 103° 14′ E)—Dong Yai Wildlife Sanctuary (DYWS), Khao Yai National Park (KYNP), Pang Sida National Park (PSNP), Thap Lan National Park (TLNP), and Ta Phraya National Park (TPNP). Map generated with ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Red-lands, CA, USA, 2011) with forest cover derived from Hansen et al. (2013).

greatest survey effort (camera-trap nights [CTN]). A more detailed description of surveys is provided in Ash et al. (2020) and supplementary online materials (Online Resource 1).

2.3 Predictor variables

We compiled a set of nine environmental predictor variables based on previous studies of tigers throughout their range (Wibisono et al. 2011; Sunarto et al. 2012; Ngoprasert et al. 2012; Kafley et al. 2016; Thapa and Kelly 2017). These primary variables were further transformed into more biologically informative predictor variables (Table 1) using class and landscape level spatial statistics (McGarigal et al. 2012). Variables were prepared in 30m resolution to ensure representation of fine-scale variations in the environment.

We used SRTM 1 (Shuttle Radar Topography Mission) arc-second global elevation data (Jarvis et al. 2008), which we further transformed into several variables measuring topographic heterogeneity using the Geomorphometry & Gradient Metrics Toolbox (Evans et al. 2014) in ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011). These included terrain roughness index (degree of elevation difference between adjacent cells), slope position (surface to area ratio) and compound topographic index (CTI). CTI is a measure of flow accumulation (Beven and Kirkby 1979), with low CTI values associated with ridges and mountaintops and high values associated with large, low-lying drainage areas.

Percent forest cover (Hansen et al. 2013) was reclassified into three classes, non-forest (0–20%), open forest (20–40%) and closed forest (>40%). Furthermore, the global land cover map (European Space Agency 2015) was classified into eight study-relevant area classes. Since some forest types (Royal Forestry Department 2000) were similar or under-represented in our study area, we reclassified eight forest types from an original 12 classes. Streams and rivers were included, but were reclassified to only include perennial rivers/streams (Royal Forestry Department 2000).

To test associations at different spatial scales, we transformed variables into seven multi-scale predictor variables (250m, 500m, 1km, 2km, 4km, 8km, and 16km). For continuous variables, we generated focal statistics (focal mean and standard deviation) in ArcGIS using a moving circular window with radius equal to each scale. For categorical variables, we calculated landscape metrics in FRAGSTATS (McGarigal et al. 2012) using moving windows for each spatial scale. For class-level statistics, we calculated area-weighted mean radius of gyration (GYR, also known as correlation length), which is a measure of mean potential travel distance within a habitat patch, or habitat extent, and percentage of habitat within the focal landscape (PLAND). At the landscape-level we calculated contrast-weighted edge density (CWED), which quantifies the influence of habitat edges via the degree of contrast between adjacent patches. We also calculated patch density (PD), a measure of the subdivision of habitat within the landscape (i.e., number of patches divided by area). Lastly, we calculated aggregation index (AI), which quantifies the degree of dispersion of habitat patches within the landscape. In total, we prepared 47 variables to investigate how spatial composition and configuration of the landscape at various scales influences tiger detections (Table 1).

2.4 Data analysis

To assess the influence of scale- and shape-optimization on model performance, we compared four approaches: (1) Single-scale optimized models (SSO); (2) A multi-scale optimized model (MSO); (3) Single-scale shape-optimized models (SSSO); and (4) A multi-scale-and shape-optimized model (MSSO).

2.5 Model 1 – Single-scale optimized model approach

To provide a baseline for assessing the effects of optimization on model performance, we developed a suite of seven independent models, one for each scale (250m to 16km), in which no optimization steps were applied (single-scale optimized [SSO]). This corresponds to what McGarigal et al. (2016) termed *pseudo-optimized single-scale* (ms4). For these models, the number of variables was reduced through a series of filtering steps. (1) Using the *glmer* function in the *lme4* package in R (Bates et al. 2014; R Development Core Team 2017), we produced a univariate generalized linear model (GLM) with a logit link function for each variable at each scale. (2) We required that p <0.05 for each variable. (3) For all variables with a Pearson's correlation coefficient $|r|$> 0.6, we selected the variable with the lowest AICc value in each univariate GLM (Burnham and Anderson 2002).

These filtering steps resulted in the inclusion of 11 to 19 variables, including survey effort (CTN), among each of the seven scales (Online Resource 2, Table 2). To find the most parsimonious model for each spatial scale we used the 'biostats' package in R (McGarigal 2018), a set of functions which (1) produced models for all combinations of the standardized predictor variables, subsetting the best performing models ranked by ΔAICc (defined in our models as ΔAICc < 2); (2) averaged a final set of models and calculated goodness-of-fit statistics, including proportion deviance explained for each candidate model; and (3) ranked variable importance in the final model with averaged coefficients based on Akaike's model weight (w_i).

2.6 Model 2 – Multi-scale optimized model approach

For the multi-scale optimized (MSO) model, we selected the scale of best fit for each variable prior to the filtering steps and inclusion in the final model. For each variable, we developed a univariate GLM for each scale and selected among correlated variables (Pearson's coefficient $|r|$> 0.6) by lowest AICc value.

Table 1 Variables included in univariate model selection, metrics, and data sources. Landscape statistics include focal mean and standard deviation (SD). Landscape metrics include percentage of landscape (PLAND), area weighted mean of radius of gyration/correlation length (GYR), contrast-weighted edge density (CWED), patch density (PD), and aggregation index (AI).

Variable	ID	Metric	Data Source
Elevation	DEM	Focal mean & SD	Jarvis et al. 2008; http://srtm.csi.cgiar.org)
Protected area boundary	BOUND	Focal mean	Royal Forestry Department (2000)
Forest class: 1-Non-forest (0–20%); 2-Open canopy (20–40%); 3-Closed canopy ([40%)	TC	PLAND & GYR	Reclassified from Hansen et al. (2013)
Forest type: 1-Evergreen; 2-Mixed Deciduous; 3-Dry Dipterocarp; 4-Reforested Areas; 5-Bamboo Forest; 6-Secondary Forest/Old Clearing; 7-Grassland/Scrubland	FT	PLAND & GYR	Reclassified from Royal Forestry Department (2000)
Terrain Roughness Index (TRI)	TRI	Focal mean & SD	Derived from Jarvis et al. 2008; http://srtm.csi.cgiar.org) and Evans et al. (2014)
Slope position	SLOPE	Focal mean & SD	Derived from Jarvis et al. 2008; http://srtm.csi.cgiar.org) and Evans et al. (2014)
Streams/Rivers	STRC1	Focal mean	Reclassified from Royal Forestry Department (2000)
Compound topographic index (i.e., flow accumulation)	CTI	Focal mean & SD	Derived from Jarvis et al. 2008; http://srtm.csi.cgiar.org) and Evans et al. (2014)
Land cover classes: 1-Cropland; 2-Mosaic cropland; 3-Forest/Natural vegetation; 4-Shrubland/grassland; 5-Sparse vegetation & bare areas; 6-Urban Areas; 7-Water	LC	PLAND, GYR, CWED, PD, AI	Reclassified from European Space Agency (2015; www.esa-landcover-cci.org/?q=node/175)

Scale-specific variables were then included in a multivariate GLM using the 'biostats' set of functions (McGarigal 2018) to subset best performing models, calculate goodness-of-fit statistics, and rank variable importance in the final model. This approach is what McGarigal et al. (2016) termed (*pseudo-)optimized multiple scales (ms5)*, as we optimized our model based on a range of scales determined *a priori* rather than selecting among an unconstrained range of continuous scales.

2.7 Model 3 – Single-scale and shape-optimized model approach

To investigate the effects of shape-optimization on model performance, we developed seven independent single-scale shape-optimized (SSSO) models, one for each scale (250m to 16km), in which variables were included at an optimal functional form. To determine candidate functional forms to investigate, we plotted nonlinear splines using *plsmo* in the R package *Hmisc* (Harrell 2018) between variables and binomial tiger detections. Among resulting plots, we identified four potential functional forms (quadratic, logarithmic, exponential, and negative exponential). These functions were used to transform variables at their optimal scales in univariate GLMs, as described above. Unmodified linear forms were also included, resulting in five functional forms tested in this model approach. The best performing shape for each variable was determined by lowest AICc value before conducting, as previously described, filtering based on p-values and collinearity. In the final multivariate GLM for each scale, for quadratic variables, we included both linear and quadratic terms as separate explanatory variables. We were able to include these quadratic terms using 'biostats' (McGarigal 2018), while running all combinations of models, providing an advantage over other similar approaches, such as *dredge* (Bartoń 2018).

2.8 Model 4 – Multi-scale- and shape-optimized model approach

In the multi-scale and shape-optimized (MSSO) model, we include both scale- and shape-optimization. As in MSO and SSSO models, we determined the best performing shape and scale for each variable by lowest AICc value before conducting filtering based on p-values and collinearity. In effect, variables were included in a final multivariate GLM at their optimal scale and functional form. As in the SSSO approach, for quadratic variables, we included both linear and quadratic terms as separate explanatory variables using 'biostats' (McGarigal 2018).

2.9 Evaluating model performance and variable importance

We evaluated model performance in three ways. First, we calculated sensitivity (*correctly predicted presence/total points present*), specificity (*correctly predicted absence/total points absent*), percent correctly classified (*PCC; summary of correctly predicted points at a defined threshold*), Kappa (*proportion correctly*

Table 2 Summary of model performance statistics for single-scale optimized (SSO) models, single-scale shape-optimized (SSSO) models, the multi-scale optimized (MSO) model, and the multi-scale and shape-optimized (MSSO) model.

Model	Threshold	PCC	Sensitivity	Specificity	Kappa	AUC
SSO - 250m	0.37	0.8700	0.5965	0.9462	0.5873	0.85
SSSO - 250m	0.46	0.8719	0.5175	0.9707	0.5651	0.86
SSO - 500m	0.41	0.8719	0.6140	0.9438	0.5975	0.87
SSSO - 500m	0.41	0.8681	0.5877	0.9462	0.5798	0.88
SSO - 1km	0.39	0.8413	0.5526	0.9218	0.5047	0.86
SSSO - 1km	0.35	0.8375	0.6579	0.8875	0.5336	0.87
SSO - 2km	0.27	0.8145	0.8246	0.8117	0.5391	0.88
SSSO - 2km	0.27	0.8222	0.7632	0.8386	0.5357	0.88
SSO - 4km	0.32	0.8509	0.7456	0.8802	0.5886	0.90
SSSO - 4km	0.33	0.8547	0.7807	0.8753	0.6062	0.90
SSO - 8km	0.40	0.8700	0.6667	0.9267	0.6087	0.91
SSSO - 8km	0.45	0.8795	0.7018	0.9291	0.6410	0.91
SSO - 16km	0.54	0.8929	0.6491	0.9609	0.6601	0.93
SSSO - 16km	0.54	0.8891	0.6667	0.9511	0.6551	0.93
MSO	0.37	0.8891	0.7456	0.9291	0.6747	0.92
MSSO	0.43	0.8815	0.7018	0.9315	0.6455	0.93

predicted points accounting for probability of chance), and area under the ROC curve (AUC). We measured variable importance via AICc variable importance from the model averaging table and magnitude of the standardized coefficients (Wasserman et al. 2012). We tested the influence of each variable importance from the model averaging table and magnitude of the standardized coefficients (Wasserman et al. 2012). We also tested the influence of each variable on model performance by calculating the difference in probability of tiger detections when the variable increases from the 10th to 100th percentile using standardized values and holding all other variables constant at their medians. Variables were back-transformed to original values and plotted to evaluate changes in probability of tiger presence relative to changes in each variable. Lastly, we generated prediction maps to investigate differences in predictions for each modelling approach. These maps depict spatial variation in predicted tiger presence, with each cell containing a predicted presence value ranging from 0 (absent) to 1 (present). To compare predictive maps between the four top models, we used three approaches. First, we calculated the correlation between the pixel values in each of the four maps. Second, we calculated the average absolute difference between the pixel values in the four maps. Third, we classified the four maps into high quality (greater than probability of 0.7) and mid-high quality habitat (greater than probability of 0.5). We then used FRAGSTATS (McGarigal et al. 2012) to calculate percentage of landscape (PLAND), patch density (PD), correlation length (GYR) and largest patch index (LPI) for each of the maps.

3. Results

3.1 Model performance

All models demonstrated high predictive performance, with AUC ranging from a low of 0.85 (for the 250m single-scale optimized [SSO] model) to 0.93 for the multi-scale and shape-optimized (MSSO) model and the top single scale-optimized 16km models (SSO and SSSO; Table 2). Similarly, the Kappa statistic, percent observations correctly classified, model sensitivity, and specificity were high for all models, with the 16km SSO, 16km SSSO, MSO, MSSO models generally out-performing smaller-scale SSO models. There was slight disagreement among these measures in terms of which of these models had the highest performance. The 16km SSO, 16km SSSO, and MSSO models had the highest performance based on AUC (0.93), MSO had the highest performance based on Kappa, and the 16km SSO had the highest performance based on PCC. All four of these models had very high performance, with AUC over 0.90, PCC greater than 0.88, and Kappa greater than 0.64, which demonstrates exceptionally high ability to correctly discriminate between detection and non-detection points.

3.2 Model interpretation

Although the top models (16km SSO, 16km SSSO, MSO, and MSSO) each had very high and very similar predictive performance, they differed substantially in model interpretation. We base model interpretation on several characteristics: (1) variables included in the model, (2) scale at which each variable is included, (3) sign of the variables included, (4) variable importance, (5) the shape of variables included in SSSO and MSSO models, and (6) differences in prediction maps.

3.3 Variables included

Camera effort (Cam_eff) was included in all four of the top models (SSO, MSO, SSSO, and MSSO), showing the universally high importance of sampling effort to model prediction. Other than camera effort, only percentage of bamboo forest (FT5_PLAND) was included in all four top models (with a positive coefficient), indicating that the extent of bamboo forest surrounding a sampling location is a ubiquitously important predictor of tiger occurrence in the study area. No other variable was included in all four of the top models, although secondary growth forest (FT_6) was included in all four top models based on slightly different FRAGSTATS metrics, which measure extensiveness of the cover type. Specifically, correlation length of secondary growth forest (FT6_GYR) was included in MSO, the 16km SSSO, and MSSO, while percentage of secondary growth forest (FT6_PLAND) was included in the 16km SSO. This suggests that the extensiveness of secondary growth forest is also an important predictor of tiger occurrence in the study area (with a negative coefficient). Similarly, the standard deviation of compound topographic index (CTI_SD), a measure of topographical complexity, was included in MSSO and the 16km SSO. Focal mean of topographical roughness index (TRI_FM) and standard deviation of elevation (DEM_SD), which measure similar attributes of topographical complexity, were also included in MSSO while standard deviation of elevation was also included in the 16km SSSO. This suggests that topographical heterogeneity is a consistently important predictor of tiger occurrence in the study area. Several variables were included in two of the four top models, with focal extensiveness of open forest (20–40% forest cover; TC2_PLAND), included in both MSO and MSSO, but not in the top SSO and SSSO models. Similarly, focal extensiveness of shrubland/grassland (LC4_PLAND), was included in the MSO and 16km SSO/SSSO. Four variables were included in only one of the four top models, with percentage evergreen forest (FT1_PLAND) and percentage mosaic cropland (LC2_PLAND) included only in the 16km SSSO, correlation length of reforested areas (FT4_GYR) included only in MSSO, and correlation length of urban areas (LC6_GYR) included only in the 16km SSO. Three variables were shared between the 16km SSO and SSSO models while four variables were shared between both shape-optimized models (SSSO and MSSO).

Table 3 Generalized linear model results for the multi-scale and shape-optimized (MSSO) model, predicting tiger presence based on 1,166 detections of tiger in DPKY (2008–2017), including standardized regression coefficients (β), adjusted standard error, z-score (*z*), and significance (*p*).

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-1.367	0.314	4.352	<0.001
% Secondary Forest (16km) ^{LOG}	FT6_PLAND_16000_LOG	-0.777	0.210	3.702	<0.001
Correlation length Secondary Forest (4km) ^{L}	FT6_GYR_4000L	-0.701	0.235	2.978	0.003
Camera effort (# trap nights)	Cam_eff	1.460	0.309	4.718	<0.001
% Bamboo (16km) ^{L}	FT5_PLAND_16000	1.028	0.525	1.960	0.050
DEM Standard Deviation (16km) ^{L}	DEM_SD_16000	0.995	0.308	3.226	0.001
% Bamboo (16km) ^{Q}	FT5_PLAND_16000Q	-0.072	0.232	0.309	0.757
DEM Standard Deviation (16km) ^{Q}	DEM_SD_16000Q	-0.866	0.336	2.575	0.010
Focal mean of terrain roughness index (16km) ^{L}	TRI_FM_16000L	1.165	0.502	2.317	0.020
Focal mean of terrain roughness index (16km) ^{Q}	TRI_FM_16000Q	-1.671	0.579	2.887	0.004
% Open forest (16km) ^{L}	TC2_PLAND_16000_L	-2.353	0.457	5.149	<0.001
Correlation length of reforested areas (8km) ^{L}	FT4_GYR_8000_L	0.968	0.321	3.011	0.003
Correlation length of reforested areas (8km) ^{Q}	FT4_GYR_8000_Q	-0.555	0.195	2.844	0.004

Shape (i.e., functional form) of each variable is indicated by: ^{L} linear, ^{Q} Quadratic, ^{LOG} Logarithmic.

3.4 Variable scales

Variables were generally represented at broad spatial scales. Almost all variables in the MSSO (six out of seven; Table 3) and MSO (five out of seven; Online Resource 2, Table 4) were selected at the broadest spatial scales (8 and 16km). In MSO, the smallest scale represented was 1km, while the smallest scale represented in the MSSO was 4km. This representation of broad scales is also evident in the similarly strong predictive performance of both single-scale optimized (i.e., SSO and SSSO) 16km models compared with multi-scale optimized models. It is notable that the worst performing model was the SSO developed at the finest spatial scale (250m).

3.5 Variable sign

The signs of shared variables remained consistent across our four top models. Variables with a positive relationship with tiger occurrence included camera effort (Cam_eff) and percentage of bamboo forest (FT5_PLAND) in all models, standard deviation of compound topographic index (CTI_SD) in the 16km SSO and MSO models, standard deviation of terrain roughness index (TRI_SD) in the MSSO model, and percentage of evergreen forest (FT1_PLAND) in the 16km SSSO. Variables with a negative relationship

Table 4 Summary of variable importance among top models, the single-scale optimized (SSO) 16km model, the single-scale shape-optimized (SSSO) 16km model, the multi-scale optimized (MSO) model and the multi-scale and shape-optimized (MSSO) model. Specific metrics include AICc variable importance, standardized coefficients, and change in probability of tiger presence with change in variable value from 10th to 100th percentiles. The SSSO and MSSO models included both linear (^{L}) and quadratic (^{Q}) terms for five variables.

	AICc Variable Importance				Standardized Coefficients				Δ Probability of Tiger Presence			
	SSO	SSSO	MSO	MSSO	SSO	SSSO	MSO	MSSO	SSO	SSSO	MSO	MSSO
Cam_eff	2	5	6	3	1.355	1.487	1.415	1.460	0.97	0.94	0.96	0.92
CTI_SD	1	-	3	-	0.720	-	0.616	-	0.22	-	0.44	-
DEM_SD	-	4	-	1	-	0.333^{L} -0.868^{Q}	-	0.995^{L} -0.866^{Q}	-	0.07	-	0.13
FT1_PLAND	-	1	-	-	-	0.733	-	-	-	0.12	-	-
FT4_GYR	-	-	-	1	-	-	-	0.968^{L} -0.555^{Q}	-	-	-	0.17
FT5_PLAND	2	5	6	2	1.964	1.556	0.988	1.028^{L} -0.072^{Q}	0.90	0.70	0.46	0.55
FT6_GYR	-	2	5	3	-	- 0.443	- 0.675	-0.701	-	-0.10	-0.06	-0.13
FT6_PLAND	2	-	-	2	-1.827	-	-	-0.777	-0.11	-	-	-0.23
LC2_PLAND	-	5	-	-	-	- 1.130^{L} -0.770^{Q}				-0.10		
LC4_PLAND	2	2	1	-	-0.647	-0.496	-0.486	-	-0.08	-0.13	-0.06	-
LC6_GYR	1	-	-	-	-0.613	-	-	-	-0.04	-	-	-
TC2_GYR	-	-	2	-	-	-	-0.704	-	-	-	-0.11	-
TC2_PLAND	-	-	5	1	-	-	-1.437	-2.353	-	-	-0.02	-0.58
TRI_FM	-	-	-	2	-	-	-	1.165^{L} -1.671^{Q}	-	-	-	0.13
TRI_SD	-	-	2	-	-	-	0.384	-	-	-	0.38	-

included correlation length of secondary forest (FT6_GYR) in the 16km SSSO, MSO, and MSSO, percentage of open forest (TC2_PLAND) in both MSO and MSSO, correlation length of open forest (TC2_GYR) in MSO, percentage of shrubland/grassland (LC4_PLAND) in the 16km SSO, 16km SSSO, and MSO models, and correlation length of urban areas (LC6_GYR) in the 16km SSO model. Three variables in shape-optimized models (16km SSSO and MSSO) exhibited a positive parabolic relationship between probability of tiger presence and increasing variable values (Fig. 2; Online Resource 3, Fig. 4). These included standard deviation of elevation (DEM_SD; SSSO/MSSO), focal mean of terrain roughness index (TRI_FM; MSSO), and correlation length of reforested areas (FT4_GYR; MSSO). This indicates the probability of tiger presence peaks at intermediate values of these variables.

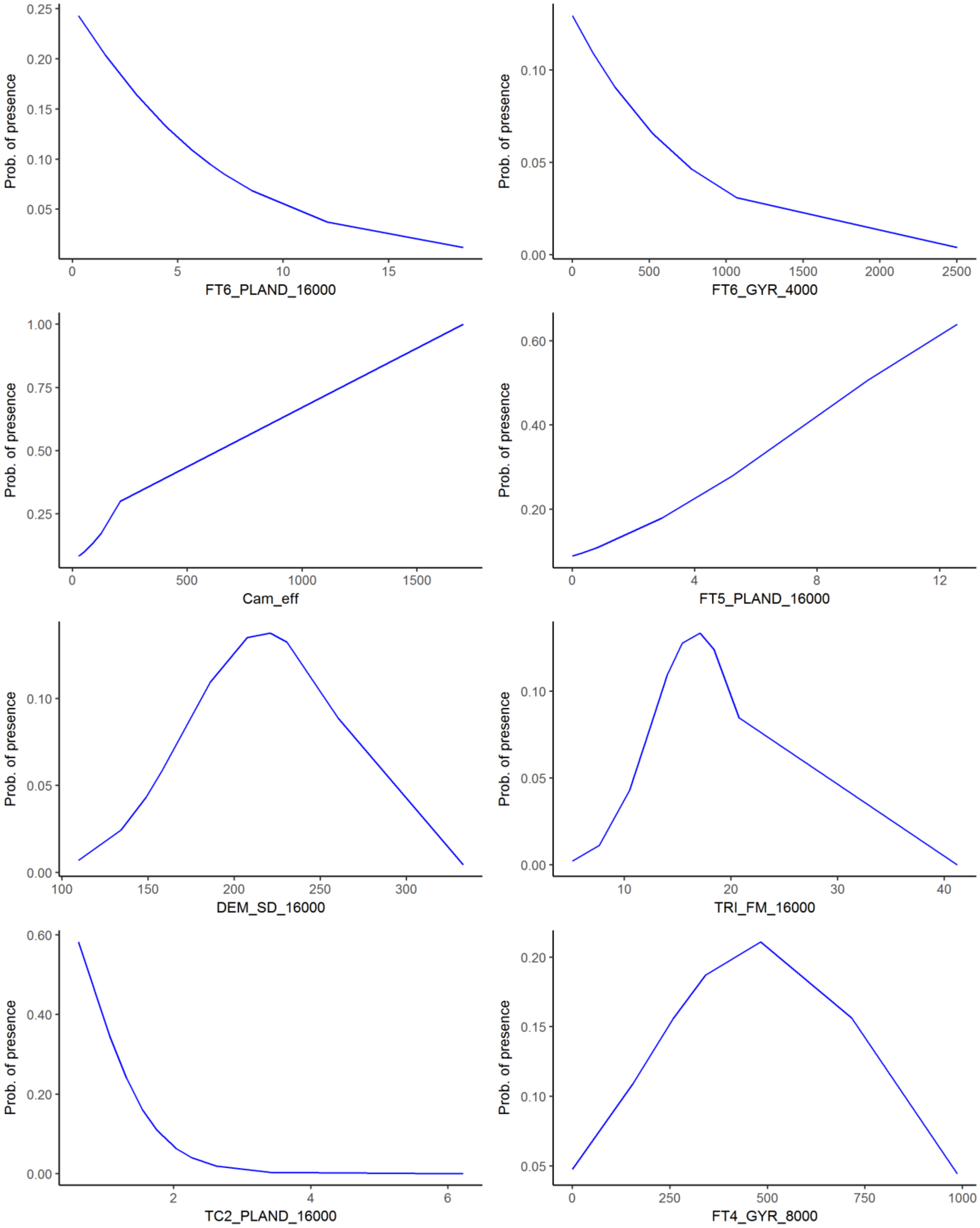

Fig. 2 Partial effects plots for the multi-scale and shape-optimized (MSSO) model showing changes in predicted probability of tiger presence when variables increase from their 10th to 100th percentile, holding other variables at their medians. Graphic generated in R (R Development Core Team 2017).

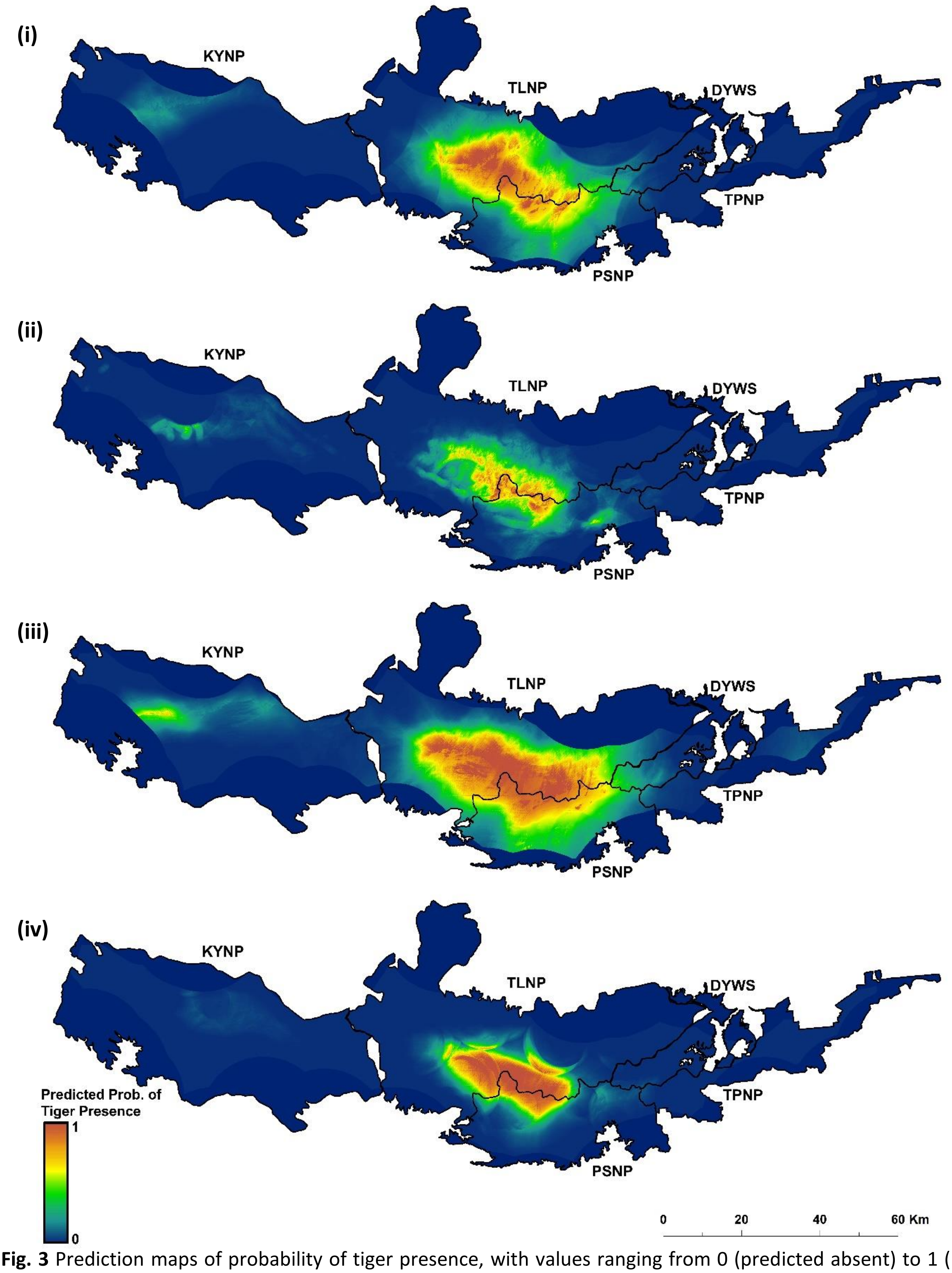

Fig. 3 Prediction maps of probability of tiger presence, with values ranging from 0 (predicted absent) to 1 (predicted present), generated from the top four fully averaged models – (i) the single-scale optimized (SSO) 16km model, (ii) the scale-optimized (MSO) model, (iii) the single-scale shape-optimized (SSSO) 16km model, and (iv) the scale- and shape-optimized (MSSO) model. Map generated with ArcGIS 10.3.1 (Environmental Systems research Incorporated, ESRI, Redlands, CA, USA, 2011).

3.6 Variable importance

In the 16km SSO model, AICc variable importance was similar across variables with the number of model subsets in which variables were represented ranging from *n = 1 to 2* (Table 4). Key variables in this model, as determined by standardized coefficients, included percentage of bamboo forest (FT5_PLAND; β = 1.964 ± 0.314), percentage of secondary forest (FT6_PLAND; β = -1.827 ± 0.424), and camera effort (Cam_eff; β = 1.355 ± 0.279). Variables which demonstrated the strongest effect on probability of tiger presence were camera effort (Δ0.97), percentage of bamboo forest (Δ0.90) and standard deviation of compound topographic index (Δ0.22).

The 16km SSSO model exhibited different patterns in AICc variable importance, with the number of model subsets in which variables were represented ranging from *n = 1 to 5*. Variables with notable standardized coefficients, included percentage of bamboo forest (FT5_PLAND; β = 1.556 ± 0.440), percentage of mosaic cropland (LC2_PLAND; β = -1.130 ± 0.495^{L}; β = -0.770 ± 0.516^{Q}), and camera effort (Cam_eff; β = 1.487 ± 0.311). The strongest effect on probability of tiger presence was evident in camera effort (Δ0.94) and percentage of bamboo forest (Δ0.70).

The MSO model had notable variation in AICc variable importance, ranging from *n = 1* for percentage shrubland/grassland (LC4_PLAND) to *n = 6* for camera effort (Cam_eff) and percentage of bamboo forest (FT5_PLAND). Variable importance, in terms of the magnitude of standardized coefficients, was strongest for percentage open forest (TC2_PLAND; β = -1.437 ± 0.349), camera effort (Cam_eff; β = 1.415 ± 0.299), and percentage of bamboo forest (FT5_PLAND; β = 0.988 ± 0.238). Changes in probability of tiger presence were greatest among camera effort (Δ0.96), standard deviation of compound topographic index (CTI_SD; Δ0.46), percentage of bamboo forest (Δ0.44), and standard deviation of terrain roughness index (TRI_SD; Δ0.38).

The MSSO model had some degree of variation in AICc variable importance, ranging from *n = 1* for standard deviation of elevation (DEM_SD), correlation length of reforested areas (FT4_GYR), and percentage of open forest (TC2_PLAND) to *n = 3* for camera effort (Cam_eff) and correlation length of secondary forest (FT6_GYR). Standardized coefficients indicated the importance of percentage of open forest (TC2_PLAND; β

= -2.353 ± 0.457), camera effort (β = 1.460 ± 0.309), focal mean of terrain roughness index (TRI_FM; β = 1.165 ± 0.502^{L}; β = -1.671 ± 0.579^{Q}) and percentage of bamboo forest (FT5_PLAND; β = 1.028 ± 0.525^{L}; β = -0.072 ± 0.232^{Q}). Variables with the strongest effect on probability of tiger presence included camera effort (Cam_eff; Δ0.92), percentage of open forest (TC2_PLAND; Δ-0.58), and percentage of bamboo forest (Δ0.55).

3.7 Shape of variables

While five functional forms were tested during variable selection for the 16km SSSO and MSSO models—linear, quadratic, logarithmic, exponential, and negative exponential—only three were represented in fully averaged models. Quadratic relationships (for which linear terms were also included) were evident in percentage of bamboo forest (FT5_PLAND) at 16km (SSSO/MSSO), standard deviation of elevation (DEM_SD) at 16km (SSSO/MSSO), focal mean of terrain roughness index (TRI_FM) at 16km (MSSO), percentage of mosaic cropland (LC2_PLAND) at 16km (SSSO) and correlation length of reforested areas (FT4_GYR) at 8km (MSSO). Three variables—percentage of secondary forest (FT6_PLAND) at 16km (MSSO), correlation length of secondary forest (FT6_GYR) at 16km (SSSO), and percentage of evergreen forest (FT1_PLAND) at 16km (SSSO)—exhibited logarithmic relationships. Linear relationships were observed in correlation length of secondary forest (FT6_GYR) at 4km (MSSO), percentage of reforested areas (LC4_PLAND; SSSO), and percentage of open forest (TC2_PLAND; MSSO) at 16km.

3.8 Model prediction

Correlation between prediction maps (Fig. 3) for the four top models was reasonably high. Correlation of the prediction maps for SSSO–SSO was the highest (0.95), followed by MSSO–MSO (0.92), and MSSO–SSO (0.84; Table 5). Differences between pixel values were generally highest in the central part of the landscape, within TLNP and PSNP, with SSSO and SSO 16km models having a notably higher predicted presence of tigers over a broader area compared to MSSO and MSO models (Online Resource 3, Fig. 5). Between these models, SSSO had higher predicted values elsewhere in the complex. Predicted tiger presence was higher in a smaller core area of the complex in MSSO and lower predicted presence outside this area

Table 5 Matrix of correlation (COR) and average absolute difference (AAD) between prediction maps between the single-scale optimized (SSO) 16km model, multi-scale optimized (MSO) model, single-scale shape-optimized (SSSO) 16km model, and multi-scale and shape-optimized (MSSO) model.

	SSO	MSO	SSSO	MSSO	
SSO		0.09	0.10	0.08	*AAD*
MSO	0.84		0.17	0.04	
SSSO	0.95	0.83		0.15	
MSSO	0.84	0.92	0.83		
		COR			

compared with other models. The MSO generally had lower predicted tiger presence in more central areas compared to other models though predicted higher probability of presence in certain areas elsewhere in the complex such as in small areas of PSNP and KYNP. Average absolute difference was highest between SSSO and MSO maps (0.17) and lowest between MSSO and MSO maps (0.04; Table 4).

Percentage of high-quality habitat (> 0.7 predicted tiger presence) in the landscape was highest in the 16km SSSO (~ 12.3%), followed by the MSSO (~ 5.5%), the 16km SSO (~ 4.7%), and was notably low in MSO (~ 0.7%; Table 6). Extent of mid-high quality habitat (> 0.5 predicted tiger presence) was also highest in the 16km SSSO (~ 20.8%), followed by the 16km SSO (~ 11.7%), MSSO (~ 7.9%), and MSO (~ 4.1%). Mid- to high-quality habitat was generally more dispersed in MSO than other models, as indicated by relatively higher PD, and lower LPI and GYR values, characterized by several distinct patches. In the 16km SSSO/SSO and MSSO, both mid-high and high quality habitat were largely represented by single patches.

4. Discussion

The focus of this study was to quantitatively evaluate the relative impacts of scale- and functional shape-optimization on model performance, prediction and interpretation in habitat selection studies, using a globally important tiger population as a case study. Our study confirms the scale-dependence of habitat selection in tigers, and our results suggest it is important for further habitat selection research to formally evaluate and optimize scale as a component of the modelling process. In contrast, we did not find strong and clear effects of optimizing models to account for different, nonlinear functional shapes of relationship

Table 6 Landscape metrics of high (> 0.7) and mid-high (> 0.5) probability of tiger presence among the four top models. Landscape metrics include percentage of landscape (PLAND), patch density (PD), largest patch index (LPI), and radius of gyration/correlation length (GYR).

Habitat Quality	Model	PLAND	PD	LPI	GYR
HIGH	SSO	4.6680	0.0005	4.668	6106
	MSO	0.7400	0.0013	0.275	1557
	SSSO	12.3025	0.0003	12.303	9767
	MSSO	5.4998	0.0005	5.388	6812
MID-HIGH	SSO	11.6668	0.0003	11.6668	9599
	MSO	4.0950	0.0059	4.0534	6673
	SSSO	20.7904	0.0006	20.7506	12,173
	MSSO	7.8861	0.0008	7.7687	7739

between species occurrence and environmental variables.

Consistent with our first hypothesis, we found that tiger occurrence probability is highly scale dependent. There were strong differences in the univariate strength of relationship between most variables across scale. In addition, we found large differences in model performance and interpretation, indicating that the ability to predict tiger occurrence is strongly affected by the scale in which variables are measured. This scale-dependence in model interpretation is particularly stark between top models and smaller scale single-scale models (SSO/SSSO). Nine variables in top models were not present in fine-scale single-scale optimized (SSO) models (250m–4km) and ten variables represented in these fine-scale SSOs/SSSOs were not present in top models. This is particularly important, as most past tiger habitat modelling, similar to past modelling for other large carnivores (Mateo-Sanchez et al. 2014), have used SSO models with a relatively fine (~ 500m–1km) focal scale.

Our results reinforce that the lens with which the niche of organism is evaluated, specifically its relationships with habitat, has a considerable influence in the interpretation of models. This high degree of scale-dependence is evident in other tiger studies (Rostro-García et al. 2016; Krishnamurthy et al. 2016; Reddy et al. 2017), as well as studies on cheetah (Rostro-García et al. 2015), leopard (Pitman et al. 2017; Kittle et al. 2018), puma (Zeller et al. 2014) and clouded leopard (Hearn et al. 2018; Macdonald et al. 2019). Substantial differences in model interpretation and identification of optimal habitat based on the scale of analysis is also consistent with numerous studies of other taxonomic groups (Thompson and McGarigal 2002; Wasserman et al. 2012; Mateo-Sanchez et al. 2014; Wan et al. 2017). Scale-dependence in habitat relationships is a foundational idea in wildlife ecology (Wiens 1989; Levin 1992; Thompson and McGarigal 2002) and critical for analyses which aim to quantify species niches (Hegel et al. 2010). Our results strongly reinforce this and demonstrate the importance of the scale of analysis for predicting tiger presence.

A majority of variables were most strongly associated with tiger occurrence at the broadest spatial scales, which was consistent with our second hypothesis. In the multi-scale optimized (MSO) model, 71% of the included variables were measured at the broadest (16km) or second broadest (8km) scale. Similarly, in the multi-scale and shape optimized (MSSO) model, 88% were selected at the broadest or second broadest scale, with more than half at the broadest scale. Notably, there were clear patterns of improvement in AUC in both single-scale model approaches (SSO/SSSO) from fine to broad scales. The 16km SSO and SSSO models, in which all variables were measured at the broadest scale, were the best performing among these single-scale models. The high consistency among these top models clearly suggests that habitat selection for tigers in our study is largely related to broad-scale habitat factors. These results are aligned with previous studies on tigers (Krishnamurthy et al. 2016; Rostro-García et al. 2016; Reddy et al. 2017), brown bear (Mateo-Sánchez et al. 2015), leopard (Kittle et al. 2018), and clouded leopard (Hearn et al. 2018), all of which found dominant effects of environmental variables at broad scales. Importantly, however, most habitat relationship studies, even for large bodied and highly mobile animals, typically have utilized single-scale analysis of fine scale (e.g., 500m–1km) environmental data (McGarigal et al. 2016). Our analysis suggests that such fine-scale analysis would fail to accurately or fully elucidate species habitat selection patterns, even if model performance is reasonably strong, such as with single, fine-scale models in our study.

Our third hypothesis was that the multi-scale optimized models (MSO and MSSO) would outperform any single-scale optimized (SSO/SSSO) model. This follows from arguments and observations made by McGarigal et al. (2016) who reviewed a large number of habitat modelling papers and found that, in nearly all cases that were formally evaluated, multi-scale optimization outperformed single-scale modelling of habitat relationships. The habitat niche of any species consists of a number of dimensions, each composed of environmental variation at particular characteristic scales. Our results are not fully consistent with this third hypothesis. Both the multi-scale optimized and the best single-scale optimized models (16km SSO/SSSO) performed exceptionally and equivalently well. These results suggest that a single-scale model may sometimes perform as well as a multi-scale optimized model, but only when organism-habitat relationships are dominated by a single-scale response and that the appropriate scale of analysis is evaluated. This has also been observed in other studies (Martin and Fahrig 2012; Krishnamurthy et al. 2016; Timm et al. 2016). In the case of tigers (Krishnamurthy et al. 2016; Reddy et al. 2017), a single, broad-scale model might produce very similar results to a multi-scale optimized model. However, we emphasize that it is impossible to assess the appropriate scale of analyses for a single-scale model *a priori*. Further, even when a single, large scale may be optimal, broad application can result in potentially important fine-scale niche dynamics being under-represented (Mateo-Sanchez et al. 2014) leading to oversimplified and potentially misleading interpretations of model results. Therefore, even when a single-scale model provides the strongest prediction, it requires use of scale-optimization to identify and confirm this. Further, when a single-scale model isn't optimal, multi-scale optimization is required to identify the optimal multi-scale model.

Perhaps the most novel aspect of our study is the comparison of the multi-scale and shape-optimized model (MSSO) with multi-scale optimized (MSO) and single-scale optimized (SSO/SSSO) models. We expected that the multi-scale and shape-optimized model and single-scale shape-optimized (SSSO) models would out-perform non-shape-optimized models. This is because, like scale-dependence, species occurrence probability may have a different functional response shape for each variable, with some responses being linear, some unimodal, and some curvilinear (Austin et al. 1990). Results of similar studies suggest that optimizing for functional form may have meaningful influence in the selection of top models (Mateo-Sánchez et al. 2015; Devoe et al. 2015), potentially allowing for the expression of otherwise obscure environmental effects (Carle 2006), which may improve explanatory power. We hypothesised that optimizing the response shape of variables, like optimizing the scale of response, would measurably improve the predictive ability of the model. Our results do not support this.

While the multi-scale and shape-optimized models were tied as the highest performing model based on the most widely used criterion (AUC), the 16km single-scale optimized model performed equally well. Furthermore, the multi-scale optimized and the single-scale optimized 16km models performed slightly better based on other measures. The single-scale optimized (SSO) and single-scale shape-optimized (SSSO) models exhibited similar patterns in model performance, with AUC values generally increasing with scale. While AUC was slightly higher (0.01) in finer-scale shape-optimized models compared to corresponding non-optimized models, this was not the case at broader scales. This suggests that shape-optimization may be less important than scale-optimization.

While model performance was not substantially improved by shape-optimization in our study, the inclusion of variables at their optimal functional form clarified relationships between habitat characteristics and species response. For example, topographic variables (i.e., elevation and terrain roughness) are present exclusively in non-linear forms (i.e., quadratic and logarithmic) in shape-optimized models (SSSO/MSSO). In effect, the multi-scale and shape-optimized model suggested a more complex relationship between species presence and topographic heterogeneity than in non-optimized models. Expression of these types of relationships are also evident in other species-habitat modelling studies, in particular, the representation of quadratic relationships in final models (Mashintonio et al. 2014; Devoe et al. 2015; Timm et al. 2016; Macdonald et al. 2018, 2019). Notably, inclusion of variables at their optimal functional form influenced representation of variables in final, fully averaged models with differences in variables included between optimized (SSSO) and non-optimized (SSO) models. For example, in 8 and 16km models, only two variables were included in both SSSO and SSO models out of 12 and 11 total variables in these models, respectively. Further, only two out of 11 total variables were represented in both SSO and MSSO models. This illustrates that models may be sensitive to optimizing for functional form, as with scale, and may lead to considerable differences in model interpretation and conclusions about species–habitat relationships.

4.1 Limitations/caveats

Our fundamental goal in this study was to evaluate the effect of scale- and shape-optimization on the performance, prediction and interpretation of habitat relationships models. We use a single case study species and system (tigers in Thailand) for this evaluation, which limits the generality of our conclusions, however, in exchange we feel our example provides realism in that it reflects actual relationships of a focal species of ecological and conservation importance. We suggest future work employ simulation studies which can control scale and shape effects and, therefore, more reliably and completely evaluate the sensitivity of modelling methods to scale- and shape-optimization. Second, given our focus was on exploring the novel question of impacts of scale- and shape-optimization simultaneously, rather than evaluating the best approaches for scale optimization, our example uses GLM modelling because it is the most well understood and widely-used method in habitat modelling, and the dominant approach in multi-scale habitat modelling studies published to date (McGarigal et al. 2016). This approach to scale selection is consistent with many other species-habitat modelling studies (Rostro-García et al. 2016; Kittle et al. 2018; Macdonald et al. 2018). However, with the rapid emergence and adoption of other modelling methods, in particular machine learning approaches (e.g., Evans et al. 2011; Cushman and Wasserman 2018), we suggest future work should focus on comparing performance of scale- and shape-optimization in a wider range of modelling approaches. In particular, tree-based machine learning approaches like random forests perhaps can automatically optimize nonlinear functional shape (Evans et al. 2011), which could be a great advantage, while others, like Maxent, do not (Elith et al. 2011). While there are a myriad of approaches for habitat–selection analysis, we opted to utilize GLMs given their intuitiveness, flexibility, and their wide-spread use in studies investigating scale in similar studies (McGarigal et al. 2016).

We also note that our definition of optimization closely follows the definition proposed by McGarigal et al. (2016) of pseudo-optimization as the scales we evaluated were selected *a priori*. Importantly, this approach does not optimize scale relationships across a continuous range, and does not optimize them multivariately and simultaneously. A true optimized approach may have allowed for inclusion of more specific scales that best explain variation in tiger occurrence. However, we feel that the scales selected for evaluation were sufficient for understanding relevant scales of relationships between covariates and tiger occurrence and, most importantly, allowed for a more effective and straightforward evaluation of scale-dependence in our study compared to a true-optimized approach. However, improvement of scale-optimization approaches is an important current topic in habitat relationships modelling (McGarigal et al. 2016), and we strongly suggest future research to explore the performance of a range of continuous and multivariate simultaneous optimization approaches.

4.2 Species management implications

We recommend central DPKY, particularly areas of closed forest cover containing bamboo forest patches within a 16km window, should be managed as an area of high conservation priority for tigers in this landscape. Our models reinforce the importance of protecting surrounding broad-scale (8 to 16km) forest within protected areas with low human impact as part of a landscape-scale management strategy. Protection of this core area and facilitating unconstrained movement to other available habitat will be critical to the long-term recovery of this population. Scale-dependence in species-habitat relationships, as demonstrated by this and other studies (Wasserman et al. 2012; Mateo-Sanchez et al. 2014) can have monumental implications for species management. As such, efforts to develop management and recovery strategies should account for scale-dependence of tigers in this landscape. Our results are consistent with other literature highlighting the importance of large protected areas and low human disturbance for tiger populations (Trisurat et al. 2010; Sunarto et al. 2012; Ngoprasert et al. 2012; Hebblewhite et al. 2014; Reddy et al. 2017).

It is pertinent to highlight that our results reflect an expression of the tigers' realized niche within DPKY that may be severely constrained in comparison with its theoretical fundamental niche. The tigers' range itself has suffered considerable declines and its current range likely reflect its refuge in areas less likely to be impacted by human activities, which are the chief driver of range and population declines (Goodrich et al. 2015). In our study area, areas of the landscape with flat topography are typically highly affected by human activities, which may explain their lower selection. Historically, Thailand's lowland forests, now converted by human activity, would have likely represented preferable habitat due to high prey densities (Rabinowitz 1993; Sunquist et al. 1999).

5. Conclusion

While shape-optimization did not substantially improve performance over other models, it did allow for the expression of potentially important relationships between tigers and covariates that were not apparent in the models assuming linear forms. Importantly, our study clearly reinforces previous studies (McGarigal and Cushman 2002; McGarigal et al. 2016) which highlight the importance of accounting for scale when modelling habitat selection and other ecological relationships, particularly for wide-ranging species such as tigers. We recommend that habitat-selection studies on tigers and other species incorporate a robust, ecologically-relevant scale-optimization framework and consider the inclusion and evaluation of shape-optimization in model development.

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References

Ash E, Kaszta Ż, Noochdumrong A, et al (2020) Opportunity for Thailand's Forgotten Tigers: Assessment of Indochinese tiger Panthera tigris corbetti and prey from camera-trap surveys in Eastern Thailand. Oryx 55:204–211.

https://doi.org/10.1017/S0030605319000589

Austin MP, Nicholls AO, Margules CR (1990) Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. Ecol Monogr 60:161–177. https://doi.org/doi:10.2307/1943043

Bar-Massada A, Wood EM, Pidgeon AM, Radeloff VC (2011) Complex effects of scale on the relationships of landscape pattern versus avian species richness and community structure in a woodland savanna mosaic. Ecography (Cop) 35:393–411. https://doi.org/10.1111/j.1600-0587.2011.07097.x

Barber-Meyer SM, Jnawali SR, Karki JB, et al (2013) Influence of prey depletion and human disturbance on tiger occupancy in Nepal. J Zool 289:10–18. https://doi.org/10.1111/j.1469-7998.2012.00956.x

Bartoń K (2018) Multi-Model Inference (MuMIn). Comprehensive R Archive Network (CRAN), Version 1.40.4

Bates D, Mächler M, Bolker B, Walker S (2014) Fitting Linear Mixed-Effects Models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Beven KJ, Kirkby MJ (1979) A physically based, variable contributing area model of basin hydrology. Hydrol Sci Bull 24:43–69. https://doi.org/10.1080/02626667909491834

Blonder B (2018) Hypervolume concepts in niche- and trait-based ecology. Ecography (Cop) 41:1441–1455. https://doi.org/10.1111/ecog.03187

Bosco L, Wan HY, Cushman SA, et al (2019) Separating the effects of habitat amount and fragmentation on invertebrate abundance using a multi-scale framework. Landsc Ecol 34:105–117. https://doi.org/10.1007/s10980-018-0748-3

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference. Springer, New York

Carle RJ (2006) Factors affecting nest survival of three species of migrant songbirds in the Greater Yellowstone Ecosystem. Masters Thesis, University of Montana

Cushman S (2007) Research agenda for integrated landscape modeling. US Department of Agriculture, Forest Service, Rocky Mountain Research Station

Cushman SA, Wasserman TN (2018) Landscape Applications of Machine Learning: Comparing Random Forests and Logistic Regression in Multi-Scale Optimized Predictive Modeling of American Marten Occurrence in Northern Idaho, USA. In: Humphries G, Magness DR, Huettmann F (eds) Machine Learning for Ecology and Sustainable Natural Resource Management. Springer International Publishing, Cham, pp 185–203

Devoe JD, Garrott RA, Rotella JJ, et al (2015) Summer range occupancy modeling of non-native mountain goats in the greater Yellowstone area. Ecosphere 6:1–20. https://doi.org/10.1890/ES15-00273.1

DNP (2004) Submission for Nomination of the Dong Phayayen- Khao Yai Forest Complex. Department of National Parks, Wildlife and Plant Conservation, The Royal Thai Government, Bangkok

Dzialak MR, Olson C V., Webb SL, et al (2015) Incorporating within- and between-patch resource selection in identification of critical habitat for brood-rearing greater sage-grouse. Ecol Process 4:5. https://doi.org/10.1186/s13717-015-0032-2

Elith J, H. Graham C, P. Anderson R, et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography (Cop) 29:129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elith J, Phillips SJ, Hastie T, et al (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17:43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

European Space Agency (2015) 300 m annual global land cover time series from 1992 to 2015. Climate Change Initiative (CCI), European Space Agency (ESA)

Evans JS, Cushman SA, Theobald D (2014) An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, version 2.0-0.

Evans JS, Murphy MA, Holden ZA, Cushman SA (2011) Modeling Species Distribution and Change Using Random Forest. In: Drew CA, Wiersma YF, Huettmann F (eds) Predictive Species and Habitat Modeling in Landscape Ecology: Concepts and Applications. Springer

New York, New York, NY, pp 139–159

Fisher TJ, Anholt B, Volpe JP (2011) Body mass explains characteristic scales of habitat selection in terrestrial mammals. Ecol Evol 1:517–528. https://doi.org/10.1002/ece3.45

Gonthier DJ, Ennis KK, Farinas S, et al (2014) Biodiversity conservation in agriculture requires a multi-scale approach. Proc R Soc B Biol Sci 281:20141358–20141358. https://doi.org/10.1098/rspb.2014.1358

Goodrich JM, Lynam A, Miquelle DG, et al (2015) Panthera tigris. IUCN Red List Threat. Species 2015 e.T15955A50659951

Goodwin BJ, Fahrig L (1998) Spatial scaling and animal population dynamics. In: Peterson DL, Parker VT (eds) Ecological Scale: Theory and Applications. Columbia University Press, New York, pp 193–206

Hansen MC, Potapov P V., Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science (80-) 342:850–853. https://doi.org/10.1126/science.1244693

Harrell FEJ (2018) Harrell Miscellaneous (Hmisc). Comprehensive R Archive Network (CRAN), Version 4.1-1

Hearn AJ, Cushman SA, Ross J, et al (2018) Spatio-temporal ecology of sympatric felids on Borneo. Evidence for resource partitioning? PLoS One 13:e0200828. https://doi.org/10.1371/journal.pone.0200828

Hebblewhite M, Miquelle DG, Robinson H, et al (2014) Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. Biol Conserv 178:50–64. https://doi.org/10.1016/j.biocon.2014.07.013

Hegel TM, Cushman SA, Evans J, Huettmann F (2010) Current State of the Art for Statistical Modelling of Species Distributions. In: Cushman SA, Huettmann F (eds) Spatial Complexity, Informatics, and Wildlife Conservation. Springer Japan, Tokyo, pp 273–311

Hutchinson GE (1957) Concluding Remarks. Cold Spring Harb Symp Quant Biol 22:415–427

Jarvis A, Reuter HI, Nelson A, Guevara E (2008) Hole-filled seamless SRTM data V4. In: Int. Cent. Trop. Agric. http://srtm.csi.cgiar.org

Johnson AR, Wiens JA, Milne BT, Crist TO (1992) Animal Movements and Population-Dynamics in Heterogeneous Landscapes. Landsc Ecol 7:63–75. https://doi.org/10.1007/bf02573958

Kafley H, Gompper ME, Sharma M, et al (2016) Tigers (Panthera tigris) respond to fine spatial-scale habitat factors: occupancy-based habitat association of tigers in Chitwan National Park, Nepal. Wildl Res 43:398–410. https://doi.org/10.1071/WR16012

Kanagaraj R, Wiegand T, Kramer-Schadt S, et al (2011) Assessing habitat suitability for tiger in the fragmented Terai Arc Landscape of India and Nepal. Ecography (Cop) 34:970–981. https://doi.org/10.1111/j.1600-0587.2010.06482.x

Karanth KU, Chundawat RS (2002) Ecology of the Tiger: Implications for Population Monitoring. In: Karanth KU, Nichols JD (eds) Monitoring tigers and their prey : a manual for researchers, managers, and conservationists in tropical Asia. Centre for Wildlife Studies, Bangalore, pp 9–22

Kittle AM, Watson AC, Cushman SA, Macdonald DW (2018) Forest cover and level of protection influence the island-wide distribution of an apex carnivore and umbrella species, the Sri Lankan leopard (Panthera pardus kotiya). Biodivers Conserv 27:235–263. https://doi.org/10.1007/s10531-017-1431-8

Krishnamurthy R, Cushman SA, Sarkar MS, et al (2016) Multi-scale prediction of landscape resistance for tiger dispersal in central India. Landsc Ecol 31:1355–1368. https://doi.org/10.1007/s10980-016-0363-0

Levin SA (1992) The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology 73:1943–1967. https://doi.org/10.2307/1941447

Lynam A, Nowell K (2011) Panthera tigris ssp. corbetti. IUCN Red List Threat. Species 2011 e.T136853A4346984

Macdonald DW, Bothwell HM, Hearn AJ, et al (2018) Multi-scale habitat selection modeling identifies threats and conservation opportunities for the Sunda clouded leopard (Neofelis diardi). Biol Conserv 227:92–103. https://doi.org/10.1016/j.biocon.2018.08.027

Macdonald DW, Bothwell HM, Kaszta Ż, et al (2019) Multi-scale habitat modelling identifies spatial conservation priorities for mainland clouded leopards (Neofelis nebulosa). Divers Distrib 25:1639–1654. https://doi.org/10.1111/ddi.12967

Martin AE, Fahrig L (2012) Measuring and selecting scales of effect for landscape predictors in species–habitat models. Ecol Appl 22:2277–2292. https://doi.org/10.1890/11-2224.1

Mashintonio AF, Pimm SL, Harris GM, et al (2014) Data-driven discovery of the spatial scales of habitat choice by elephants. PeerJ 2:e504. https://doi.org/10.7717/peerj.504

Mateo-Sánchez MC, Balkenhol N, Cushman S, et al (2015) A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow? Landsc Ecol 30:1405–1420. https://doi.org/10.1007/s10980-015-0194-4

Mateo-Sanchez MC, Cushman SA, Saura S (2014) Scale dependence in habitat selection: the case of the endangered brown bear (Ursus arctos) in the Cantabrian Range (NW Spain). Int J Geogr Inf Sci 28:1531–1546. https://doi.org/10.1080/13658816.2013.776684

Mayor S, Schneider D, Schaefer J, P. Mahoney S (2009) Habitat Selection at Multiple Scales. Ecoscience 16:238–247. https://doi.org/10.2980/16-2-3238

McGarigal K (2018) BIOSTATS. Department of Environmental Conservation, University of Massachusetts. v. 9 February 2018

McGarigal K, Cushman S, Neel MC, Ene E (2012) FRAGSTATS: Spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst.

McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12:335–345. https://doi.org/10.1890/1051-0761(2002)012[0335:CEOEAT]2.0.CO;2

McGarigal K, Wan HY, Zeller KA, et al (2016) Multi-scale habitat selection modeling: a review and outlook. Landsc Ecol 31:1161–1175. https://doi.org/10.1007/s10980-016-0374-x

Nelder JA, Wedderburn RWM (1972) Generalized Linear Models. J R Stat Soc Ser A 135:370–384. https://doi.org/10.2307/2344614

Ngoprasert D, Lynam AJ, Sukmasuang R, et al (2012) Occurrence of Three Felids across a Network of Protected Areas in Thailand: Prey, Intraguild, and Habitat Associations. Biotropica 44:810–817. https://doi.org/10.1111/j.1744-7429.2012.00878.x

Oksanen J, Minchin PR (2002) Continuum theory revisited: what shape are species responses along ecological gradients? Ecol Modell 157:119–129. https://doi.org/10.1016/S0304-3800(02)00190-4

Pitman RT, Fattebert J, Williams ST, et al (2017) Cats, connectivity and conservation: incorporating data sets and integrating scales for wildlife management. J Appl Ecol 54:1687–1698. https://doi.org/10.1111/1365-2664.12851

R Development Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing. v.3.4.2. Vienna

Rabinowitz A (1993) Estimating the Indochinese tiger (Panthera tigris corbetti) population in Thailand. Biol Conserv 65:213–217. https://doi.org/10.1016/0006-3207(93)90055-6

Reddy PA, Cushman SA, Srivastava A, et al (2017) Tiger abundance and gene flow in Central India are driven by disparate combinations of topography and land cover. Divers Distrib 23:863–874. https://doi.org/10.1111/ddi.12580

Redfern J V, Ferguson MC, Becker EA, et al (2006) Techniques for cetacean–habitat modeling. Mar Ecol Prog Ser 310:271–295. https://doi.org/10.3354/meps310271

Rostro-García S, Kamler JF, Hunter LTB (2015) To Kill, Stay or Flee: The Effects of Lions and Landscape Factors on Habitat and Kill Site Selection of Cheetahs in South Africa. PLoS One 10:e0117743. https://doi.org/10.1371/journal.pone.0117743

Rostro-García S, Tharchen L, Abade L, et al (2016) Scale dependence of felid predation risk: identifying predictors of livestock kills by tiger and leopard in Bhutan. Landsc Ecol 31:1277–1298. https://doi.org/10.1007/s10980-015-0335-9

Royal Forestry Department (2000) Study of the Status and Database Design of Natural Resources in Khao Yai, Thap Lan, Pang Sida, and Ta Phraya National Parks [Thai]. Royal Forestry Department, Government of Thailand and Geo Asia Co. Ltd., Bangkok, Thailand

Shirk AJ, Cushman SA, Waring KM, et al (2018) Southwestern white pine (Pinus strobiformis) species distribution models project a large range shift and contraction due to regional climatic changes. For Ecol Manage 411:176–186. https://doi.org/10.1016/j.foreco.2018.01.025

Shirk AJ, Raphael MG, Cushman SA (2014) Spatiotemporal variation in resource selection: Insights from the American marten (Martes americana). Ecol Appl 24:1434–1444. https://doi.org/10.1890/13-1510.1

Smith JLD (1993) The Role of Dispersal in Structuring the Chitwan Tiger Population. Behaviour 124:165–195. https://doi.org/10.1163/156853993X00560

Sunarto S, Kelly MJ, Parakkasi K, et al (2012) Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS One 7:e30859. https://doi.org/10.1371/journal.pone.0030859

Sunquist M (2010) What Is a Tiger? Ecology and Behavior. In: Tilson R, Nyhus PJ (eds) Tigers of the World, Second Edition. Elsevier, New York, pp 19–33

Sunquist M, Karanth UK, Sunquist F (1999) Ecology, behaviour and resilience of the tiger and its conservation needs. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 5–18

Thapa K, Kelly MJ (2017) Prey and tigers on the forgotten trail: high prey occupancy and tiger habitat use reveal the importance of the understudied Churia habitat of Nepal. Biodivers Conserv 26:593–616. https://doi.org/10.1007/s10531-016-1260-1

Thompson CM, McGarigal K (2002) The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). Landsc Ecol 17:569–586. https://doi.org/10.1023/A:1021501231182

Timm BC, McGarigal K, Cushman SA, Ganey JL (2016) Multi-scale Mexican spotted owl (Strix occidentalis lucida) nest/roost habitat selection in Arizona and a comparison with single-scale modeling results. Landsc Ecol 31:1209–1225. https://doi.org/10.1007/s10980-016-0371-0

Toews M (2011) Managing human footprint with respect to its effects on large mammals: implications of spatial scale, divergent responses and ecological thresholds. MSc Thesis. University of British Columbia

Trisurat Y, Pattanavibool A, Gale GA, Reed DH (2010) Improving the viability of large-mammal populations by using habitat and landscape models to focus conservation planning. Wildl Res 37:401–212. https://doi.org/10.1071/WR09110

UNESCO (2017) Dong Phayayen-Khao Yai Forest Complex. In: UNESCO World Herit. Cent. http://whc.unesco.org/en/list/590. Accessed 27 Nov 2017

Wan HY, McGarigal K, Ganey JL, et al (2017) Meta-replication reveals nonstationarity in multi-scale habitat selection of Mexican Spotted Owl. Condor 119:641–658. https://doi.org/10.1650/CONDOR-17-32.1

Wasserman TN, Cushman SA, Wallin DO, Hayden J (2012) Multi scale habitat relationships of Martes americana in northern Idaho, U.S.A. USDA For Serv - Res Pap RMRS-RP 1–21

Wibisono HT, Linkie M, Guillera-Arroita G, et al (2011) Population Status of a Cryptic Top Predator: An Island-Wide Assessment of Tigers in Sumatran Rainforests. PLoS One 6:e25931. https://doi.org/10.1371/journal.pone.0025931

Wiens J (1976) Population Responses to Patchy Environments. Annu Rev Ecol Syst 7:81–120. https://doi.org/10.1146/annurev.es.07.110176.000501

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397. https://doi.org/10.2307/2389612

Zeller KA, McGarigal K, Beier P, et al (2014) Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study. Landsc Ecol 29:541–557. https://doi.org/10.1007/s10980-014-9991-4

Supplementary Materials 1

1. Camera-trap Survey Design

Data for modelling was based on extensive camera-trap tiger surveys conducted by Ash et al. (2020b). These surveys were conducted opportunistically (non-random) beginning March 2008 and running relatively uninterrupted (Fig. 1) until February 2017. Although these ongoing surveys continue at the time of this writing, a cut-off of early 2017 is used for analysis. During this period, all five protected areas in the Dong Phayayen-Khao Yai Forest Complex were surveyed opportunistically, constrained by available resources. Surveys were expanded as resources became available to fill gaps in survey coverage over time. Extensive surveys were conducted in Khao Yai National Park (KYNP), Pang Sida National Park (PSNP), Dong Yai Wildlife Sanctuary (DYWS), and Ta Phraya National Park (TPNP). Long-term surveys were conducted in Thap Lan National Park (TLNP) and Pang Sida National Park (PSNP). Camera placement was maintained as a series of semi-permanent and roving surveys to cover all areas of DPKY. In addition, data includes results from spatially extensive surveys conducted in 2013 (DNP/Freeland/WWF, unpublished) and 2016 (Ash et al. 2020a) designed to generate density estimates of tigers in PSNP and TLNP. As such, TLNP and PSNP had disproportionately higher levels of survey effort during the survey period (Table 1).

Cameras were placed to maximize detection of tigers by prioritizing camera placement in areas with previous tiger or prey records and identifying topographic (e.g., ridges, river valleys) or other features (e.g., roads, trails) likely used by tigers (Karanth and Chundawat 2002; Sunarto et al. 2012; Barber-Meyer et al. 2013). Detections at one camera station were considered to be independent if they occurred after a 30-minute period (O'Brien et al. 2003).

To reduce spatial autocorrelation, if more than one camera was present within a 300m radius, we selected the camera with the highest number of tiger detections or, if no tigers were detected, by greatest survey effort (camera-trap nights [CTN]). This resulted in a total of 1,166 tiger detections for analysis from 56,214 trap nights (Table 1).

Table 1 Survey data summary in DPKY (2008-2017) following filtering to reduce potential spatial autocorrelation, including number of camera stations, camera-trap nights (CTN), and resulting tiger detections.

	Total	DYWS	KYNP	PSNP	TLNP	TPNP
Stations	523	51	68	155	194	55
CTN	56,214	3,427	7,276	18,321	22,168	5,022
Tiger Detections	1,166	7	0	322	837	0

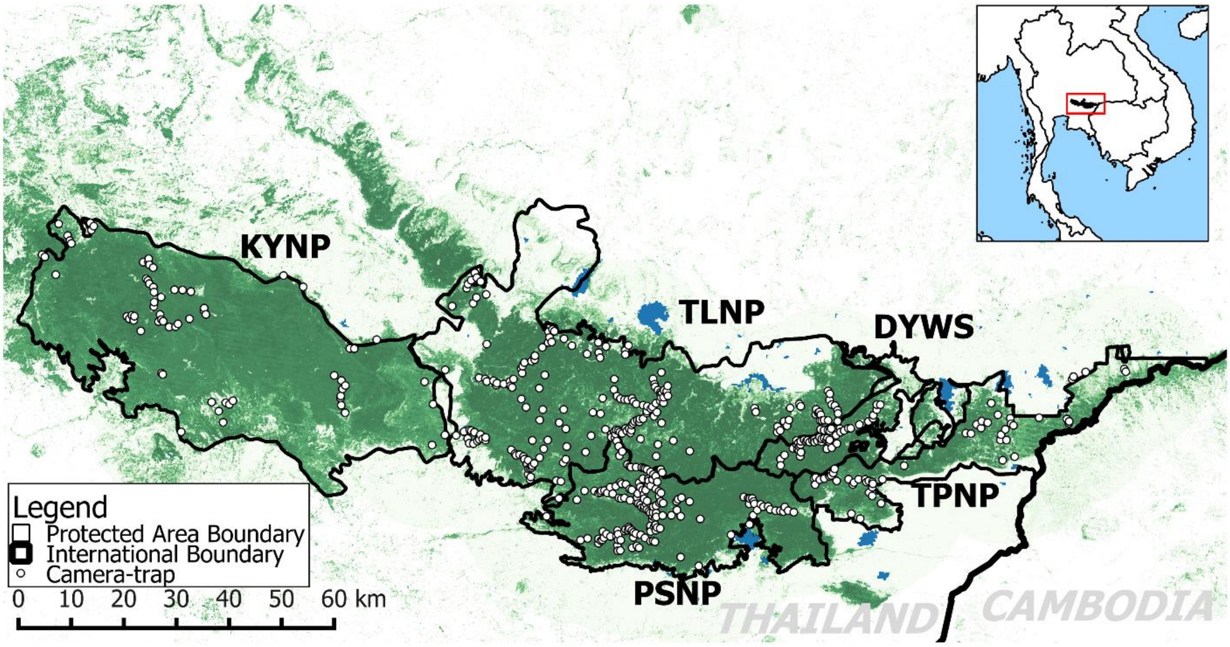

Fig. 1 Map of camera-trap stations in the Dong Phayayen-Khao Yai forest complex (DPKY) and its five protected areas (~14°00' to 14°33'N and ~101°05' to 103°14'E) – Dong Yai Wildlife Sanctuary (DYWS), Khao Yai National Park (KYNP), Pang Sida National Park (PSNP), Thap Lan National Park (TLNP), and Ta Phraya National Park (TPNP). Map generated with ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011) with forest cover derived from Hansen et al. (2013).

References

Ash E, Hallam C, Chanteap P, et al (2020a) Estimating the density of a globally important tiger (Panthera tigris) population: Using simulations to evaluate survey design in Eastern Thailand. Biol Conserv 241:108349. https://doi.org/10.1016/j.biocon.2019.108349

Ash E, Kaszta Ż, Noochdumrong A, et al (2020b) Opportunity for Thailand's Forgotten Tigers: Assessment of Indochinese tiger Panthera tigris corbetti and prey from camera-trap surveys in Eastern Thailand. Oryx 55:204–211. https://doi.org/10.1017/S0030605319000589

Barber-Meyer SM, Jnawali SR, Karki JB, et al (2013) Influence of prey depletion and human disturbance on tiger occupancy in Nepal. J Zool 289:10–18. https://doi.org/10.1111/j.1469-7998.2012.00956.x

Hansen MC, Potapov P V., Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science (80-) 342:850–853. https://doi.org/10.1126/science.1244693

Karanth KU, Chundawat RS (2002) Ecology of the Tiger: Implications for Population Monitoring. In: Karanth KU, Nichols JD (eds) Monitoring tigers and their prey : a manual for researchers, managers, and conservationists in tropical Asia. Centre for Wildlife Studies, Bangalore, pp 9–22

O'Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim Conserv 6:131–139. https://doi.org/10.1017/S1367943003003172

Sunarto S, Kelly MJ, Parakkasi K, et al (2012) Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS One 7:e30859. https://doi.org/10.1371/journal.pone.0030859

Supplementary Materials 2

Table 1 Final variables included in the multi-scale and shape-optimized (MSSO) global model from an original 47 variables. The optimal functional form (shape) of each variable indicated by: L-linear, Q-Quadratic, EXP-Exponential, LOG-Logarithmic.

Variable	Optimal Scale (m)	Optimal Functional Form	ID
Correlation length of secondary forest	4000	L	FT6_GYR_4000_L
Percentage of shrubland/grassland	4000	L	LC4_PLAND_4000_L
Correlation length of mixed deciduous forest	8000	Q	FT2_GYR_8000_Q
Correlation length of reforested areas	8000	Q	FT4_GYR_8000_Q
Correlation length of grassland	8000	Q	FT7_GYR_8000_Q
Correlation length of mosaic cropland	8000	Q	LC2_GYR_8000_Q
Correlation length of water	8000	Q	LC7_GYR_8000_Q
Correlation length of open forest	8000	LOG	TC2_GYR_8000_LOG
Focal mean of park boundary	16000	L	BOUND_FM_16000_L
Standard deviation of CTI	16000	Q	CTI_SD_16000_Q
Standard deviation of DEM	16000	Q	DEM_SD_16000_Q
Percentage of bamboo forest	16000	Q	FT5_PLAND_16000_Q
Percentage of secondary forest	16000	LOG	FT6_PLAND_16000_LOG
Correlation length of urban areas	16000	L	LC6_GYR_16000_L
Focal mean of slope position	16000	Q	SLOPE_FM_16000_Q
Percentage of open forest	16000	L	TC2_PLAND_16000_L
Focal mean of TRI	16000	Q	TRI_FM_16000_Q
Camera effort	-	-	Cam_eff

Table 2 Final variables included in the (a) single-scale optimized (SSO) and (b) single-scale shape-optimized (SSSO) global models from an original 47 variables. The shape (i.e., functional form) of each variable in the SSSO model is indicated by: ^{L} linear, ^{Q} Quadratic, ^{LOG} Logarithmic, ^{EXP} Exponential; $^{-EXP}$ Negative Exponential.

250m	500m	1km	2km	4km	8km	16km
DEM_FM	CTI_FM	CTI_FM	CTI_FM	CTI_FM	CTI_FM	BOUND_FM
DEM_SD	DEM_FM	DEM_FM	DEM_FM	DEM_FM	CTI_SD	CTI_SD
FT1_GYR	FT1_GYR	DEM_SD	DEM_SD	DEM_SD	FT2_PLAND	FT3_PLAND
FT5_GYR	FT5_GYR	FT1_PLAND	FT2_GYR	FT2_PLAND	FT4_GYR	FT5_PLAND
FT6_GYR	FT6_GYR	FT2_GYR	FT5_GYR	FT4_GYR	FT5_PLAND	FT6_PLAND
FT7_GYR	FT7_GYR	FT5_GYR	FT6_PLAND	FT5_GYR	FT7_PLAND	FT7_PLAND
STRC1_FM	STRC1_FM	FT6_GYR	FT7_GYR	FT6_PLAND	LC6_GYR	LC2_GYR
TC2_PLAND	TC2_GYR	FT7_GYR	LC2_GYR	FT7_GYR	LC7_GYR	LC4_PLAND
TC3_GYR	TC3_PLAND	LC1_GYR	STRC1_FM	LC2_GYR	STRC1_FM	LC6_PLAND
		STRC1_FM	TC1_GYR	LC4_GYR	TC2_GYR	LC7_PLAND
		TC1_GYR	TC2_GYR	LC7_GYR	TC2_PLAND	SLOPE_FM
		TC2_GYR		STRC1_FM		SLOPE_SD
				TC1_GYR		TC2_GYR
				TC2_GYR		TC2_PLAND

250m	500m	1km	2km	4km	8km	16km
CTIFM^{L}	DEMFM^{LOG}	CTISD^{EXP}	CTISD^{-EXP}	BOUNDFM^{L}	CTISD^{-EXP}	CTISD^{-EXP}
DEMFM^{LOG}	FT1_GYR^{L}	DEMFM^{Q}	DEMFM^{LOG}	CTISD^{-EXP}	DEMFM^{LOG}	DEMSD^{Q}
FT1_GYR^{L}	FT6_GYR^{L}	FT1_GYR^{L}	FT2_GYR^{L}	DEMFM^{LOG}	DEMSD^{LOG}	FT4_GYR^{Q}
FT5_GYR^{EXP}	FT7_GYR^{L}	FT2_GYR^{L}	FT4_GYR^{LOG}	DEMSD^{Q}	FT2_GYR^{Q}	FT6_GYR^{LOG}
FT6_GYR^{L}	FT5_PLAND^{-EXP}	FT5_GYR^{EXP}	FT5_GYR^{L}	FT5_GYR^{L}	FT4_GYR^{Q}	FT1_PLAND^{LOG}
FT7_GYR^{L}	LC2_GYR^{LOG}	FT6_GYR^{L}	FT7_GYR^{L}	FT7_GYR^{Q}	FT5_GYR^{Q}	FT2_PLAND^{L}
SLOPEFM^{EXP}	SLOPEFM^{EXP}	FT7_GYR^{L}	LC2_GYR^{L}	FT2_PLAND^{L}	FT6_GYR^{L}	FT3_PLAND^{L}
SLOPESD^{Q}	SLOPESD^{Q}	FT2_PLAND^{EXP}	LC1_PLAND^{-EXP}	FT4_PLAND^{-EXP}	FT7_GYR^{Q}	FT4_PLAND^{LOG}
STRC1FM^{L}	STRC1FM^{L}	FT4_PLAND^{-EXP}	LC4_PLAND^{-EXP}	FT6_PLAND^{L}	FT1_PLAND^{LOG}	FT5_PLAND^{Q}
TC2_GYR^{-EXP}	TC2_GYR^{Q}	FT5_PLAND^{Q}	STRC1FM^{L}	FT7_PLAND^{-EXP}	FT7_PLAND^{-EXP}	FT7_PLAND^{Q}
TC3_GYR^{L}	TC2_PLAND^{-EXP}	SLOPESD^{LOG}	TC1_GYR^{Q}	LC2_GYR^{Q}	LCai^{L}	LC2_GYR^{L}
	TC3_PLAND^{L}	STRC1FM^{L}	TC2_GYR^{L}	LC3_GYR^{LOG}	LC2_GYR^{L}	LC7_GYR^{Q}
		TC1_GYR^{L}	TRIFM^{LOG}	LC7_GYR^{L}	LC4_GYR^{Q}	LC2_PLAND^{Q}
		TC2_GYR^{Q}		LC4_PLAND^{-EXP}	LC6_GYR^{L}	LC4_PLAND^{LOG}
		TC2_PLAND^{-EXP}		STRC1FM^{L}	LC4_PLAND^{-EXP}	LC5_PLAND^{LOG}
				TC1_GYR^{Q}	LC7_PLAND^{-EXP}	SLOPEFM^{EXP}
				TC2_GYR^{Q}	STRC1FM^{L}	TC2_GYR^{Q}
				TRIFM^{LOG}	TC2_GYR^{Q}	TRIFM^{LOG}
					TRISD^{EXP}	

Table 3 Final variables included in the multi-scale optimized (MSO) global model from an original 47 variables.

Variable	Best Scale (m)	ID
Terrain roughness index SD	1000	TRI_SD_1000
Correlation length of secondary forest	4000	FT6_GYR_4000
Slope SD	4000	SLOPE_SD_4000
CTI SD	8000	CTI_SD_8000
Correlation length of reforested areas	8000	FT4_GYR_8000
% Mixed deciduous forest	8000	FT2_PLAND_8000
% Grassland	8000	FT7_PLAND_8000
Correlation length of mosaic cropland	8000	LC2_GYR_8000
Correlation length of water bodies	8000	LC7_GYR_8000
% Shrubland/grassland	8000	LC4_PLAND_8000
Correlation length of open forest	8000	TC2_GYR_8000
Focal mean of park boundary	16000	BOUND_FM_16000
% Dry dipterocarp forest	16000	FT3_PLAND_16000
% Bamboo forest	16000	FT5_PLAND_16000
Correlation length of urban areas	16000	LC6_GYR_16000
% water bodies	16000	LC7_GYR_8000
Focal mean of slope	16000	SLOPE_FM_16000
% Open forest	16000	TC2_PLAND_16000

Table 4 Change in probability of tiger presence with change in variable value from 10th to 100th percentiles for fully averaged single-scale optimized (SSO) and single-scale shape-optimized (SSSO) models.

	250m		500m		1km		2km		4km		8km		16km	
	SSO	**SSSO**	**SSO**	**SSSO**	**SSO**	**SSSO**	**SSO**	**SSSO**	**SSO**	**SSSO**	**SSO**	**SSSO**	**SSO**	**SSSO**
Cam_eff	0.87	0.84	0.84	0.76	0.73	0.79	0.71	0.83	0.85	0.83	0.92	0.92	0.97	0.94
CTI_FM	-	-	-0.39	-	-0.47	-	-0.48	-	-0.25	-	-0.09	-	-	-
CTI_SD	-		-		-		-		-	-	0.24	-	0.22	-
DEM_FM	-	-	-	-	-	0.19	-	-	-	-	-	-	-	-
DEM_SD	0.67	-	-	-	-	-	-	-	0.43	-	-	0.14	-	0.07
FT1_GYR	0.18	-	0.23	0.23	0.38	0.32	-	-	-	-	-	-	-	-
FT1_PLAND	-	-	-	-	-	-	-	-	-	-	-	0.16	-	0.12
FT2_GYR	-	-	-	-	-	-0.27	-0.35	-0.21	-	-	-	-	-	-
FT4_PLAND	-	-	-	-	-	-0.03	-	-	-	-	-	-	-	-
FT5_GYR	0.73	-	0.69	-	0.58	-	0.34	0.41	0.47	0.31	-	-	-	-
FT5_PLAND	-	-	-	<0.01	-	0.12	-	-	-	-	0.31	-	0.90	0.70
FT6_GYR	-0.22	-0.21	-	-0.29	-0.32	-0.24	-	-	-	-	-	-0.15	-	-0.10
FT6_PLAND	-	-	-	-	-	-	-0.36	-	-0.20	-0.22	-	-	-0.11	-
FT7_GYR	-	-0.20	-	-	-0.33	-	-0.44	-0.25	-0.30	-	-	-	-	-
FT7_PLAND	-	-	-	-	-	-	-	-	-	0.36	-	0.48	-	-
LC2_PLAND	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.10
LC4_GYR	-	-	-	-	-	-	-	-	-	-	-	0.50	-	-0.13
LC4_PLAND	-	-	-	-	-	-	-	-	-	-	-	-	-0.08	-
LC6_GYR	-	-	-	-	-	-	-	-	-	-	-	-	-0.04	-
SLOPE_SD	-	0.36	-	-0.47	-	0.80	-	-	-	-	-	-	-	-
STRC1_FM	-0.21	-0.28	-0.24	-0.36	-0.42	-0.31	-0.42	-0.24	-	-0.26	-	-0.14	-	-
TC1_GYR	-		-		-		-0.42	-0.29	-0.26	-0.28	-	-	-	-
TC2_GYR	-	-	-0.24	-0.30	-0.50	-0.30	-	-	-0.30	-	-0.19	-0.12	-	-
TC2_PLAND	-	-	-	-	-	-	-	-	-	-	-0.19	-	-	-
TC3_GYR	0.20	0.34	-	-	-	-	-	-	-	-	-	-	-	-
TC3_PLAND	-	-	0.13	-	-	-	-	-	-	-	-	-	-	-
TRI_FM	-	-	-	-	-	-	-	0.55	-	0.47	-	-	-	-

Table 5 Generalized linear model results for the multi-scale optimized (MSO) model, predicting tiger presence based on 1,166 detections of tiger in DPKY (2008-2017), including optimal scale, standardized regression coefficients (β), adjusted standard error (SE(Adj)), z-score (*z*), and significance (*p*).

Variable	**ID**	**β**	**SE (Adj)**	***z***	***p***
(Intercept)	-	-2.405	0.260	9.242	<0.001
% Open forest (16km)	TC2_PLAND_16000	-1.437	0.349	4.120	<0.001
% Bamboo (16km)	FT5_PLAND_16000	0.988	0.238	4.158	<0.001
Correlation length secondary forest (4km)	FT6_GYR_4000	-0.675	0.246	2.744	0.006
Standard deviation of compound topographic index (8km)	CTI_SD_8000	0.616	0.193	3.199	0.001
Camera effort (# trap nights)	Cam_eff	1.415	0.299	4.728	<0.001
% Shrubland/grassland (8km)	LC4_PLAND_8000	-0.486	0.202	2.404	0.016
Standard Deviation of terrain roughness index (1km)	TRI_SD_1000	0.384	0.158	2.423	0.015
Correlation length of open forest (8km)	TC2_GYR_8000	-0.704	0.344	2.045	0.041

Table 6 Generalized linear model results for the single-scale optimized (SSO) model at each scale, predicting tiger presence based on 1,166 detections of tiger in DPKY (2008-2017), including standardized regression coefficients (β), adjusted standard error (SE(Adj)), z-score (*z*), and significance (*p*).

(a) SSO - 250m

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-1.849	0.198	9.355	<0.001
Standard deviation of DEM	DEM_SD	0.620	0.123	5.038	<0.001
Focal mean of streams/rivers	STRC1_FM	-1.090	0.426	2.559	0.011
Correlation length of bamboo forest	FT5_GYR	0.702	0.149	4.724	<0.001
Correlation length of evergreen forest	FT1_GYR	0.981	0.262	3.747	<0.001
Camera effort (# of trap nights)	Cam_eff	1.513	0.253	5.973	<0.001
Correlation length of closed canopy forest	TC3_GYR	0.920	0.484	1.901	0.057

(b) SSO - 500m

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-1.912	0.200	9.575	<0.001
Standard deviation of DEM	DEM_SD	-0.761	0.151	5.054	<0.001
Focal mean of streams/rivers	STRC1_FM	0.684	0.140	4.880	<0.001
Correlation length of bamboo forest	FT5_GYR	-0.872	0.426	2.047	0.041
Correlation length of evergreen forest	FT1_GYR	1.040	0.295	3.530	<0.001
Camera effort (# of trap nights)	Cam_eff	1.543	0.261	5.920	<0.001
Correlation length of closed canopy forest	TC3_GYR	-0.450	0.203	2.214	0.027
Standard deviation of DEM	DEM_SD	0.630	0.336	1.873	0.061

(c) SSO - 1km

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-2.025	0.244	8.282	<0.001
Focal mean of compound topographic index	CTI_FM	-0.771	0.168	4.588	<0.001
Correlation length of bamboo forest	FT5_GYR	0.649	0.137	4.727	<0.001
Correlation length of open forest	TC2_GYR	-0.691	0.198	3.492	<0.001
Correlation length of evergreen forest	FT1_GYR	0.877	0.275	3.185	0.001
Camera effort (# of trap nights)	Cam_eff	1.498	0.247	6.068	<0.001
Correlation length of grassland/shrubland	FT7_GYR	-0.868	0.272	3.195	0.001
Focal mean of streams/rivers	STRC1_FM	-1.592	0.458	3.477	0.001
Correlation length of secondary forest/old clearing	FT6_GYR	-0.783	0.221	3.540	<0.001

(d) SSO - 2km

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-2.234	0.262	8.523	<0.001
Correlation length of grassland/shrubland	FT7_GYR	-1.090	0.398	2.741	0.006
Focal mean of compound topographic index	CTI_FM	-0.894	0.224	4.000	<0.001
% secondary forest/old clearing	FT6_PLAND	-0.735	0.277	2.656	0.008
Correlation length of mixed deciduous forest	FT2_GYR	-0.818	0.322	2.538	0.011
Camera effort (# of trap nights)	Cam_eff	1.515	0.289	5.246	<0.001
Focal mean of streams/rivers	STRC1_FM	-1.426	0.483	2.952	0.003
Correlation length of non-forest	TC1_GYR	-1.320	0.517	2.554	0.011
Correlation length of bamboo forest	FT5_GYR	0.288	0.121	2.369	0.018

(e) SSO - 4km

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-2.506	0.314	7.978	<0.001
Correlation length of non-forest	TC1_GYR	-1.659	0.606	2.739	0.006
Correlation length of open forest	TC2_GYR	-0.769	0.292	2.630	0.009
Correlation length of bamboo forest	FT5_GYR	0.480	0.182	2.645	0.008
Standard deviation of DEM	DEM_SD	0.443	0.159	2.785	0.005
Camera effort (# of trap nights)	Cam_eff	1.595	0.314	5.081	<0.001
Correlation length of grassland/shrubland	FT7_GYR	-1.176	0.421	2.794	0.005
Focal mean of compound topographic index	CTI_FM	-0.676	0.259	2.607	0.009
% secondary forest/old clearing	FT6_PLAND	-0.543	0.304	1.789	0.074

(f) SSO - 8km

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-2.394	0.289	8.288	<0.001
Correlation length of open forest	TC2_GYR	-0.668	0.264	2.528	0.011
% Open forest	TC2_PLAND	-1.558	0.470	3.313	0.001
% Bamboo forest	FT5_PLAND	0.489	0.161	3.042	0.002
Standard deviation of compound topographic index	CTI_SD	0.321	0.163	1.968	0.049
Camera effort (# of trap nights)	Cam_eff	1.041	0.230	4.520	<0.001
Focal mean of compound topographic index	CTI_FM	-0.384	0.253	1.515	0.130

(g) SSO - 16km

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-2.513	0.273	9.215	<0.001
% Bamboo forest	FT5_PLAND	1.964	0.314	6.264	<0.001
% secondary forest/old clearing	FT6_PLAND	-1.827	0.424	4.311	<0.001
% Shrubland/grassland	LC4_PLAND	-0.647	0.247	2.620	0.009
Standard deviation of compound topographic index	CTI_SD	0.720	0.284	2.537	0.011
Camera effort (# of trap nights)	Cam_eff	1.355	0.279	4.853	<0.001
Correlation length of urban areas	LC6_GYR	-0.613	0.348	1.762	0.078

Table 7 Generalized linear model results for the single-scale shape-optimized (SSSO) model at each scale, predicting tiger presence based on 1,166 detections of tiger in DPKY (2008-2017), including optimal shape (functional form), standardized regression coefficients (β), adjusted standard error (SE(Adj)), z-score (*z*), and significance (*p*). The optimal functional form (shape) of each variable is indicated by: L-linear, Q-Quadratic, EXP-Exponential, LOG-Logarithmic.

(a) SSSO - 250m

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-2.056	0.251	8.189	<0.001
Camera effort (# of trap nights)	Cam_eff	1.747	0.280	6.237	<0.001
Focal mean of streams/rivers ^{L}	STRC1FM_L	-1.462	0.459	3.188	0.001
Correlation length of grassland/shrubland ^{L}	FT7_GYR_L	-0.673	0.282	2.389	0.017
Correlation length of secondary forest/old clearing ^{L}	FT6_GYR_L	-1.065	0.382	2.790	0.005
Standard deviation of slope position ^{L}	SLOPESD_L	0.979	0.197	4.964	<0.001
Standard deviation of slope position ^{Q}	SLOPESD_Q	-0.128	0.064	1.991	0.047
Correlation length of closed canopy forest ^{L}	TC3_GYR_L	1.340	0.618	2.169	0.030

(b) SSSO - 500m

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-1.157	0.262	4.424	<0.001
Camera effort (# of trap nights)	Cam_eff	1.620	0.272	5.960	<0.001
% Bamboo forest $^{-EXP}$	FT5_PLAND_NExp	-0.428	0.144	2.970	0.003
Correlation length of evergreen forest ^{L}	FT1_GYR_L	0.619	0.238	2.601	0.009
Standard deviation of slope position ^{L}	SLOPESD_L	1.109	0.231	4.804	<0.001
Correlation length of open forest ^{L}	TC2_GYR_L	-0.757	0.328	2.305	0.021
Standard deviation of slope position ^{Q}	SLOPESD_Q	-0.283	0.119	2.379	0.017
Correlation length of open forest ^{Q}	TC2_GYR_Q	-1.084	0.420	2.582	0.010
Focal mean of streams/rivers ^{L}	STRC1FM_L	-1.145	0.469	2.442	0.015

(c) SSSO - 1km

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-1.572	0.249	6.320	<0.001
Camera effort (# of trap nights)	Cam_eff	1.522	0.266	5.725	<0.001
Standard deviation of slope position ^{LOG}	SLOPESD_LOG	0.898	0.235	3.816	<0.001
Correlation length of secondary forest/old clearing ^{L}	FT6_GYR_L	-0.549	0.230	2.392	0.017
Correlation length of mixed deciduous forest ^{L}	FT2_GYR_L	-0.863	0.306	2.820	0.005
Correlation length of open forest ^{L}	TC2_GYR_L	-0.919	0.322	2.854	0.004
Correlation length of open forest ^{Q}	TC2_GYR_Q	-0.663	0.286	2.322	0.020
% Bamboo forest ^{L}	FT5_PLAND_L	0.891	0.330	2.703	0.007
% Bamboo forest ^{Q}	FT5_PLAND_Q	-0.134	0.073	1.850	0.064
Focal mean of streams/rivers ^{L}	STRC1FM_L	-0.990	0.500	1.981	0.048
% Reforested areas $^{-EXP}$	FT4_PLAND_NExp	-0.356	0.160	2.221	0.026
Focal mean of DEM ^{L}	DEMFM_L	0.429	0.180	2.380	0.017
Focal mean of DEM ^{Q}	DEMFM_Q	-0.166	0.098	1.707	0.088
Correlation length of evergreen forest ^{L}	FT1_GYR_L	0.860	0.321	2.684	0.007

(d) SSSO - 2km

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-2.328	0.328	7.101	<0.001
Camera effort (# of trap nights)	Cam_eff	1.504	0.280	5.375	<0.001
Focal mean of terrain roughness index ^{LOG}	ROUGHFM_LOG	0.763	0.245	3.117	0.002
Correlation length of bamboo forest ^{L}	FT5_GYR_L	0.362	0.119	3.035	0.002
Correlation length of mixed deciduous forest ^{L}	FT2_GYR_L	-0.649	0.316	2.050	0.040
Correlation length of non-forest ^{L}	TC1_GYR_L	-1.773	0.595	2.981	0.003
Correlation length of non-forest ^{Q}	TC1_GYR_Q	0.253	0.239	1.060	0.289
Correlation length of grassland/shrubland ^{L}	FT7_GYR_L	-0.699	0.382	1.830	0.067
Focal mean of streams/rivers ^{L}	STRC1FM_L	-0.682	0.453	1.508	0.132

(e) SSSO - 4km					
Variable	**ID**	**β**	**SE (Adj)**	***z***	***p***
(Intercept)	-	-2.708	0.415	6.531	<0.001
Camera effort (# of trap nights)	Cam_eff	1.440	0.304	4.733	<0.001
Focal mean of terrain roughness index ^{LOG}	ROUGHFM_LOG	0.784	0.309	2.534	0.011
% Grassland/shrubland $^{-EXP}$	FT7_PLAND_NExp	0.864	0.267	3.237	0.001
Correlation length of bamboo forest ^{L}	FT5_GYR_L	0.316	0.124	2.551	0.011
Correlation length of non-forest ^{L}	TC1_GYR_L	-1.795	0.755	2.376	0.017
Correlation length of non-forest ^{Q}	TC1_GYR_Q	0.290	0.336	0.863	0.388
% Secondary forest/old clearing ^{L}	FT6_PLAND_L	-0.802	0.379	2.117	0.034
Focal mean of streams/rivers ^{L}	STRC1FM_L	-1.637	0.562	2.915	0.004

(f) SSSO - 8km					
Variable	**ID**	**β**	**SE (Adj)**	***z***	***p***
(Intercept)	-	-2.417	0.354	6.821	<0.001
Camera effort (# of trap nights)	Cam_eff	1.248	0.256	4.878	<0.001
Standard deviation of DEM ^{LOG}	DEMSD_LOG	0.468	0.236	1.982	0.047
% Evergreen forest ^{LOG}	FT1_PLAND_LOG	1.070	0.475	2.256	0.024
% Grassland/shrubland $^{-EXP}$	FT7_PLAND_NExp	1.140	0.204	5.576	<0.001
Correlation length of shrubland/grassland ^{L}	LC4_GYR_L	0.701	0.335	2.093	0.036
Correlation length of shrubland/grassland ^{Q}	LC4_GYR_Q	-0.051	0.122	0.422	0.673
Focal mean of streams/rivers ^{L}	STRC1FM_L	-1.967	0.843	2.335	0.020
Correlation length of secondary forest/old clearing ^{L}	FT6_GYR_L	-0.571	0.249	2.290	0.022
Correlation length of open forest ^{L}	TC2_GYR_L	-0.518	0.303	1.708	0.088
Correlation length of open forest ^{Q}	TC2_GYR_Q	-0.392	0.393	0.997	0.319

(g) SSSO - 16km					
Variable	**ID**	**β**	**SE (Adj)**	***z***	***p***
(Intercept)	-	-1.334	0.435	3.069	0.002
Camera effort (# of trap nights)	Cam_eff	1.487	0.311	4.788	0.000
Correlation length of secondary forest/old clearing ^{LOG}	FT6_GYR_LOG	-0.443	0.239	1.856	0.063
% Mosaic cropland ^{L}	LC2_PLAND_L	-1.130	0.495	2.285	0.022
% Bamboo forest ^{L}	DEMSD_L	0.333	0.336	0.990	0.322
Standard deviation of DEM ^{L}	FT5_PLAND_L	1.556	0.440	3.534	0.000
% Mosaic cropland ^{Q}	LC2_PLAND_Q	-0.770	0.516	1.493	0.136
Standard deviation of DEM ^{Q}	DEMSD_Q	-0.868	0.361	2.402	0.016
% Bamboo forest ^{Q}	FT5_PLAND_Q	-0.192	0.216	0.892	0.372
% Scrubland/grassland ^{LOG}	LC4_PLAND_LOG	-0.496	0.286	1.736	0.083
% Evergreen forest ^{LOG}	FT1_PLAND_LOG	0.733	0.499	1.470	0.142

Supplementary Materials 3

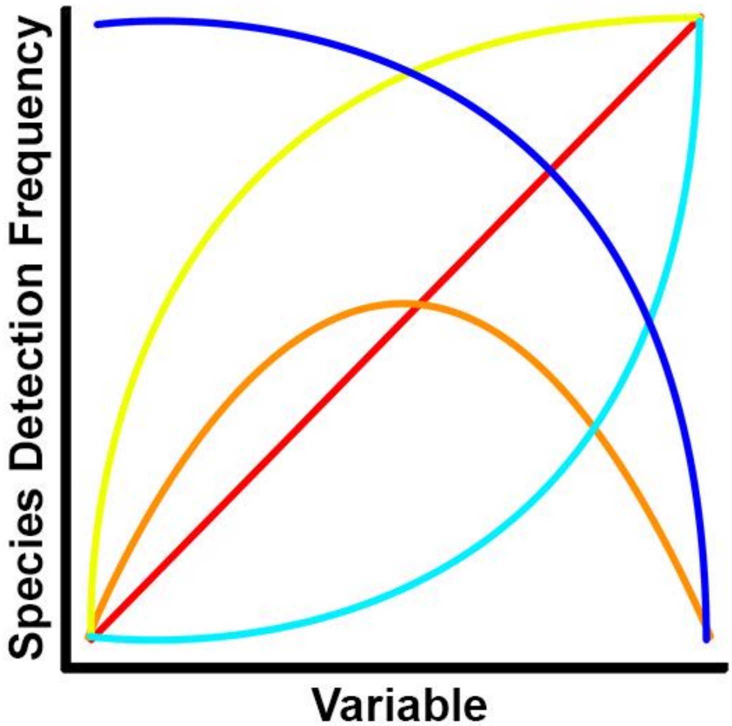

Fig. 1 A graphical representation of the functional form relationships between variables and species detection frequencies, including: linear (red); quadratic (orange); logarithmic (yellow); exponential (cyan) and negative exponential (blue).

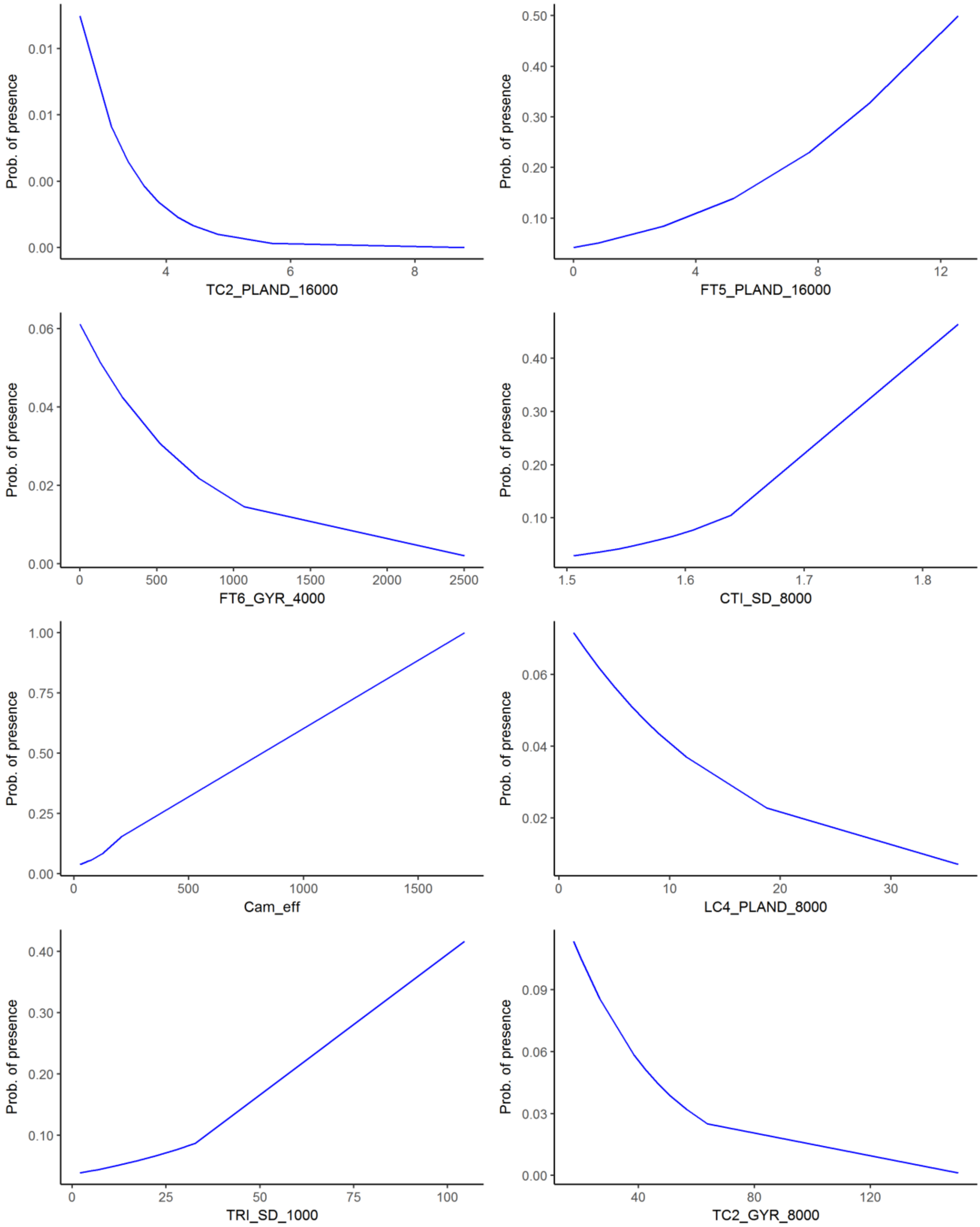

Fig. 2 Partial effects plots for the multi-scale optimized (MSO) model showing changes in predicted probability of tiger presence when variables increase from their 10th to 100th percentile, holding other variables at their medians. Graphic generated in R (R Development Core Team 2017).

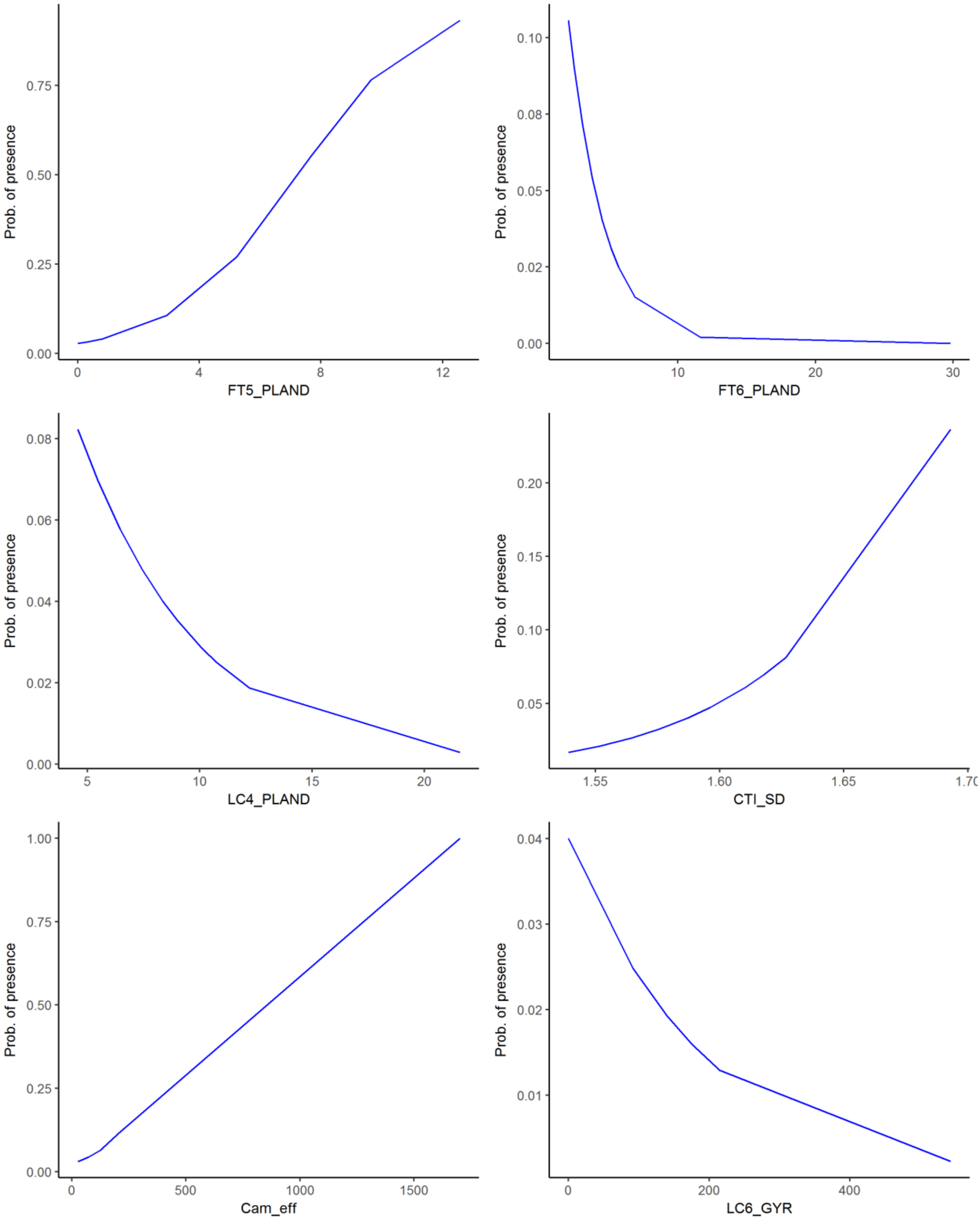

Fig. 3 Partial effects plots for the top-performing single-scale optimized (SSO) model (16km) showing changes in predicted probability of tiger presence when variables increase from their 10th to 100th percentile, holding other variables at their medians. Graphic generated in R (R Development Core Team 2017).

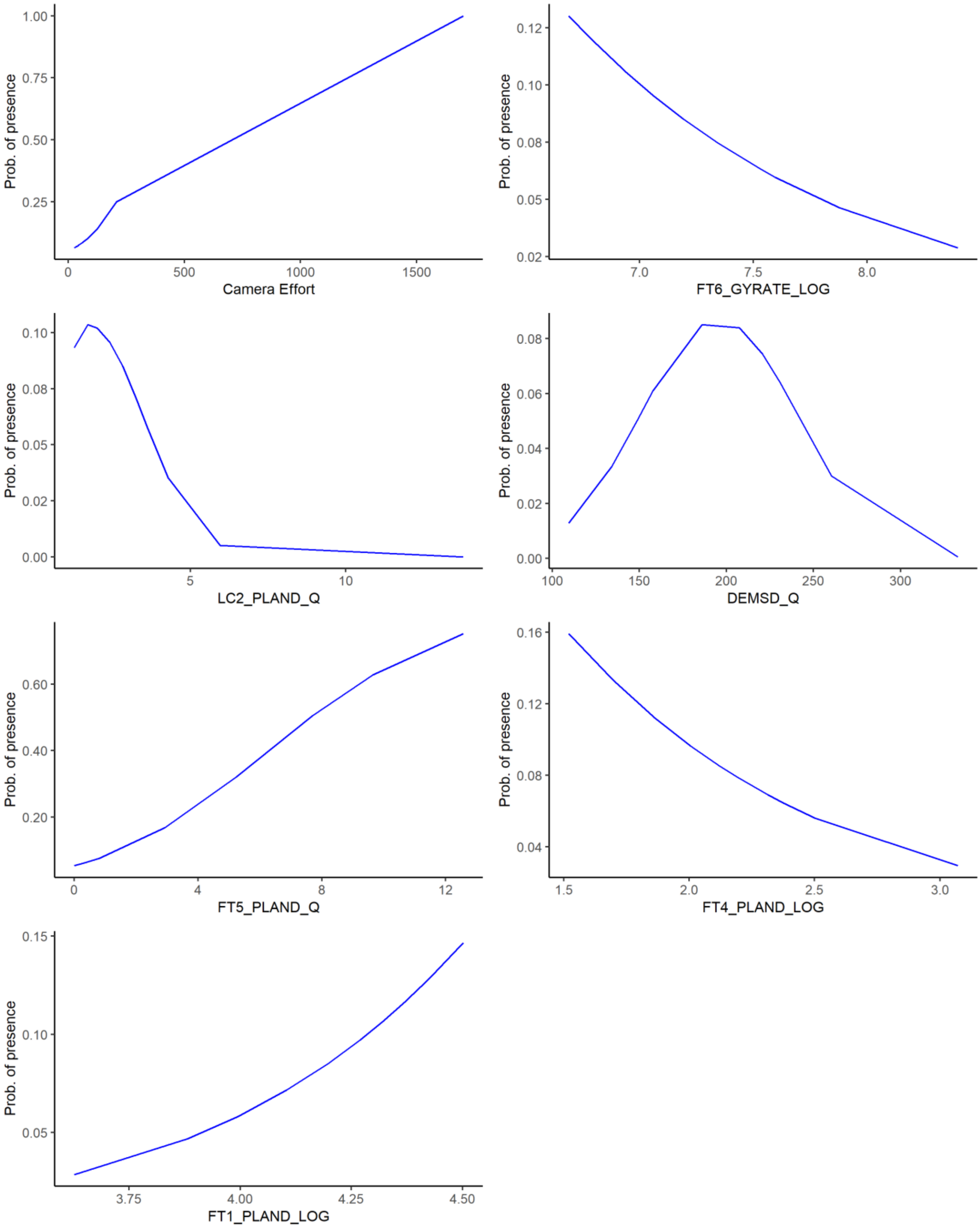

Fig. 4 Partial effects plots for the top-performing single-scale shape-optimized (SSSO) model (16km) showing changes in predicted probability of tiger presence when variables increase from their 10^{th} to 100^{th} percentile, holding other variables at their medians. Graphic generated in R (R Development Core Team 2017).

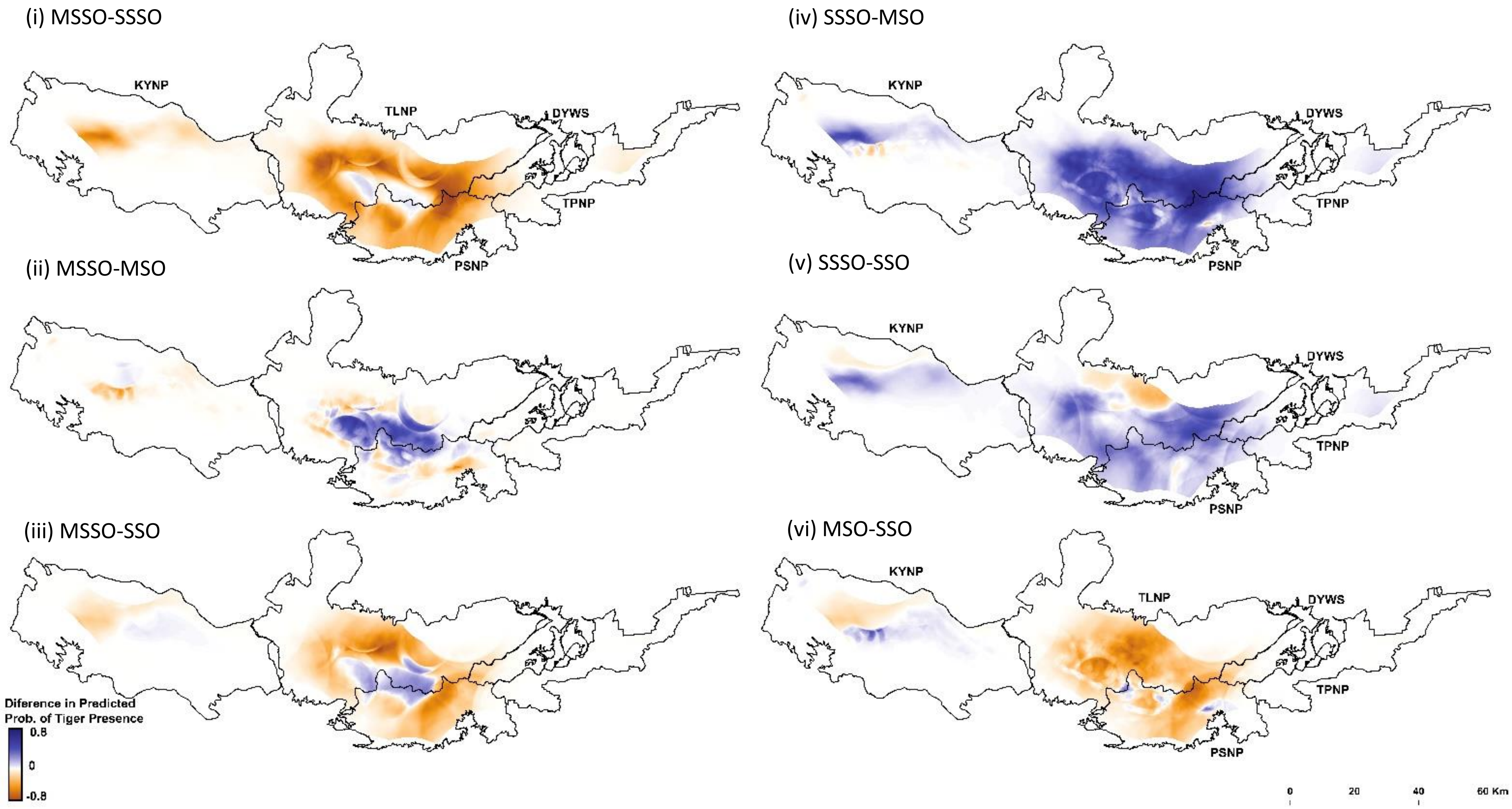

Fig. 5 Differences in prediction maps of probability of tiger presence generated from the top four fully averaged models – (i) MSSO-SSSO (ii) MSSO-MSO, (iii) MSSO-SSO, (iv) SSSO-MSO; (v) SSSO-SSO; and (vi) MSO-SSO. Maps were generated with ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011).

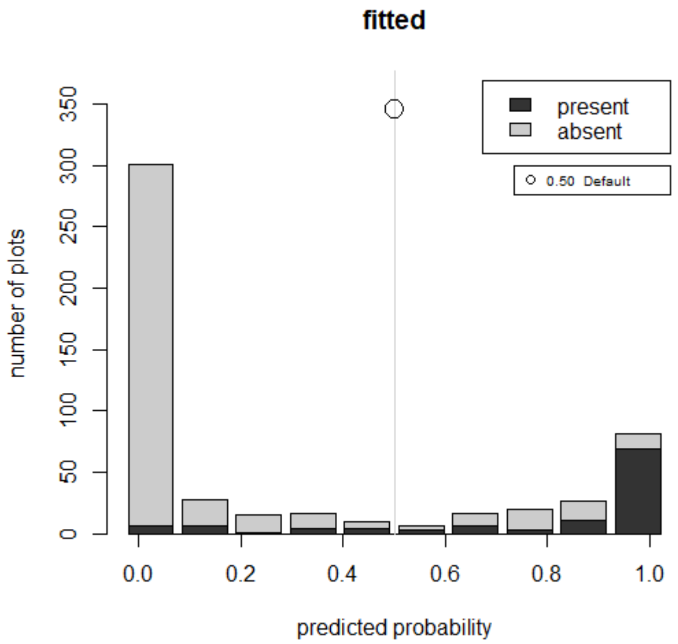

Fig. 6 Presence-absence across predicted probability values for the multi-scale and shape-optimized (MSSO) model. Graphic generated in R (R Development Core Team 2017).

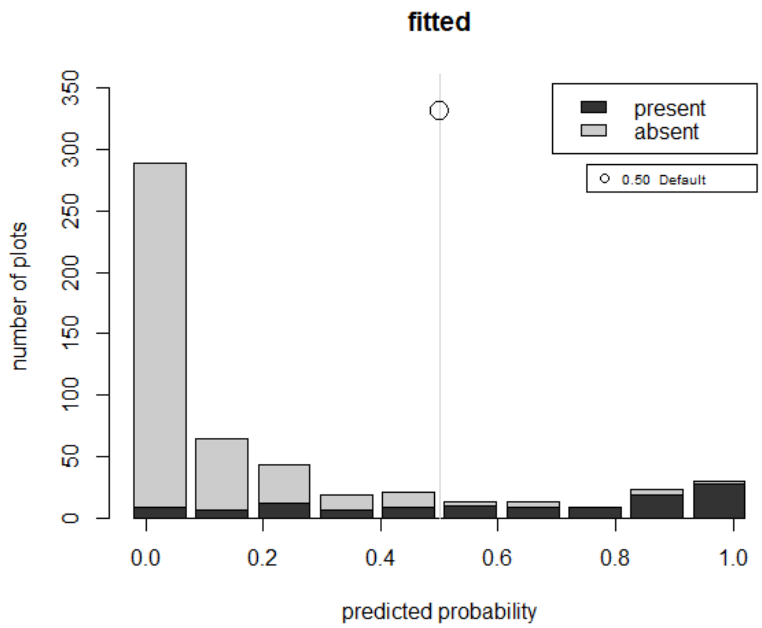

Fig. 7 Presence-absence across predicted probability values for the multi-scale-optimized (MSO) model. Graphic generated in R (R Development Core Team 2017).

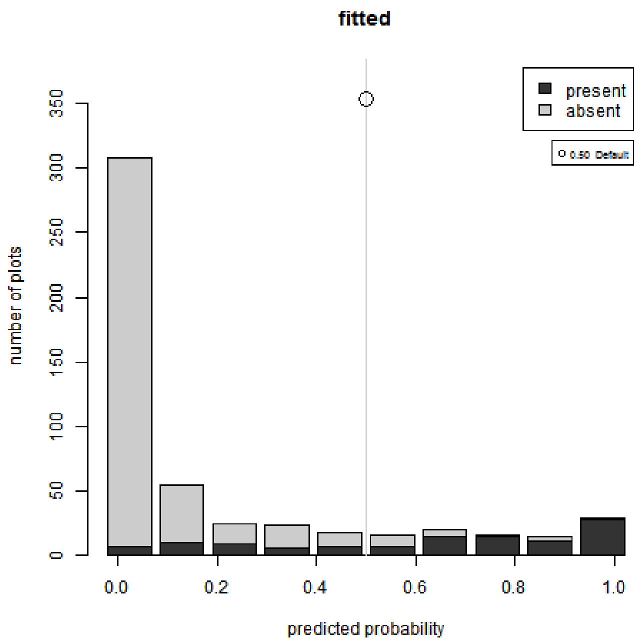

Fig. 8 Presence-absence across predicted probability values for the top-performing single scale optimized (SSO) model (16km). Graphic generated in R (R Development Core Team 2017).

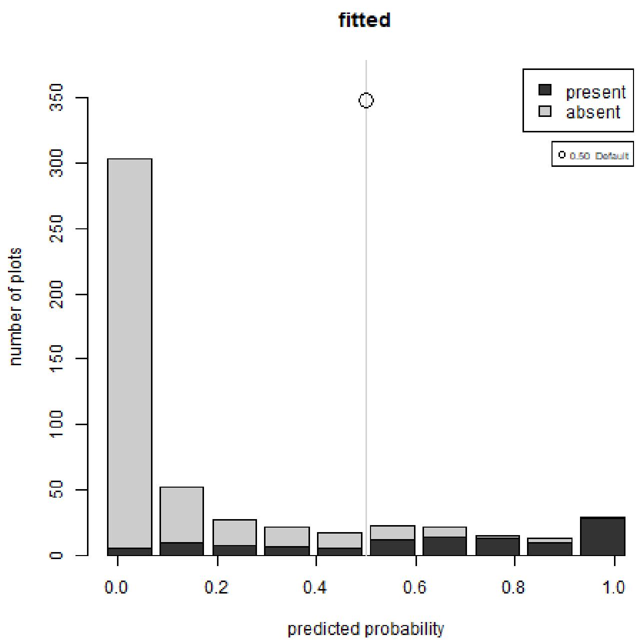

Fig. 9 Presence-absence across predicted probability values for the top-performing single scale shape-optimized (SSSO) model (16km). Graphic generated in R (R Development Core Team 2017).

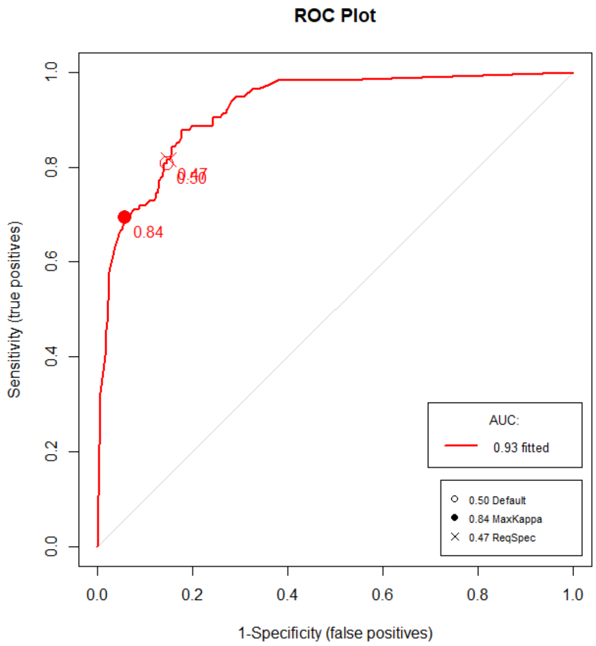

Fig. 10 Relative Operator Characteristic (ROC) plot with MaxKappa and area under the ROC curve (AUC) for the multi-scale- and shape-optimized (MSSO) model. Graphic generated in R (R Development Core Team 2017).

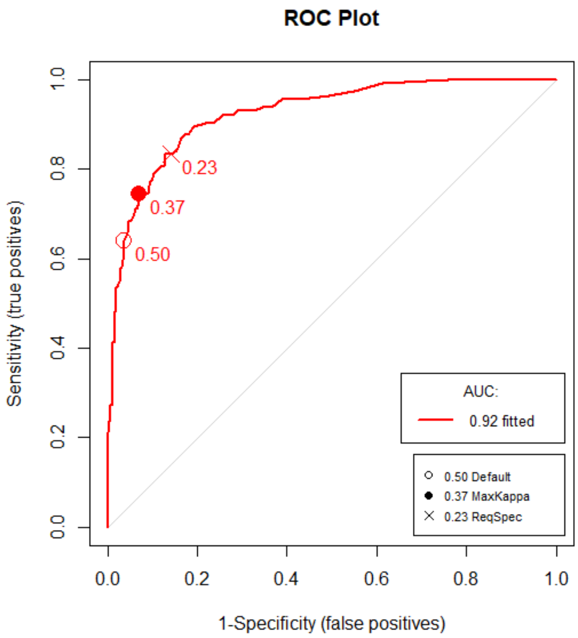

Fig. 11 Relative Operator Characteristic (ROC) plot with MaxKappa and area under the ROC curve (AUC) for the multi-scale optimized (MSO) model. Graphic generated in R (R Development Core Team 2017).

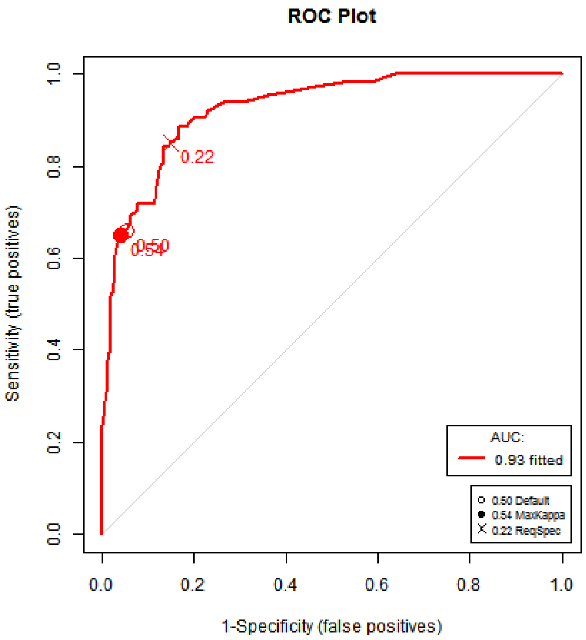

Fig. 12 Relative Operator Characteristic (ROC) plot with MaxKappa and area under the ROC curve (AUC) for the top performing single scale optimized (SSO) model (16km). Graphic generated in R (R Development Core Team 2017).

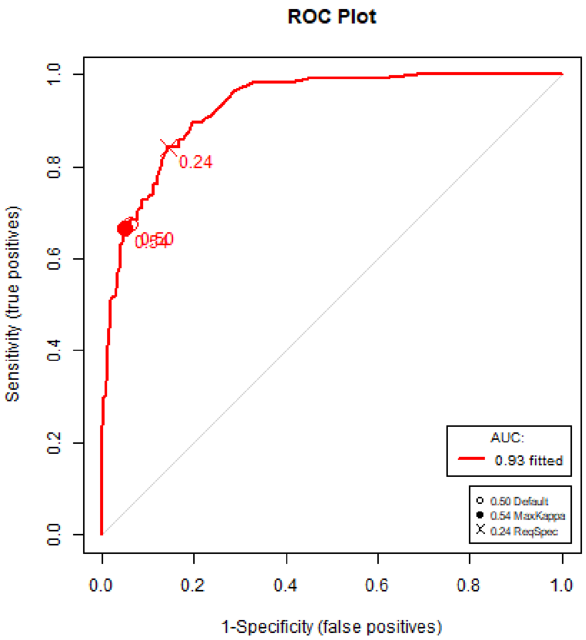

Fig. 13 Relative Operator Characteristic (ROC) plot with MaxKappa and area under the ROC curve (AUC) for the top performing single scale shape-optimized (SSSO) model (16km). Graphic generated in R (R Development Core Team 2017).

Chapter 4

Environmental factors, human presence, and prey interact to explain patterns of tiger presence in Eastern Thailand

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Title

Environmental factors, human presence and prey interact to explain patterns of tiger presence in Eastern Thailand

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Abstract

Thailand is one of the last strongholds for tigers *Panthera tigris* in mainland Southeast Asia. Evidence suggests heterogeneity in tiger presence in a globally important landscape in Eastern Thailand is potentially influenced by a complex interaction of prey, human presence and environmental conditions. Understanding these dynamics is of considerable importance for the conservation of tigers both in this landscape and elsewhere in their range. In this study, we examine which factors, among prey, human presence and environmental characteristics, best explain tiger presence in the Dong Phayayen–Khao Yai Forest Complex (DPKY). We collated survey data from 56,214 camera trap nights and evaluated the relationship between tiger presence and a suite of five prey, 11 human presence and eight environmental variables. We then used variance partitioning to discern the degree of variance in tiger presence explained by these factors. We documented strong, positive associations with wild boar *Sus scrofa* presence and prey richness, and strong, negative associations with human settlement density, public roads and presence of poachers. Environmental characteristics explained a greater relative proportion of variance (19.6%) in tiger presence than prey

covariates alone (3.1%), particularly confounded with human presence (31.1%). This suggests that environmental variables, especially when accompanied by anthropogenic factors, could be used to model potential tiger occurrence where other data may be lacking. Our approach may be helpful in providing guidance for prioritizing habitat, evaluating the effect of human presence and identifying key prey to provide a foundation for tiger protection and recovery.

Keywords tiger; Dong Phayayen–Khao Yai Forest Complex; prey; variance partitioning; wild boar; wildlife monitoring; anthropogenic disturbance; camera trapping.

1. Introduction

Catastrophic population declines over the past century, driven by hunting, habitat loss and prey depletion, have pushed the tiger *Panthera tigris* precipitously close to extinction (Nowell and Jackson 1996; Goodrich et al. 2015). In response, the species has been the focus of considerable funding, research and management efforts (Walston et al. 2010). Such investments appear to be generating positive results, such as recent announcements of a rise in global tiger numbers, though not without debate (Karanth et al. 2016; WWF 2016a, b; Harihar et al. 2017).

In contrast to recent cautious optimism, dramatic declines in tiger populations (Lynam and Nowell 2011; Goodrich et al. 2015) and habitat (Joshi et al. 2016) in Southeast Asia cast doubt on the future of the Indochinese tiger *Panthera tigris corbetti*, one of the most poorly understood subspecies. It is now possible that Cambodia, Lao PDR and Viet Nam have lost viable tiger populations (Lynam and Nowell 2011; Gray et al. 2017; Rasphone et al. 2019). The potential loss of populations from these countries and continuing loss of habitat would represent a considerable challenge for meaningful recovery of tigers in the region.

These overall trends are evident in Thailand, one of the last remaining strongholds for tigers in Southeast Asia. While there are suggestions that the tiger population in Thailand is relatively low and has suffered national range restriction in recent years (Pisdamkam et al. 2010; DNP 2016), long-term investments in law enforcement capacity may be providing a foundation for recovery in its largest source population

(Duangchantrasiri et al. 2016). Further, a recent study in the Dong Phayayen-Khao Yai forest complex (DPKY) in eastern Thailand has established this understudied landscape as one of the few remaining breeding populations known for the Indochinese subspecies (Ash et al. 2020). DPKY has become a landscape of global conservation significance for tigers, underscoring the importance of improving scientific understanding of its population.

The landscape has been defined by considerable changes throughout its history which have played a major role in shaping the current state of wildlife conservation in the area. Over the past century, the interaction of environmental factors and anthropogenic activity have led to modification of habitat, such as conversion of lowland forests, and proliferation of roads and settlements, facilitating varying degrees of human presence (Rabinowitz 1993; Lynam et al. 2006; Stokes 2017). This complex history has had direct influence on tigers and the prey species which underpin their survival.

Given DPKY's history, the interaction of environmental, prey and human factors on recent tiger distribution is likely complex. In tiger studies elsewhere in their range, prey emerges as the strongest, or among the strongest, predictors of tiger presence (Karanth et al. 2011; Harihar and Pandav 2012; Ngoprasert et al. 2012; Barber-Meyer et al. 2013) with evidence suggesting an optimal tiger-prey body mass ratio of approximately 1:1 (~60-250kg; Hayward et al. 2012). Conversely, studies also report strong negative associations between tiger presence and anthropogenic disturbance, such as roads (Kerley et al. 2002) and proximity to settlements (Sunarto et al. 2012), though these relationships may not be ubiquitous (Carter et al. 2012). Understanding the degree to which these factors broadly explain tiger presence on their own and are confounded could provide critical information for managers to develop protection strategies and inform additional, focused research.

At this critical juncture for tigers in Southeast Asia, understanding how tiger presence is affected by prey, threats and landscape characteristics is of considerable importance. Therefore, our goal in this study was to examine which factors, among prey, human and environmental characteristics, best explain the patterns of tiger presence in DPKY. To do so, we modelled several prey, human and landscape variables and compared the extent to which tiger occurrence is explained by these factors using variance partitioning. We tested three hypotheses in this study. First, we predict that tigers will have strong, positive associations with large-bodied (>175 kg) prey species. Second, tigers will have strong, negative associations with human habitation and, to a lesser degree, human presence. Third, we predict prey will better explain tiger presence compared to human or environmental characteristics, given the established importance of prey as a major limiting factor in tiger presence.

2. Materials & Methods

2.1 Study area

The Dong Phayayen-Khao Yai Forest Complex (DPKY) spans 6,155km^2 in eastern Thailand and includes five protected areas (PAs): Khao Yai National Park (KYNP), Thap Lan National Park (TLNP), Pang Sida National Park (PSNP), Ta Phraya National Park (TPNP) and Dong Yai Wildlife Sanctuary (DYWS; Fig. 1). Designated as a UNESCO World Heritage Site for its outstanding natural value, the complex is believed to host at least 112 mammal, 392 bird and 200 reptile/amphibian species (UNESCO 2017), among them, the flagship Indochinese tiger. Ash et al. (2020) identified six prey species potentially supporting presence of tigers in DPKY: banteng *Bos javanicus*, gaur *Bos gaurus*, Northern red muntjac *Muntiacus vaginalis*, sambar *Rusa unicolor*, Chinese serow *Capricornis milneedwardsii* and wild boar *Sus scrofa*.

Potential sources of disturbance through human activities are diverse. DPKY is situated almost completely within a human-dominated matrix of villages, agriculture, silviculture and infrastructure. The complex supports a substantial tourism industry in some areas and major roads occur between KYNP-TLNP and TPNP-DYWS. Smaller roads also facilitate varying degrees of controlled and uncontrolled vehicle access into these PAs. Human incursions into DPKY include local collectors of non-timber forest products, wildlife poachers and illegal loggers. Law enforcement patrols by park rangers are conducted regularly.

2.2 Camera-trap surveys

Species presence data were collated from non-invasive tiger camera-trap surveys conducted from 2008 to 2017 (Fig. 1; see Ash et al. 2020). Surveys were conducted opportunistically, varying in coverage and

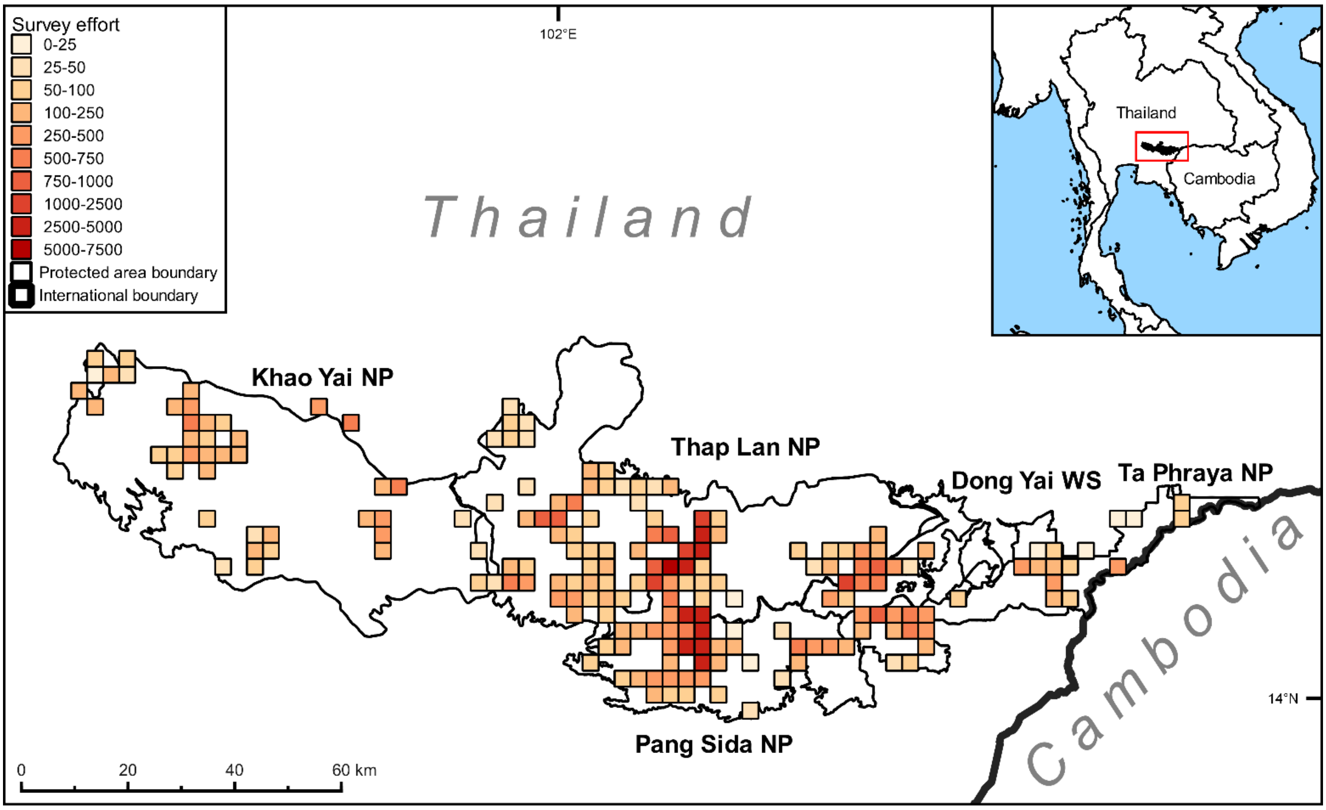

Fig.1 Map of the five protected areas within the Dong Phayayen-Khao Yai forest complex (DPKY; ~14°00' to 14°33'N and ~101°05' to 103°14'E; derived from Ash et al. [2020]) – Dong Yai Wildlife Sanctuary (DYWS), Khao Yai National Park (KYNP), Pang Sida National Park (PSNP), Thap Lan National Park (TLNP) and Ta Phraya National Park (TPNP). Survey locations are represented by 3km x 3km grids, shaded by total survey effort (total camera-trap nights; 2008-2017).

intensity. Thap Lan NP accounted for the highest proportion of survey effort (22,168 trap nights; 39% of total) with Dong Yai WS accounting for the least amount of survey effort (3,427 trap nights; 6% of total). Survey effort generally increased as access to resources improved, covering all five PAs in the complex. Cameras were placed to maximize detection of tigers by prioritizing camera placement in areas with previous tiger or prey records and identifying topographic or other features (e.g. roads, trails) likely used by tigers (Karanth and Chundawat 2002; Sunarto et al. 2012; Barber-Meyer et al. 2013). Detections at one camera station were considered to be independent if they occurred after a 30-min period (O'Brien et al. 2003). This resulted in a total of 1,166 tiger detections for analysis, as well as 10,726 detections of potential prey species and 21,910 human or human-related detections from 56,214 trap nights (Data S1, Table 1). A more comprehensive description of surveys is provided in Ash et al. (2020).

2.3 Variables

Based on information from previous studies on tigers throughout their range (Sunarto et al. 2012; Ngoprasert et al. 2012; Barber-Meyer et al. 2013; Hebblewhite et al. 2014), we assembled a suite of relevant predictor variables to explain variability in tiger detections in relation to prey and human presence (Data S1, Table 2). Presence was incorporated via photographic capture rate indices (PCRI) of four prey species as described by Ash et al. (2020) – gaur, muntjac, sambar and wild boar. This was calculated as the number of independent detections per 100 camera-trap nights. We included a prey richness covariate as the number of prey species detected for each station; this covariate also included the detection of banteng and serow, which were considered too rare to include as separate covariates. In this study, we define large prey as species with a mean body mass > 175 kg (sambar and gaur), medium-sized prey as species with a mean body mass from 20 to 175 kg (wild boar) and small prey species with a body mass < 20 kg (muntjac), designations similar to those in other tiger studies (Karanth and Sunquist 1995; Karanth and Nichols 1998; Andheria et al. 2007; Steinmetz et al. 2013).

Human variables were determined based on direct human presence detected on camera traps and at broader scales. Among covariates related to human presence, we included PCRI for poachers (identified via weapons, equipment, carrying dead wildlife/timber etc.), domestic dogs, park rangers, vehicles, and other humans (which include all humans and vehicles, except rangers and poachers). To evaluate broader scale human influence, we generated several GIS-based covariates at 30m resolution to match the resolution of environmental variables from Ash et al. (2021). Using ArcGIS (ESRI 2015), we calculated Euclidean distance to roads (Royal Forestry Department, 2000; GISTDA, 2005; 2018 Google, US Dept of State Geographer, Image Landsat/Copernicus) for two classes: uncontrolled public roads, most of which occur just inside or outside the parks, and controlled private (park) roads, which are managed by parks to regulate access. We also calculated distance to park substation (Royal Forestry Department 2000). To evaluate the potential influence of settlements, we calculated kernel density of settlements surrounding DPKY in ArcGIS (ESRI 2015; 2018 Google, US Dept of State Geographer, Image Landsat/Copernicus). We also included the Global Human

Influence Index dataset (WCS and CIESIN 2005), summarizing population density, human land use and infrastructure and human access.

In addition to prey and human covariates, we also included relevant environmental variables developed for the multiple-scale shape-optimized model in Ash et al. (2021). In this study, authors tested the effect of 47 environmental variables (Data S2, Table 1) on tiger occurrence based on the same camera-trap dataset (Ash et al. 2020) at seven spatial scales (250m to 16km), derived from spatial statistics and including several landscape metrics (focal mean/percentage of landscape, standard deviation, correlation length, contrast-weighted edge density, patch density and aggregation index), generated by moving windows of size corresponding to each scale. The authors also tested variables transformed by five different functional shapes (linear, quadratic, log, exponential and negative exponential). Variables were evaluated at each scale and functional form in univariate models with tiger presence as the response variable, with optimal scale and functional form determined by AICc. Following filtering of variables based on $p > 0.05$ and Pearson's correlation, remaining variables were included in a fully averaged multivariate model with performance evaluated via area under the relative operating characteristic (ROC) curve (AUC). The model, which performed exceptionally well (AUC 0.93), included eight variables: percentage of secondary forest (log, 16km), correlation length of secondary forest (linear, 4km), camera effort, percentage of bamboo forest (linear/quadratic; 16km), standard deviation of elevation (linear/quadratic, 16km), focal mean of terrain roughness index (linear/quadratic 16km), percentage of open forest (linear, 16km) and correlation length of reforested areas (linear/quadratic, 8km). Environmental factors in our study were defined by the same set of variables and their coefficients as in Ash et al. (2021) at their appropriate spatial scales and functional forms (Table 2c; see Data S2).

2.4 Tiger occurrence models

To evaluate the within-group effect of each covariate on tiger detections, we developed generalized linear models (GLM) for each of the three factors (prey, human and environment). The models included binomial tiger detection data as the response variable, covariate data as the explanatory variable, and survey effort (CTN) as a fixed effect, with binomial distribution using a logit link function. To eliminate within-group collinearity and maintain collinearity across the groups for variance partitioning analysis, we conducted a Pearson's correlation test between variables in each category (prey and human) with correlation threshold of $|r| > 0.6$, removing variables of higher AICc value via univariate regression (Burnham and Anderson 2002). The best combination of remaining covariates in each group were determined by subsetting best performing GLMs in 'BIOSTATS' (McGarigal 2018), ranked by ΔAICc (defined in our model as ΔAICc < 2), ranking variable importance in final models and generating averaged coefficients based on Akaike's model weight (w_i). These steps were also carried out for the environmental model generated by Ash et al. (2021).

To evaluate model performance, we calculated and compared statistics indicating model discriminatory ability. Specifically, we evaluated sensitivity, specificity, percent correctly classified (PCC), kappa and AUC. Second, we tested the influence of each covariate on probability of tiger presence by calculating the difference observed when the covariate increases from the 10th to 100th percentile, using standardized values while holding other covariates at their medians. Covariates were transformed to non-standardized values and plotted to evaluate changes in probability of tiger presence relative to changes in covariate values.

2.5 Variance partitioning

We used all final variables in each group (five prey, 11 human and eight environmental variables) to conduct variance partitioning analysis (Borcard et al. 1992), in order to quantify the extent to which prey, human and environmental factors account for variation in tiger detections across DPKY. Variance partitioning has been used in a number of ecological modelling studies (Cushman and McGarigal 2004; Bhattarai and Kindlmann 2013; Timm et al. 2016) and is useful in discerning the explanatory power of independent and confounded models on a shared response.

Variance partitioning was conducted using the function *varpart* within the package '*vegan*' in R (R Development Core Team 2017; Oksanen et al. 2018), including the three described types of covariates (prey, human, and environment) with camera effort as a fourth explanatory component, and binomial tiger detections as the response.

3. Results

Among an original 11 covariates for human presence and five covariates for prey, four human presence covariates were dropped (domestic dog, other humans, distance to park sub-station and distance to all roads) and one prey covariate was dropped (muntjac) due to $p > 0.05$. Pearson's correlation test for variables within the two groups did not indicate correlation ($|r| > 0.6$) between remaining covariates.

Overall model performance was strong for all groups of covariates (AUC > 0.80; Table 1). The environmental model from Ash et al. (2021), exhibited the strongest performance by AUC (0.93), followed by human factors (0.90) and prey (0.80). For other model performance statistics, human factors outperformed others in percent observations correctly classified (PCC) and specificity with the environmental model performing better based on sensitivity. Further, Kappa for human factors (0.65) was similar to the environmental model (0.65), but notably higher than that of prey (0.41), demonstrating exceptional ability to correctly discriminate between detection and non-detection points. All groups had relatively high specificity values – 0.96 for human factors, 0.93 for environment and 0.86 for prey – indicating a strong ability to predict non-detection points.

3.1 Prey model

All four prey covariates were included in the fully averaged model (Table 2a) together with camera effort. AIC variable importance was highest for wild boar, prey richness and camera effort, both present in $n=3$ model subsets, and lowest for sambar and gaur ($n = 1$).

Variable importance, as determined by standardized coefficients, was highest for camera effort (β = 0.990 ± 0.241), followed by prey richness (β = 0.442 ± 0.167) and wild boar (β = 0.297 ± 0.111). Both gaur (β = -0.074 ± 0.132) and sambar (β = -0.104 ± 0.119) had adjusted standard errors crossing zero.

Predicted tiger presence had a strong, positive association with camera effort, with a change (Δ) of

Table 1 A summary of performance statistics for prey, human and environmental models, the latter derived from Ash et al. (2021).

Model	Max Kappa Cut-point	PCC	Sensitivity	Specificity	Kappa	AUC
Prey	0.2700	0.7954	0.5526	0.8631	0.4092	0.80
Human	0.4700	0.8891	0.6491	0.9560	0.6504	0.90
Env.	0.4300	0.8815	0.7018	0.9315	0.6455	0.93

0.87 as camera effort values increased from 10^{th} to 100^{th} percentiles. Wild boar appeared to be a strong predictor of tiger presence, with predicted probability increasing from 0.14 to 0.65 (Δ0.51) as PCRI values increased to 0-58 detections per 100 CTN. There was a moderate increase in predicted probability in tiger presence from 0.15 to 0.48 (Δ0.33) as sambar PCRI increased from 0 to extreme values at the 100^{th} percentile (288 detections/100 trap nights). The presence of gaur appeared to have a marginally negative influence on predicted tiger presence, with predicted probabilities declining from 0.15 to 0.08 (Δ-0.07) as PCRI increased from 0 to 28. However, these relationships for gaur and sambar are uncertain given adjusted SE for their standardized coefficients cross zero. Predicted tiger presence was also positively associated with overall prey species richness, increasing from 0.08 to 0.32 (Δ0.24) as richness increased from 0 to 5 prey species detected.

3.2 Human model

A total of six human covariates were included in the fully averaged model (Table 2b) – vehicles, camera effort, distance to park roads, distance to public roads, poacher PCRI and settlement density. AIC variable importance varied marginally across covariates with highest values for camera effort, distance to public roads and settlement density ($n = 3$), followed by vehicles and distance to park roads ($n = 2$), and poacher presence ($n = 1$). Influential covariates positively associated with tiger presence, as determined by standardized coefficients, included camera effort (β = 1.426 ± 0.270) and distance to public roads (β = 1.005 ± 0.197). Conversely, covariates with a notably strong negative association included settlement density (β = -1.614 ± 0.485) and, to a lesser degree, poacher PCRI (β = -0.678 ± 0.517).

Predicted tiger presence relative to changing covariate values was positively associated with camera effort (Δ0.91) and vehicles (Δ0.75). Tigers were also positively associated with distance to public roads with probabilities increasing from 0.04 to 0.71 (Δ0.67) as distance to public roads increased from 570m to over 17,400m. Changes in predicted tiger presence was less pronounced in cases where tigers were negatively associated with covariates. Predicted tiger presence with increasing settlement density decreased from 0.19 to 0 (Δ-0.19) as density increased from almost 0 to 0.13. Predicted tiger presence steeply declined from 0.12 to almost 0 (Δ-0.12) as poacher PCRI increased from 0 to 100 detections per 100 trap nights. Similarly, as distance to park roads increased from less than 100m to over 27,000m, we observed a moderate decline in predicted tiger presence from 0.14 to 0.03 (Δ-0.11).

3.3 Environmental model

As discussed in Ash et al. (2021), the environmental model (Table 2c) describes positive associations between tigers and percentage of bamboo forest ($\beta = 1.028 \pm 0.525$), moderate topographic heterogeneity (standard deviation of elevation [$\beta = 0.995 \pm 0.308$] and focal mean of terrain roughness index [$\beta = 1.165 \pm 0.502$]) and reforested areas ($\beta = 0.968 \pm 0.321$), and negative associations with secondary ($\beta = -0.777 \pm 0.210$) and open forest ($\beta = -2.353 \pm 0.457$). Additional information on changes in predicted tiger presence as variables increase from 10^{th} to 100^{th} percentiles can be found in Table 2c and Data S2.

3.4 Variance partitioning

The relative proportion of variance explained among the three main groups of variables (prey, human, environment), and camera effort varied considerably with a high degree of collinearity (Fig. 2). Environmental factors, independent and confounded with others, accounted for 81.6% of the relative proportion of variance explained, followed by 59.3% for human factors, 36.7% for camera effort and 33.2% for prey. However, the relative proportion of variance explained exclusively by independent factors was highest for environment (19.6%), followed by camera effort (5.2%), prey (3.1%), and human presence (2.1%). Environmental and human factors jointly explained 31.1% of relative proportion of variance, the highest among confounded

Table 2 Fully averaged model results for (a) human presence, (b) prey and (c) the environmental model (Ash et al. 2021) including standardized regression coefficients (*β*), standard error (SE), adjusted standard error (Adjusted SE), z-value (z), significance (*p*), AIC variable importance (AIC Var. Imp), and change in probability with increasing variable values from 10th to 100th percentile (Δprob). Vehicle, poacher, wild boar, sambar and gaur covariates were derived from photographic capture-rate index values (PCRI; detections per 100 camera-trap nights). The environmental model includes optimal scale and functional form (^{L} linear, ^{Q} Quadratic, ^{LOG} Logarithmic).

(a)

Variable	**β**	**Adjusted SE**	***z***	***p***	**AIC Var. Imp**	**Δprob**
(Intercept)	-1.459	0.133	10.984	<0.001	-	-
Wild Boar	0.297	0.111	2.674	0.008	3	0.51
Prey Richness	0.442	0.167	2.647	0.008	3	0.24
Camera effort	0.990	0.241	4.108	<0.001	3	0.87
Sambar	0.104	0.119	0.872	0.383	1	0.33
Gaur	-0.074	0.132	0.556	0.578	1	-0.07

(b)

Variable	**β**	**Adjusted SE**	***z***	***p***	**AIC Var. Imp**	**Δprob**
(Intercept)	-2.349	0.268	8.775	<0.001	-	-
Vehicle	0.286	0.154	1.860	0.063	2	0.75
Distance to Public Road	1.005	0.197	5.112	<0.001	3	0.67
Distance to Park Road	-0.355	0.182	1.955	0.051	2	-0.11
Settlement Density	-1.614	0.485	3.327	0.001	3	-0.19
Camera effort	1.426	0.270	5.287	<0.001	3	0.91
Poacher	-0.678	0.517	1.313	0.189	1	-0.12

(c)

Variable	**β**	**Adjusted SE**	***z***	***p***	**AIC Var. Imp**	**Δprob**
(Intercept)	-1.367	0.314	4.352	<0.001	-	-
% Secondary Forest (16km) ^{LOG}	-0.777	0.210	3.702	<0.001	2	-0.23
Correlation length Secondary Forest (4km) ^{L}	-0.701	0.235	2.978	0.003	3	-0.13
Camera effort (# trap nights)	1.460	0.309	4.718	<0.001	3	0.92
% Bamboo (16km) ^{L}	1.028	0.525	1.960	0.050	2	0.55
DEM Standard Deviation (16km) ^{L}	0.995	0.308	3.226	0.001	1	0.13
% Bamboo (16km) ^{Q}	-0.072	0.232	0.309	0.757	2	0.55
DEM Standard Deviation (16km) ^{Q}	-0.866	0.336	2.575	0.010	1	0.13
Focal mean of terrain roughness index (16km) ^{L}	1.165	0.502	2.317	0.020	2	0.13
Focal mean of terrain roughness index (16km) ^{Q}	-1.671	0.579	2.887	0.004	2	0.13
% Open forest (16km) ^{L}	-2.353	0.457	5.149	<0.001	1	-0.58
Correlation length of reforested areas (8km) ^{L}	0.968	0.321	3.011	0.003	1	0.17
Correlation length of reforested areas (8km) Q	-0.555	0.195	2.844	0.004	1	0.17

factors (Data S1; Table 3). Relative proportion of variance explained jointly for environment, prey and human factors was 7.3%.

4. Discussion

We evaluated the degree to which prey, human and environmental characteristics explain tiger presence in the Dong Phayayen-Khao Yai Forest Complex, a tiger landscape of global conservation priority.

Environmental variables, particularly confounded with human factors, explained a greater proportion of variance in tiger presence than any other factor in our study, potentially due to environmental covariates more comprehensively accounting for factors influencing tiger presence, including presence of prey and human access, than either of these factors independently. Importantly, we documented strong associations with medium-sized prey (wild boar) and areas of high prey richness while also documenting strong negative associations with anthropogenic factors, particularly settlement density, public roads and increased poaching presence.

Our first hypothesis predicted that tigers would have strong, positive associations with large-bodied (> 175kg) prey species, in particular, sambar and gaur. The presence of prey species is a critical factor in the presence and persistence of tigers (Karanth and Stith 1999; Karanth et al. 2004) and a number of studies throughout the tiger's range indicate a preference for large prey (Karanth and Sunquist 1995; Biswas and Sankar 2002; Bagchi et al. 2003). Results do not support our hypothesis. In our study, tiger presence had strong, positive associations with wild boar, considered in our study a medium-sized species, while positive or negative relationships could not be determined for sambar and gaur, the two largest prey species evaluated. Wild boar are relatively widespread in the complex compared to sambar and differences in availability of these prey species across the complex may have been a factor in the strength of variable coefficients for these species. These results are partially consistent with other studies in Thailand. In Ngoprasert et al. (2012), tigers had strong overall associations with wild boar; however, in contrast to our results, gaur was considered to have the highest importance in both national and Khao Yai NP models and tiger presence was also positively associated with sambar. In Western Thailand, studies have suggested wild boar (Steinmetz et al. 2013), gaur, sambar and banteng to be important prey species (Petdee 2000; Prommakul 2003). Wild boar and deer species, such as sambar, are suggested to be important prey species elsewhere in the tiger's range (Sunquist et al. 1999; Biswas and Sankar 2002; Hayward et al. 2012; Petrunenko et al. 2016), in some cases, more so compared to gaur and muntjac (Sunquist et al. 1999; Biswas and Sankar 2002). Hayward et al. (2012) suggest tigers optimally select prey with a similar body mass, corresponding roughly to large cervids (e.g. sambar) and wild boar which we considered 'large' and 'medium' prey species, respectively. In future studies testing similar hypotheses, prey size classifications may be more appropriate relative to tiger body mass (e.g. wild boar and sambar as 'optimally sized' prey).

In addition to strong positive associations with wild boar, we also documented relatively strong positive associations with overall prey richness. Availability of diverse prey of different size classes is thought to be an important factor in the persistence of large felids (Sandom et al. 2017) and, more broadly, richness and persistence of large carnivores may be underpinned by richness of prey species (Sandom et al. 2013). It is possible that prey species richness, in addition to specific prey species, augments tiger presence in certain areas in DPKY.

In our second hypothesis, we predicted that tigers would have strong, negative associations with human habitation and, to a lesser degree, human presence. Our results are consistent with this hypothesis. Tiger presence in our study had strong, negative associations with public roads and settlement density, and relatively strong negative associations with the presence of poachers. These results are consistent with evidence in other studies suggesting broad negative associations with human activity overall (Karanth et al. 2011; Harihar and Pandav 2012; Ngoprasert et al. 2012; Barber-Meyer et al. 2013). More specifically, strong negative associations with settlements and public roads is supported by studies elsewhere in the tiger's range (Kerley et al. 2002; Linkie et al. 2006; Sunarto et al. 2012). The negative association with the presence of poachers is also consistent with studies highlighting the potentially catastrophic impacts of poaching on tiger and prey populations, even in seemingly intact forest (Kenney et al. 1995; Chapron et al. 2008; Steinmetz et al. 2010). Negative associations with human settlements, public roads and poaching presence appears to be almost universal across the tiger's range (Kerley et al. 2002; Kanagaraj et al. 2011; Hebblewhite et al. 2012; Sunarto et al. 2012; Barber-Meyer et al. 2013), part of a broader trend of these factors being associated with declines of large carnivores globally (Ripple et al. 2014; Wolf and Ripple 2017). Our results suggest these factors are a major influence in tiger distribution in DPKY.

Our results depart somewhat from our second hypothesis with positive associations with park roads and vehicles. In our study, we distinguished between public roads, primarily occurring outside park boundaries, and park roads maintained by PAs which facilitate access for patrolling and, in some areas,

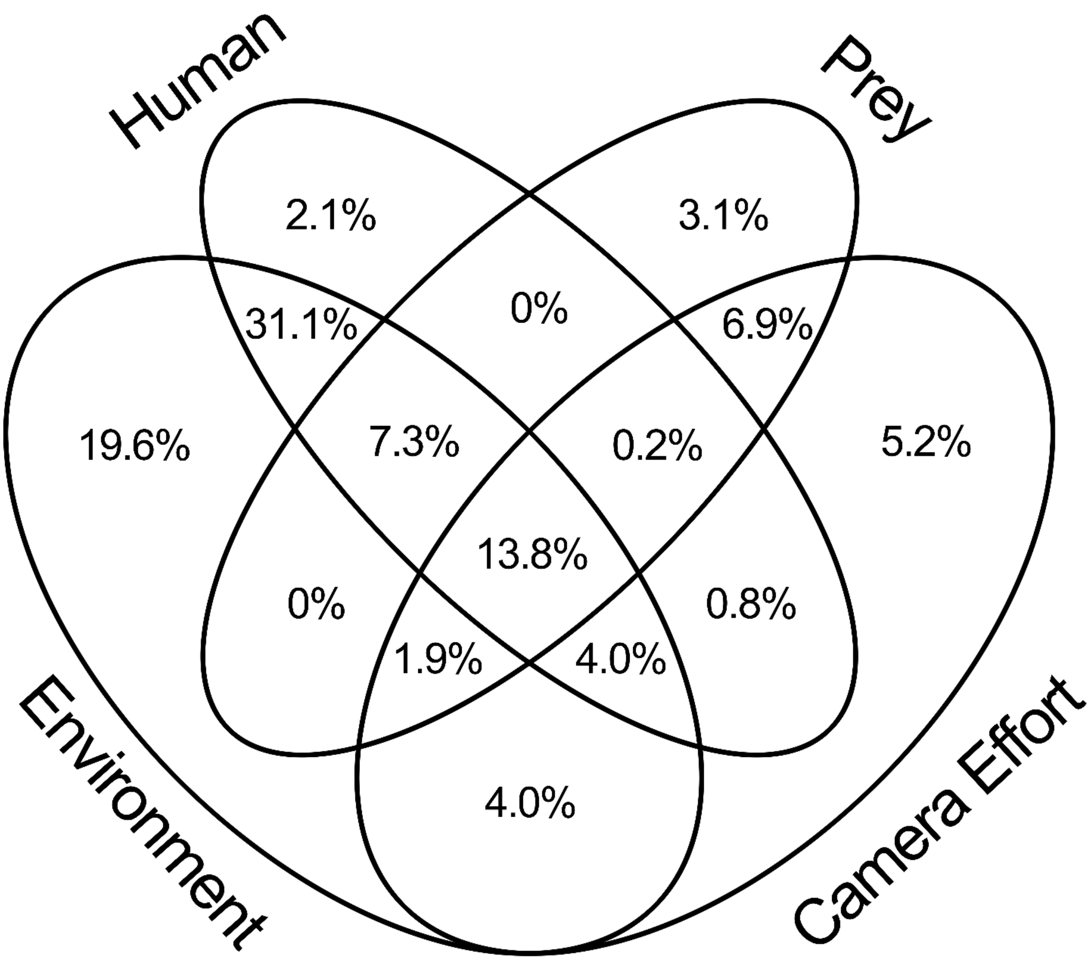

Fig.2 Relative proportion of variance in tiger detections explained by environmental, human and prey factors and camera effort. Confounded factors (areas of overlap) describe variance which cannot be explained by a single model.

tourism. Our study is distinguished in this regard from studies reviewing effects of public roads of varying intensity of use or navigability rather than uncontrolled versus controlled access (Kerley et al. 2002). Positive associations with park roads in our study are likely a result of tigers using certain roads for efficient travel through the landscape (Kerley et al. 2002; Sunquist 2010; Carter et al. 2012). Further, many of the vehicles documented in this study were vehicles used by PA staff for patrolling which may overlap with areas of protection priority, such as areas that support the presence of tigers. Elsewhere in Thailand, a study by Ngoprasert et al. (2007), did not document significant differences in detection rates of leopard among different categories of vehicle traffic rates. The authors speculate this may be due to temporal separation, a factor in patterns of co-occurrence in Carter et al. (2012). This may have also been a factor in our study. Regular use of roads by felids and other species have been documented in other studies (Di Bitetti et al. 2010, 2014). However, the relationship between these species and roads is likely complex. Due to the study design, we were unable to evaluate fine-scale effects of vehicle presence on tigers. Thus, associations with vehicles do not necessarily imply tolerance or the absence of negative influence.

Our third hypothesis was that prey itself would better explain tiger presence compared to human presence or environmental characteristics, given the established importance of prey as a major limiting factor in tiger presence (Karanth and Stith 1999; Karanth et al. 2004) and high importance of prey in other modelling studies (Karanth et al. 2011; Kanagaraj et al. 2011; Barber-Meyer et al. 2013; Steinmetz et al. 2013). This hypothesis was not supported by our results. Independently, tigers had strong positive associations with prey and a lack of prey would certainly preclude tiger presence. However, contrary to our hypothesis, in terms of relative variance explained, variance partitioning indicated that prey alone explained less variance (3.1%) compared to other factors. In contrast to our predictions, environmental factors explained the greatest overall proportion of variance (19.6%), particularly confounded with human factors (31.1%).

Variance partitioning in our study indicated that tiger relationships with prey, in some cases, could be explained by a combination of environmental and human factors. Ash et al. (2021) described strong positive associations with habitat suitable for important prey species described in our study, strong positive associations with core habitat away from human habituation and strong negative associations with habitat near settlements that were heavily impacted by human activity. In effect, environmental covariates, including habitat, terrain and proxies of human and prey effects, may have been a more comprehensive predictor of tiger presence overall than prey or human factors on their own, resulting in higher explanatory performance. Specifically, it is possible that environmental covariates better accounted for important limiting factors for the presence of prey, including human presence, resulting in a high degree of collinearity. Importantly, this suggests that in some cases an environmental model, especially coupled with anthropogenic factors, could be used to model tiger occurrence where other data may be lacking. However, this approach would merit a high degree of caution since, regardless of environmental characteristics, poaching and prey depletion can eradicate tigers and other species from otherwise intact habitat (Benítez-López et al. 2019). Application of this approach may be beneficial in poorly understood areas by identifying factors of notable influence on tiger presence to guide more specific and robust scientific enquiry. Rigorous studies to assess prey abundance and human pressure should be employed wherever possible to more comprehensively understand the influence of these factors on tiger presence.

Human presence explained a relatively large amount of variance in our study, and the effects of its variables on tiger presence were particularly strong. This relationship between human and environmental factors is evident in the high relative proportion of variance explained by confounded human and environmental factors. In DPKY, mountainous habitat has been the least prone to disturbance historically, with landscape characteristics limiting patterns of human influence. Overall, tiger presence in DPKY may be explained in broad terms by the fact that little alternative habitat remains outside of more central areas and that variance in tiger presence is explained by differences in broad-scale environmental conditions, available habitat for prey, and refugia in which prey are subject to lower poaching pressure.

While our study reveals important associations with certain prey species, these associations should be distinguished from prey selection, which was outside the scope of this study and would require methods of diet analysis (Karanth and Nichols 1998; Andheria et al. 2007). Further, we did not include smaller potential prey species (<20 kg) given the presence of several larger prey species in our study area and strong representation of larger prey as being critically important in studies throughout the tigers range (Karanth and Sunquist 1995; Biswas and Sankar 2002; Bagchi et al. 2003). Such species were not included in Ngoprasert et al. (2012) in modelling tiger associations with prey elsewhere in Thailand. Study design precluded adherence to key assumptions of occupancy modelling particularly those pertaining to independence and population closure necessary for calculating reliable estimates of detection probability. Thus, prey covariates were developed using detection rates (PCRI) as a surrogate to evaluate the influence of prey presence. We recommend future studies strive to incorporate data from studies explicitly designed for occupancy or capture-recapture frameworks where possible. Further, given spatial overlap of human presence with tiger and prey species, additional studies exploring the potential risk from disease transmission, such as from canine distemper virus (CDV; Seimon et al. 2013) or African swine fever (Guberti et al. 2019) may be warranted.

4.1 Implications for conservation

Our study suggests explanatory factors for tiger presence in the Dong Phayayen–Khao Yai Forest Complex are more nuanced than initially hypothesized. We documented strong, positive associations with wild boar (*Sus scrofa*) and prey richness, and strong, negative associations with human settlements, public roads, and poachers. However, environmental characteristics, particularly confounded with human presence, explained a greater relative proportion of variance in tiger presence than prey covariates. Given the patterns of tiger presence in our study and consistent with studies from elsewhere in the tigers' range, we recommend prioritizing protection of key habitat, minimizing human presence and securing prey rich areas as part of ongoing tiger protection strategies in DPKY. We echo the sentiment of Kanagaraj et al. (2011) that, although these seemingly intuitive results, such as negative associations with anthropogenic factors, are not new, these are nonetheless important to quantify. Negative impacts of human influence have been documented broadly (Crooks 2002; Foley et al. 2005; Coffin 2007), as well as more specifically for other large, wide-ranging species such as wolves (Lesmerises et al. 2012) and bears (Linke et al. 2013). However, the relationship between the presence of these species and anthropogenic factors may be more complex than broader trends suggest (Hebblewhite and Merrill 2008; Martin et al. 2010; Carter et al. 2012). Understanding the potential influence of human presence on tigers, particularly in concert with other factors such as prey or environmental factors, is particularly important for our study area for which landscape-scale assessments on tigers have been lacking.

Controlling poaching of prey, particularly wild boar, and minimizing disturbance to habitat will be crucial for tiger protection while restoration of degraded habitat and prey populations will improve prospects for long-term recovery of tigers in this landscape. Reducing infrastructure development that may otherwise fragment habitat or facilitate access, such as roads or dams, maintaining careful regulation of access into this landscape and additional research on potential finer-scale effects of vehicles on tiger presence is also warranted. Efforts are underway to mitigate the effects of one major roadway (UNESCO 2017) though the extent to which this will facilitate tiger movement is not yet known. Understanding the degree to which tigers can move within and beyond this landscape, particularly in areas of higher human influence, will be critical to the development of long-term, broad-scale recovery strategies. We believe this study will be beneficial in guiding such strategies in DPKY, specifically within the realm of protection of prey and mitigation of potentially adverse human activity. Our approach may be helpful in other areas for providing guidance on prioritizing habitat, evaluating the effect of human presence and identifying key prey to provide a foundation for species protection and recovery.

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Conflict of interest

None

References

Andheria AP, Karanth KU, Kumar NS (2007) Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. J Zool 273:169–175. https://doi.org/10.1111/j.1469-7998.2007.00310.x

Ash E, Kaszta Ż, Noochdumrong A, et al (2020) Opportunity for Thailand's Forgotten Tigers: Assessment of Indochinese tiger Panthera tigris corbetti and prey from camera-trap surveys in Eastern Thailand. Oryx 55:204–211. https://doi.org/10.1017/S0030605319000589

Ash E, Macdonald DW, Cushman SA, et al (2021) Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: A case study of tigers (Panthera tigris) in Thailand. Landsc Ecol 36:455–474. https://doi.org/10.1007/s10980-020-01105-6

Bagchi S, Goyal SP, Sankar K (2003) Prey abundance and prey selection by tigers (Panthera tigris) in a semi-arid, dry deciduous forest in western India. J Zool 260:285–290. https://doi.org/10.1017/S0952836903003765

Barber-Meyer SM, Jnawali SR, Karki JB, et al (2013) Influence of prey depletion and human disturbance on tiger occupancy in Nepal. J Zool 289:10–18. https://doi.org/10.1111/j.1469-7998.2012.00956.x

Benítez-López A, Santini L, Schipper AM, et al (2019) Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. PLoS Biol 17:e3000247–e3000247. https://doi.org/10.1371/journal.pbio.3000247

Bhattarai BP, Kindlmann P (2013) Effect of human disturbance on the prey of tiger in the Chitwan National Park - Implications for park management. J Environ Manage 131:343–350. https://doi.org/10.1016/j.jenvman.2013.10.005

Biswas S, Sankar K (2002) Prey abundance and food habit of tigers (Panthera tigris tigris) in Pench National Park, Madhya Pradesh, India. J Zool 256:411–420. https://doi.org/10.1017/S0952836902000456

Borcard D, Legendre P, Drapeau P (1992) Partialling out the Spatial Component of Ecological Variation. Ecology 73:1045–1055. https://doi.org/10.2307/1940179

Carter NH, Shrestha BK, Karki JB, et al (2012) Coexistence between wildlife and humans at fine spatial scales. Proc Natl Acad Sci U S A 109:15360–15365. https://doi.org/10.1073/pnas.1210490109

Chapron G, Miquelle DG, Lambert A, et al (2008) The impact on tigers of poaching versus prey depletion. J Appl Ecol 45:1667–1674. https://doi.org/10.1111/j.1365-2664.2008.01538.x

Coffin AW (2007) From roadkill to road ecology: a review of the ecological effects of roads. J Transp Geogr 15:396–406. https://doi.org/10.1016/j.jtrangeo.2006.11.006

Crooks KR (2002) Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation. Conserv Biol 16:488–502. https://doi.org/10.1046/j.1523-1739.2002.00386.x

Cushman SA, McGarigal K (2004) Patterns in the species-environment relationship depend on both scale and choice of response variables. Oikos 105:117–124. https://doi.org/10.1111/j.0030-1299.2004.12524.x

Di Bitetti MS, De Angelo CD, Di Blanco YE, Paviolo A (2010) Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta Oecologica 36:403–412. https://doi.org/10.1016/j.actao.2010.04.001

Di Bitetti MS, Paviolo A, De Angelo C (2014) Camera trap photographic rates on roads vs. off roads: Location does matter. Mastozoología Neotrop 21:37–46

DNP (2016) Practical Plan to Improve Tiger Population 2015-2035 (20 Years). Department of National Parks, Wildlife and Plant Conservation (DNP), Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

Duangchantrasiri S, Umponjan M, Simcharoen S, et al (2016) Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. Conserv Biol 30:639–648. https://doi.org/10.1111/cobi.12655

ESRI (2015) ArcGIS Desktop: Release 10.3.1. Environmental Systems Research Institute, Redlands, CA

Foley JA, DeFries R, Asner GP, et al (2005) Global consequences of land use. Science (80-) 309:570–574. https://doi.org/10.1126/science.1111772

GISTDA (2005) Thailand Roads. Geo-Informatics and Space Technology Development Agency (GISTDA), Bangkok

Goodrich JM, Lynam A, Miquelle DG, et al (2015) Panthera tigris. IUCN Red List Threat. Species 2015 e.T15955A50659951

Gray TNE, Crouthers R, Ramesh K, et al (2017) A framework for assessing readiness for tiger Panthera tigris reintroduction: a case study from eastern Cambodia. Biodivers Conserv 26:2383–2399. https://doi.org/10.1007/s10531-017-1365-1

Guberti V, Khomenko S, Masiulis M, Kerba S (2019) African Swine Fever in Wild Boar Ecology and Biosecurity. FAO Animal Production and Health Manual No. 22, FAO, OIE and EC, Rome

Harihar A, Chanchani P, Pariwakam M, et al (2017) Defensible Inference: Questioning Global Trends in Tiger Populations. Conserv Lett 10:502–505. https://doi.org/10.1111/conl.12406

Harihar A, Pandav B (2012) Influence of connectivity, wild prey and disturbance on occupancy of tigers in the human-dominated western Terai Arc landscape. PLoS One 7:e40105. https://doi.org/10.1371/journal.pone.0040105

Hayward MW, Jedrzejewski W, Jedrzewska B (2012) Prey preferences of the tiger Panthera tigris. J Zool 286:221–231. https://doi.org/10.1111/j.1469-7998.2011.00871.x

Hebblewhite M, Merrill E (2008) Modelling wildlife–human relationships for social species with mixed-effects resource selection models. J Appl Ecol 45:834–844. https://doi.org/10.1111/j.1365-2664.2008.01466.x

Hebblewhite M, Miquelle DG, Robinson H, et al (2014) Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. Biol Conserv 178:50–64. https://doi.org/10.1016/j.biocon.2014.07.013

Hebblewhite M, Zimmermann F, Li Z, et al (2012) Is there a future for Amur tigers in a restored tiger conservation landscape in Northeast China? Anim Conserv 15:579–592. https://doi.org/10.1111/j.1469-1795.2012.00552.x

Joshi AR, Dinerstein E, Wikramanayake E, et al (2016) Tracking changes and preventing loss in critical tiger habitat. Sci Adv 2:e1501675–e1501675. https://doi.org/10.1126/sciadv.1501675

Kanagaraj R, Wiegand T, Kramer-Schadt S, et al (2011) Assessing habitat suitability for tiger in the fragmented Terai Arc Landscape of India and Nepal. Ecography (Cop) 34:970–981. https://doi.org/10.1111/j.1600-0587.2010.06482.x

Karanth KU, Chundawat RS (2002) Ecology of the Tiger: Implications for Population Monitoring. In: Karanth KU, Nichols JD (eds) Monitoring tigers and their prey : a manual for researchers, managers, and conservationists in tropical Asia. Centre for Wildlife Studies, Bangalore, pp 9–22

Karanth KU, Gopalaswamy AM, Kumar NS, et al (2011) Monitoring carnivore populations at the landscape scale: Occupancy modelling of tigers from sign surveys. J Appl Ecol 48:1048–1056. https://doi.org/10.1111/j.1365-2664.2011.02002.x

Karanth KU, Miquelle D, Goodrich J, Gopalaswamy A (2016) Statement of Concern by Tiger Biologists. In: WCS Newsroom, 15 Apr 2016. https://newsroom.wcs.org/News-Releases/articleType/ArticleView/articleId/8872/Statement-of-Concern-by-Tiger-Biologists.aspx. Accessed 27 Mar 2021

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862. https://doi.org/10.2307/176521

Karanth KU, Nichols JD, Kumar NS, et al (2004) Tigers and their prey: Predicting carnivore densities from prey abundance. Proc Natl Acad Sci U S A 101:4854–4858. https://doi.org/10.1073/pnas.0306210101

Karanth KU, Stith BM (1999) Prey depletion as a critical determinant of tiger population viability. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 100–113

Karanth KU, Sunquist ME (1995) Prey Selection By Tiger, Leopard and Dhole in Tropical Forests. J Anim Ecol 64:439–450. https://doi.org/10.2307/5647

Kenney JS, Smith JLD, Starfield AM, McDougal CW (1995) The Long-Term Effects of Tiger Poaching on Population Viability. Conserv Biol 9:1127–1133. https://doi.org/10.1046/j.1523-1739.1995.9051116.x-i1

Kerley LI, Goodrich JM, Miquelle DG, et al (2002) Effects of Roads and Human Disturbance on Amur Tigers. Conserv Biol 16:97–108. https://doi.org/10.1046/j.1523-1739.2002.99290.x

Lesmerises F, Dussault C, St-Laurent M-H (2012) Wolf habitat selection is shaped by human activities in a highly managed boreal forest. For Ecol Manage 276:125–131. https://doi.org/https://doi.org/10.1016/j.foreco.2012.03.025

Linke J, McDermid GJ, Fortin M-J, Stenhouse GB (2013) Relationships between grizzly bears and human disturbances in a rapidly changing multi-use forest landscape. Biol Conserv 166:54–63. https://doi.org/10.1016/j.biocon.2013.06.012

Linkie M, Chapron G, Martyr DJ, et al (2006) Assessing the viability of tiger subpopulations in a fragmented landscape. J Appl Ecol 43:576–586. https://doi.org/10.1111/j.1365-2664.2006.01153.x

Lynam A, Nowell K (2011) Panthera tigris ssp. corbetti. IUCN Red List Threat. Species 2011 e.T136853A4346984

Lynam A, Round P, Brockelman W (2006) Status of Birds and Large Mammals in Thailand's Dong Phayayen - Khao Yai Forest Complex. Wildlife Conservation Society and Biodiversity Research Training (BRT) Programme, Bangkok

Martin J, Basille M, Van Moorter B, et al (2010) Coping with human disturbance: spatial and temporal tactics of the brown bear (Ursus arctos). Can J Zool 88:875–883. https://doi.org/10.1139/Z10-053

McGarigal K (2018) BIOSTATS. Department of Environmental Conservation, University of Massachusetts. v. 9 February 2018

Ngoprasert D, Lynam AJ, Gale GA (2007) Human disturbance affects habitat use and behaviour of Asiatic leopard Panthera pardus in Kaeng Krachan National Park, Thailand. Oryx 41:343–351. https://doi.org/10.1017/S0030605307001102

Ngoprasert D, Lynam AJ, Sukmasuang R, et al (2012) Occurrence of Three Felids across a Network of Protected Areas in Thailand: Prey, Intraguild, and Habitat Associations. Biotropica 44:810–817. https://doi.org/10.1111/j.1744-7429.2012.00878.x

Nowell K, Jackson P (1996) Wild Cats : Status Survey and Conservation Action Plan. IUCN/SSC Cat Specialist Group, International Union for the Conservation of Nature, Gland, Switzerland

O'Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim Conserv 6:131–139. https://doi.org/10.1017/S1367943003003172

Oksanen J, Blanchet FG, Friendly M, et al (2018) vegan: Community Ecology Package. Comprehensive R Archive Network (CRAN), Version 2.5-2

Petdee A (2000) Feeding habits of the tiger Panthera tigris (Linnaeus) in Huai Kha Khaeng Wildlife Sanctuary by fecal analysis. MSc Thesis, Kasetsart University, Bangkok, Thailand

Petrunenko Y, Montgomery RA, Seryodkin I V, et al (2016) Spatial variation in the density and vulnerability of preferred prey in the landscape shape patterns of Amur tiger habitat use. Oikos 125:66–75. https://doi.org/10.1111/oik.01803

Pisdamkam C, Prayurasiddhi T, Kanchanasaka B, et al (2010) Thailand Tiger Action Plan - 2010-2012. Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

Prommakul P (2003) Habitat utilization and prey of the tiger Panthera tigris (Linnaeus) in eastern ThungYai Naresuan Wildlife Sanctuary [Thai]. MSc Thesis. Kasetsart University, Bangkok

R Development Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing. v.3.4.2. Vienna

Rabinowitz A (1993) Estimating the Indochinese tiger (Panthera tigris corbetti) population in Thailand. Biol Conserv 65:213–217. https://doi.org/10.1016/0006-3207(93)90055-6

Rasphone A, Kéry M, Kamler JF, Macdonald DW (2019) Documenting the demise of tiger and leopard, and the status of other carnivores and prey, in Lao PDR's most prized protected area: Nam Et - Phou Louey. Glob Ecol Conserv 20:e00766. https://doi.org/10.1016/j.gecco.2019.e00766

Ripple WJ, Estes JA, Beschta RL, et al (2014) Status and ecological effects of the world's largest carnivores. Science (80-) 343:1241484. https://doi.org/10.1126/science.1241484

Royal Forestry Department (2000) Study of the Status and Database Design of Natural Resources in Khao Yai, Thap Lan, Pang Sida, and Ta Phraya National Parks [Thai]. Royal Forestry Department, Government of Thailand and Geo Asia Co. Ltd., Bangkok, Thailand

Sandom C, Dalby L, Fløjgaard C, et al (2013) Mammal predator and prey species richness are strongly linked at macroscales. Ecology 94:1112–1122. https://doi.org/10.1890/12-1342.1

Sandom CJ, Williams J, Burnham D, et al (2017) Deconstructed cat communities: Quantifying the threat to felids from prey defaunation. Divers Distrib 23:667–679. https://doi.org/10.1111/ddi.12558

Seimon TA, Miquelle DG, Chang TY, et al (2013) Canine distemper virus: an emerging disease in wild endangered Amur tigers (Panthera tigris altaica). MBio 4:e00410-13. https://doi.org/10.1128/mBio.00410-13

Steinmetz R, Chutipong W, Seuaturien N, et al (2010) Population recovery patterns of Southeast Asian ungulates after poaching. Biol Conserv 143:42–51. https://doi.org/10.1016/j.biocon.2009.08.023

Steinmetz R, Seuaturien N, Chutipong W (2013) Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. Biol Conserv 163:68–78. https://doi.org/10.1016/j.biocon.2012.12.016

Stokes D (2017) Thap Lan: Thailand's unsung forest gem under threat, but still abrim with life. In: Mongabay, 31 January 2017. https://news.mongabay.com/2017/01/thap-lan-thailands-unsung-forest-gem-under-threat-but-still-abrim-with-life/. Accessed 27 Mar 2021

Sunarto S, Kelly MJ, Parakkasi K, et al (2012) Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS One 7:e30859. https://doi.org/10.1371/journal.pone.0030859

Sunquist M (2010) What is a Tiger? Ecology and Behavior. In: Tilson R, Nyhus P (eds) Tigers of the World, Second Edition. Elsevier, New York, pp 19–34

Sunquist M, Karanth UK, Sunquist F (1999) Ecology, behaviour and resilience of the tiger and its conservation needs. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 5–18

Timm BC, McGarigal K, Cushman SA, Ganey JL (2016) Multi-scale Mexican spotted owl (Strix occidentalis lucida) nest/roost habitat selection in Arizona and a comparison with single-scale modeling results. Landsc Ecol 31:1209–1225. https://doi.org/10.1007/s10980-016-0371-0

UNESCO (2017) Dong Phayayen-Khao Yai Forest Complex. In: UNESCO World Herit. Cent. http://whc.unesco.org/en/list/590. Accessed 27 Nov 2017

Walston J, Robinson JG, Bennett EL, et al (2010) Bringing the tiger back from the brink-the six percent solution. PLoS Biol 8:6–9. https://doi.org/10.1371/journal.pbio.1000485

WCS, CIESIN (2005) Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic). Wildlife Conservation Society, Center for International Earth Science Information Network - Columbia University, NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY

Wolf C, Ripple WJ (2017) Range contractions of the world's large carnivores. R Soc Open Sci 4:170052. https://doi.org/10.1098/rsos.170052

WWF (2016a) Global wild tiger population increases, but still a long way to go. In: World Wildl. Fund, 10 Apr 2016. http://wwf.panda.org/wwf_news/?uNewsID=265197. Accessed 27 Mar 2021

WWF (2016b) WWF Response to Statement of Concern by Tiger Biologists. World Wildlife Fund for Nature

Supplementary Materials 1

Table 1 Cumulative detections and photographic capture rate index (PCRI; detections/100 CTN) for prey and humans in DPKY from 56,214 camera-trap nights.

		Number Stations Detected	**Detections (PCRI)**
Prey	Indochinese Tiger (*Panthera tigris*)	114 (22%)	1,166 (2.07)
	Banteng (*Bos javanicus*)	4 (<1%)	10 (0.02)
	Gaur (*Bos gaurus*)	199 (38%)	1,269 (2.26)
	Chinese Serow (*Capricornis milneedwardsii*)	33 (6%)	73 (0.13)
	Sambar (*Rusa unicolor*)	111 (21%)	4,378 (7.79)
	Northern Red Muntjac (*Muntiacus vaginalis*)	244 (47%)	1,770 (3.15)
	Wild Boar (*Sus scrofa*)	316 60%)	3,226 (5.74)
Humans	Domestic Dog	66 (13%)	211 (0.38)
	Human (Other)	511 (98%)	11,446 (20.36)
	Poacher	144 (28%)	646 (1.15)
	Ranger	168 (32%)	1,747 (3.11)
	Vehicle	85 (16%)	7,860 (13.98)

Table 2 Covariates prepared for both prey and human factors, including metrics, and data sources. Includes photographic capture rate index (PCRI; detections per 100 camera-trap nights) from camera-trap survey data.

	Variable	ID	Metric	Data Source
Prey	Gaur (*Bos gaurus*)	GAUR	PCRI	Ash et al. 2020
	Muntjac (*Muntiacus vaginalis*)	MUNTJAC	PCRI	Ash et al. 2020
	Sambar (*Rusa unicolor*)	SAMBAR	PCRI	Ash et al. 2020
	Wild Boar (*Sus scrofa*)	WBOAR	PCRI	Ash et al. 2020
	Prey Richness Banteng (*Bos javanicus*) Gaur (*Bos gaurus*) Muntjac (*Muntiacus vaginalis*) Sambar (*Rusa unicolor*) Serow (*Capricornis milneedwardsii*) Wild Boar (*Sus scrofa*)	PREY_RICH	Count of Species	Ash et al. 2020
Human	Distance to Park Substation	DIST_SS	Euclidean Distance	Derived from Royal Forestry Department 2000;ESRI 2015
	Distance to All Roads	DISTROAD_ALL	Euclidean Distance	Derived from Royal Forestry Department, 2000; GISTDA, 2005; 2018 Google, US Dept of State Geographer, Image; ESRI 2015 Landsat/Copernicus
	Distance to Public Roads (C1)	DISTROAD_C1	Euclidean Distance	
	Distance to Park Roads (C2)	DISTROAD_C2	Euclidean Distance	
	Domestic Dog	DOM_DOG	PCRI	Ash et al. 2020
	Human Influence Index	HII	HII	WCS and Center for International Earth Science Information Network - CIESIN - Columbia University 2005
	Human (Other) Monk Survey Team Tourist Unknown Vehicle Worker	HUMAN_OTHER	PCRI	Ash et al. 2020
	Poacher	POACHER	PCRI	Ash et al. 2020
	Ranger	RANGER	PCRI	Ash et al. 2020
	Settlement Density	Settlement Density	Kernel Density	Derived from 2018 Google, US Dept of State Geographer, Image Landsat/Copernicus; ESRI 2015
	Vehicle	VEHICLE	PCRI	Ash et al. 2020

Table 3 Proportion of relative and total variance explained among prey, human, and environmental (Env) covariates, and camera effort (Cam), including confounded (grouped) covariates.

	Relative Var. Explained	Total Var. Explained
Env+Human	31.1%	14.9%
Env	19.6%	9.4%
Env+Human+Prey+Cam	13.8%	6.6%
Env+Human+Prey	7.3%	3.5%
Prey+Cam	6.9%	3.3%
Cam	5.2%	2.5%
Env+Cam	4.0%	1.9%
Env+Human+Cam	4.0%	1.9%
Prey	3.1%	1.5%
Human	2.1%	1.0%
Env+Prey+Cam	1.9%	0.9%
Human+Cam	0.8%	0.4%
Human+Prey+Cam	0.2%	0.1%
Env+Prey	0.0%	0.0%
Human+Prey	0.0%	0.0%
Residuals	-	52.8%

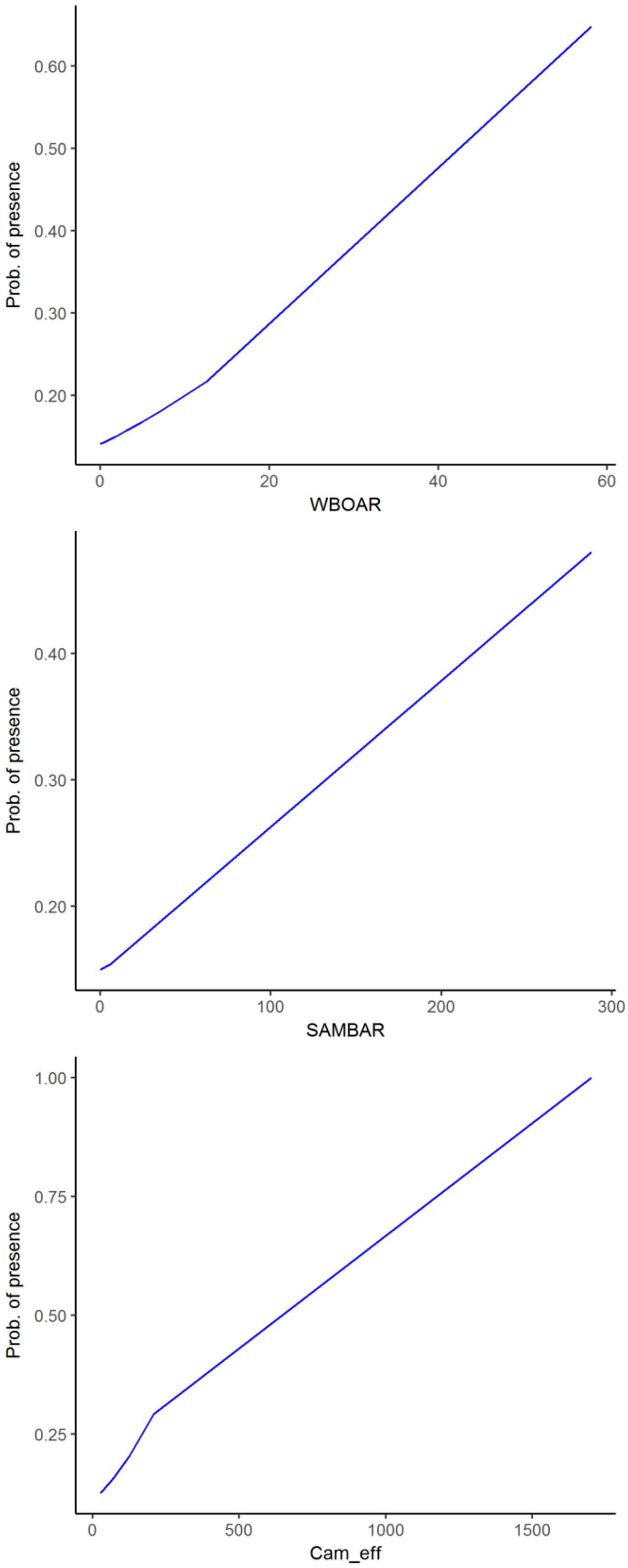

Fig. 1 Partial effects plots for prey covariates, showing changes in predicted probability of tiger presence when variable values increase from their 10th to 100th percentile, holding other variables at their medians.

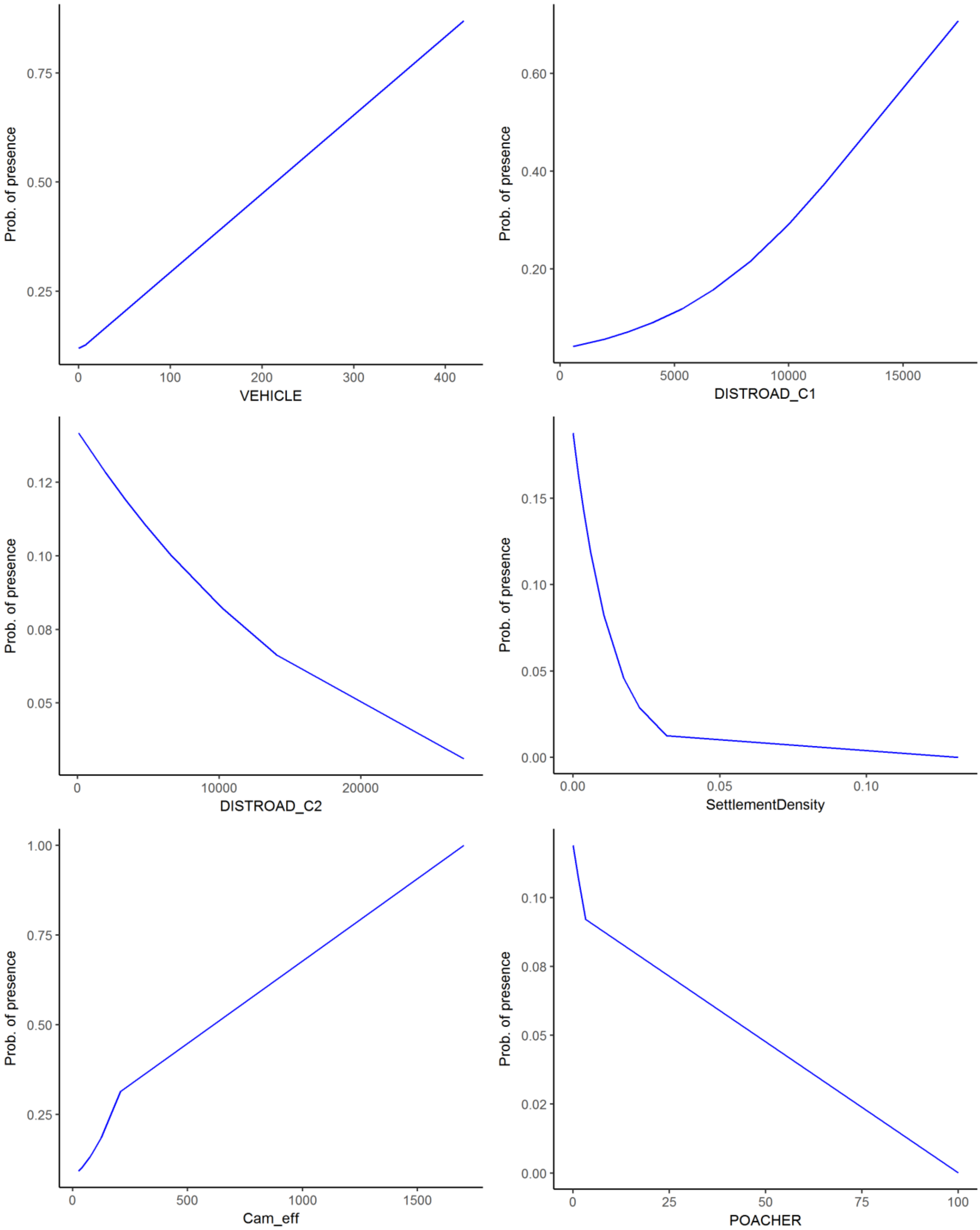

Fig. 2 Partial effects plots for human covariates, showing changes in predicted probability of tiger presence when variable values increase from their 10th to 100th percentile, holding other variables at their medians.

Supplementary Materials 2

1. Environmental Model Summary

The environmental model used in this study was derived from a multi-scale, shape-optimized (MSSO) model developed by Ash et al. (2021*; "Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: A case study of tigers (*Panthera tigris*)"*). This model was developed in the study to test the influence of spatial scale- and functional shape-optimization on the performance of habitat suitability models, in comparison to non-optimized models, and to discern the influence of spatial scale on habitat selection. This model utilizes the same camera trap-based data set (Ash et al. 2020) as described in the main text of our study which we used to develop prey and human variables. We summarize the development of this model here.

2. Method

2.1 Predictor variables

Environmental predictor variables were developed using class and landscape level spatial statistics in 30m resolution (Table 1). In total, 47 initial variables were developed. These included:

- Elevation - Derived from SRTM 1 (Shuttle Radar Topography Mission; Jarvis et al. 2008) and transformed via the Geomorphometry & Gradient Metrics Toolbox (Evans et al. 2014) in ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011):
    - Terrain roughness index (degree of elevation difference between adjacent cells)
    - Slope position (surface to area ratio)
    - Compound topographic index (CTI; flow accumulation [Beven and Kirkby 1979])
- Forest Cover – Derived from Hansen et al. (2013)
    - Non-forest (0-20%)
    - Open forest (20-40%)
    - Closed forest (>40%).
- Land Cover – Derived from global land cover map (European Space Agency 2015)
- Forest Type – Derived from Royal Forestry Department (2000)
- Streams/Rivers – Derived from Royal Forestry Department (2000).
- Protected Area Boundary – Derived from Royal Forestry Department (2000).

Variables were transformed into seven multi-scale predictor variables (250m, 500m, 1km, 2km, 4km, 8km, and 16km). Continuous variables were transformed via focal statistics (focal mean and standard deviation) in ArcGIS using a moving circular window with radius equal to each scale. Categorical variables were transformed via landscape metrics in FRAGSTATS (McGarigal et al. 2012) using moving windows for each spatial scale. Calculations included:

- Class-level statistics:
    - Area-weighted mean radius of gyration (GYR, also known as correlation length; mean potential travel distance within a habitat patch/extent)
    - Percentage of habitat within the focal landscape (PLAND).
- Landscape-level statistics:
    - Contrast-weighted edge density (CWED; degree of contrast between adjacent patches).
    - Patch density (PD; subdivision of habitat within the landscape/number of patches divided by area)
    - Aggregation index (AI; dispersion of habitat patches within the landscape).

2.2 Model development and evaluation

Development of the multi-scale, shape-optimized (MSSO) model focused on the selection of optimal spatial scale and optimal functional form (shape of relationship between variable and tiger presence as the response) among each variable. To do this, a univariate GLM was developed for seven spatial scales (250m, 500m, 1km, 2km, 4km, 8km, 16km) and five functional forms (linear, quadratic, logarithmic, exponential, and negative exponential) with optimal scale and shape selected by lowest AICc value.

Similar to the approach in our study, filtering of variables was conducted by requiring $p<0.05$ and selecting among correlated variables (Pearson's coefficient $|r|>0.6$) by lowest AICc value. This resulted in 17 variables (Table 2), which were then included with survey effort (CTN) in a multivariate GLM using the 'BIOSTATS' set of functions (McGarigal 2018) to subset best performing models, calculate goodness-of-fit statistics, and rank variable importance in the final model. For quadratic variables, both linear and quadratic terms were included as separate explanatory variables. The resulting fully averaged model was evaluated via sensitivity, specificity, percent correctly classified (PCC), Kappa, area under the ROC curve (AUC), and variable importance (AICc variable importance, standardized coefficients, and influence of each variable on probability of tiger presence from the 10^{th} to 100^{th} percentile).

Table 1 Variables included in univariate model selection, metrics, and data sources, derived from Ash et al. (2021). Landscape statistics include focal mean and standard deviation (SD). Landscape metrics include percentage of landscape (PLAND), area weighted mean of radius of gyration/correlation length (GYR), contrast-weighted edge density (CWED), patch density (PD), and aggregation index (AI).

Variable	ID	Metric	Data Source
Elevation	DEM	Focal mean & SD	Jarvis et al. (2008; http://srtm.csi.cgiar.org)
Protected area boundary	BOUND	Focal mean	Royal Forestry Department (2000)
Forest class: 1 - Non-forest (0-20%) 2- Open canopy (20-40%) 3- Closed canopy (>40%)	TC	PLAND & GYR	Reclassified from Hansen et al. (2013)
Forest type: 1 - Evergreen 2 - Mixed Deciduous 3 - Dry Dipterocarp 4 - Reforested Areas 5 - Bamboo Forest 6 - Secondary Forest/Old Clearing 7 - Grassland/Scrubland	FT	PLAND & GYR	Reclassified from Royal Forestry Department (2000)
Terrain Roughness Index (TRI)	TRI	Focal mean & SD	Derived from Jarvis et al. (2008; http://srtm.csi.cgiar.org) and Evans et al. (2014)
Slope position	SLOPE	Focal mean & SD	Derived from Jarvis et al. (2008; http://srtm.csi.cgiar.org) and Evans et al. (2014)
Streams/Rivers	STRC1	Focal mean	Reclassified from Royal Forestry Department (2000)
Compound topographic index (i.e., flow accumulation)	CTI	Focal mean & SD	Derived from Jarvis et al. (2008; http://srtm.csi.cgiar.org) and Evans et al. (2014)
Land cover classes: 1 - Cropland 2 - Mosaic cropland 3 – Forest/Natural vegetation 4 - Shrubland/grassland 5 - Sparse vegetation & bare areas 6 – Urban Areas 7 – Water	LC	PLAND, GYR, CWED, PD, AI	Reclassified from European Space Agency (2015; www.esa-landcover-cci.org/?q=node/175)

Table 2 Final variables included in the multi-scale and shape-optimized (MSSO) global model from an original 47 variables, derived from Ash et al. (2021). Optimal functional form (shape) of each variable indicated by: L-linear, Q-Quadratic, EXP-Exponential, LOG-Logarithmic.

Variable	Optimal Scale	Optimal Functional Form	ID
Correlation length of secondary forest	4000	L	FT6_GYR_4000_L
Percentage of shrubland/grassland	4000	L	LC4_PLAND_4000_L
Correlation length of mixed deciduous forest	8000	Q	FT2_GYR_8000_Q
Correlation length of reforested areas	8000	Q	FT4_GYR_8000_Q
Correlation length of grassland	8000	Q	FT7_GYR_8000_Q
Correlation length of mosaic cropland	8000	Q	LC2_GYR_8000_Q
Correlation length of water	8000	Q	LC7_GYR_8000_Q
Correlation length of open forest	8000	LOG	TC2_GYR_8000_LOG
Focal mean of park boundary	16000	L	BOUND_FM_16000_L
Standard deviation of Compound Topographic Index (CTI)	16000	Q	CTI_SD_16000_Q
Standard deviation of Digital Elevation Model (DEM)	16000	Q	DEM_SD_16000_Q
Percentage of bamboo forest	16000	Q	FT5_PLAND_16000_Q
Percentage of secondary forest	16000	LOG	FT6_PLAND_16000_LOG
Correlation length of urban areas	16000	L	LC6_GYR_16000_L
Focal mean of slope position	16000	Q	SLOPE_FM_16000_Q
Percentage of open forest	16000	L	TC2_PLAND_16000_L
Focal mean of Terrain Roughness Index (TRI)	16000	Q	TRI_FM_16000_Q
Camera effort	-	-	Cam_eff

Table 3 Fully averaged model results for the environmental model (Ash et al. 2021) including standardized regression coefficients (β), standard error (SE), adjusted standard error (Adjusted SE), z-value (*z*), significance (*p*), AIC variable importance (AIC Var. Imp), change in probability with increasing variable values from 10th to 100th percentile (Δprob), optimal scale, and optimal functional form (^{L} linear, ^{Q} Quadratic, ^{LOG} Logarithmic). This is included as Table 2c in the main text.

Variable	β	Adjusted SE	*z*	*p*	AIC Var. Imp	Δprob
(Intercept)	-1.367	0.314	4.352	<0.001	-	-
% Secondary Forest (16km) ^{LOG}	-0.777	0.210	3.702	<0.001	2	-0.23
Correlation length Secondary Forest (4km) ^{L}	-0.701	0.235	2.978	0.003	3	-0.13
Camera effort (# trap nights)	1.460	0.309	4.718	<0.001	3	0.92
% Bamboo (16km) ^{L}	1.028	0.525	1.960	0.050	2	0.55
DEM Standard Deviation (16km) ^{L}	0.995	0.308	3.226	0.001	1	0.13
% Bamboo (16km) ^{Q}	-0.072	0.232	0.309	0.757	2	0.55
DEM Standard Deviation (16km) ^{Q}	-0.866	0.336	2.575	0.010	1	0.13
Focal mean of terrain roughness index (16km) ^{L}	1.165	0.502	2.317	0.020	2	0.13
Focal mean of terrain roughness index (16km) ^{Q}	-1.671	0.579	2.887	0.004	2	0.13
% Open forest (16km) ^{L}	-2.353	0.457	5.149	<0.001	1	-0.58
Correlation length of reforested areas (8km) ^{L}	0.968	0.321	3.011	0.003	1	0.17
Correlation length of reforested areas (8km) ^{Q}	-0.555	0.195	2.844	0.004	1	0.17

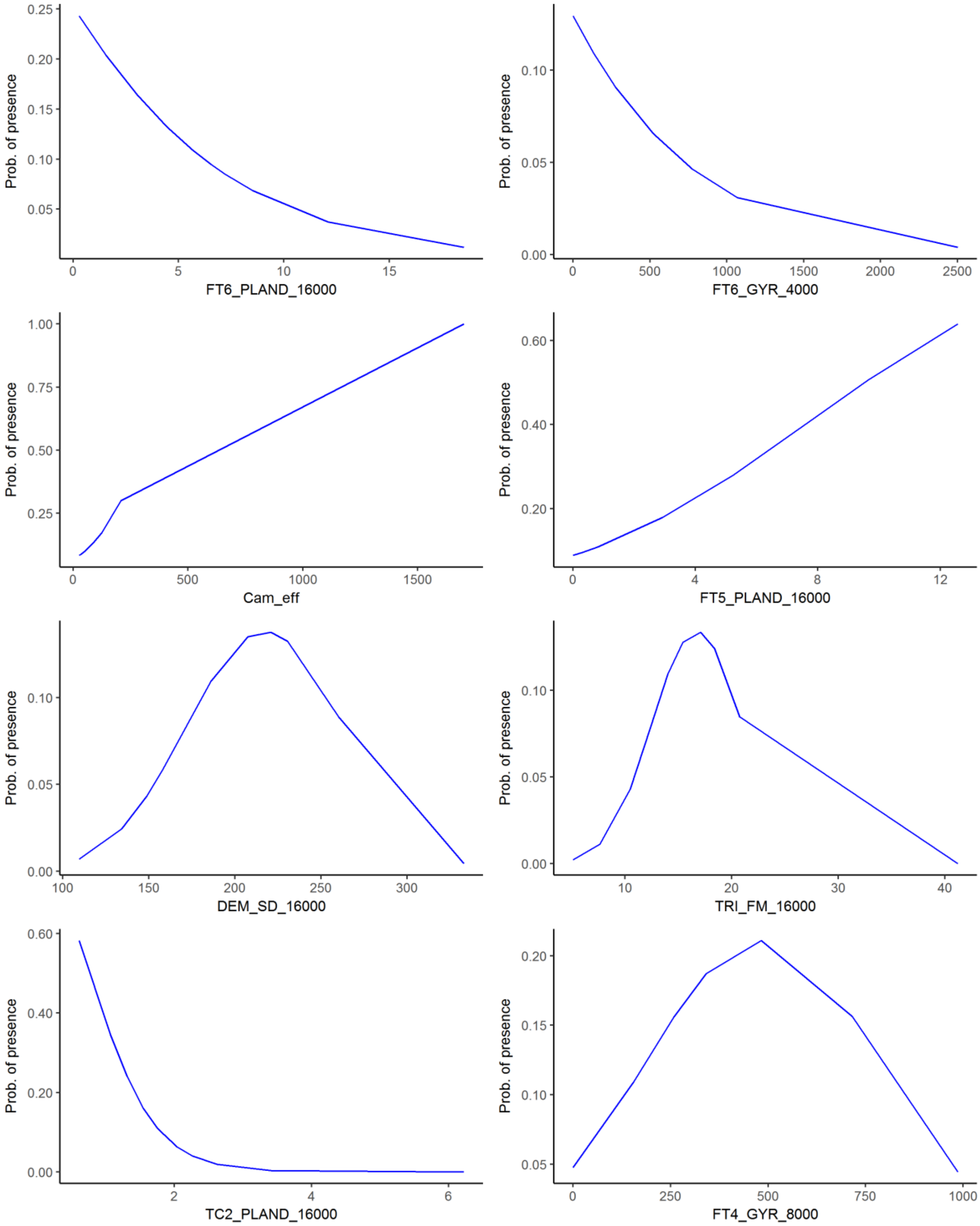

Fig. 1 Partial effects plots for the multi-scale and shape-optimized (MSSO) model from (Ash et al. 2021) showing changes in predicted probability of tiger presence when variables increase from 10th to 100th percentiles, holding other variables at their medians. Variables include: percentage secondary forest within 16km (log; FT6_PLAND_16000), correlation length of secondary forest within 4km (linear; FT6_GYR_4000), survey effort (Cam_eff), percentage of bamboo within 16km (linear/quadratic, FT5_PLAND_16000), standard deviation of elevation within 16km (linear/quadratic, DEM_SD_16000), focal mean of terrain roughness index within 16km (linear/quadratic, TRI_FM_16000), percentage of open forest within 16km (linear, TC2_PLAND_16000), and correlation length of reforested areas within 8km (linear/quadratic, FT4_GYR_8000). Graphic generated in R (R Development Core Team 2017).

References

Ash E, Kaszta Ż, Noochdumrong A, et al (2020) Opportunity for Thailand's Forgotten Tigers: Assessment of Indochinese tiger Panthera tigris corbetti and prey from camera-trap surveys in Eastern Thailand. Oryx 55:204–211. https://doi.org/10.1017/S0030605319000589

Ash E, Macdonald DW, Cushman SA, et al (2021) Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: A case study of tigers (Panthera tigris) in Thailand. Landsc Ecol 36:455–474. https://doi.org/10.1007/s10980-020-01105-6

Beven KJ, Kirkby MJ (1979) A physically based, variable contributing area model of basin hydrology. Hydrol Sci Bull 24:43–69. https://doi.org/10.1080/02626667909491834

ESRI (2015) ArcGIS Desktop: Release 10.3.1. Environmental Systems Research Institute, Redlands, CA

European Space Agency (2015) 300 m annual global land cover time series from 1992 to 2015. Climate Change Initiative (CCI), European Space Agency (ESA)

Evans JS, Cushman SA, Theobald D (2014) An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, version 2.0-0.

GISTDA (2005) Thailand Roads. Geo-Informatics and Space Technology Development Agency (GISTDA), Bangkok

Hansen MC, Potapov P V., Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science (80-) 342:850–853. https://doi.org/10.1126/science.1244693

Jarvis A, Reuter HI, Nelson A, Guevara E (2008) Hole-filled seamless SRTM data V4. In: Int. Cent. Trop. Agric. http://srtm.csi.cgiar.org

McGarigal K (2018) BIOSTATS. Department of Environmental Conservation, University of Massachusetts. v. 9 February 2018

McGarigal K, Cushman S, Neel MC, Ene E (2012) FRAGSTATS: Spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst.

R Development Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing. v.3.4.2. Vienna

Royal Forestry Department (2000) Study of the Status and Database Design of Natural Resources in Khao Yai, Thap Lan, Pang Sida, and Ta Phraya National Parks [Thai]. Royal Forestry Department, Government of Thailand and Geo Asia Co. Ltd., Bangkok, Thailand

WCS, CIESIN (2005) Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic). Wildlife Conservation Society, Center for International Earth Science Information Network - Columbia University, NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY

Chapter 5

Estimating the density of a globally important tiger (*Panthera tigris*) population: Using simulations to evaluate survey design in Eastern Thailand

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Title

Estimating the density of a globally important tiger (*Panthera tigris*) population: Using simulations to evaluate survey design in Eastern Thailand

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Abstract

Spatially explicit capture-recapture analysis is widely utilized for estimating densities of tigers (*Panthera tigris*). However, developing a robust study design capable of meeting assumptions and achieving study objectives may be difficult, particularly for low-density populations. Study design decisions for such fieldwork can be aided by simulations. Our goal was to (1) use simulations to investigate and evaluate study design and (2) generate a reliable estimate of density for a population of tigers in Thailand's Dong Phayayen-Khao Yai forest complex. Scenarios were parameterized with a range of potential density estimates ($\hat{D}$) and detection function parameters ($g0$ and σ). We designed a field-based trap configuration and compared it with simulated performance of a regular trapping array, over 45-day and 60-day sampling occasions. We compared simulation results (i.e., number of individuals [*n*], detections [*ndet*], relative standard error [*RSE*] and relative bias [*RB*]) and identified that the non-regular trapping array deployed for 60 sampling days would generate reliable density estimates. Our survey produced a density estimate of 0.63 ± SE0.22; (0.32–1.21) tigers per 100 km^2, from a model incorporating variation in sex for *g0* and σ, and a population estimate of 20 (14–33). Simulations closely reflected actual results under the null model. Our survey design performed reasonably well, generating a sufficient number of detections and individuals to estimate density of a globally important tiger population. Our results suggest simulations and use of non-regular trap arrays may be beneficial for areas with low species density in which generating sufficient detections is particularly challenging.

Keywords *Panthera tigris;* spatially-explicit capture-recapture; simulations; Dong Phayayen-Khao Yai Forest Complex; population density; Thailand

Highlights

- Tiger density in Dong Phayayen-Khao Yai (DPKY) was 0.63 (0.32-1.21) tigers/100km^2
- The estimated population for the study area was 20 (14-33) individuals.
- We used simulations to validate a non-regular survey design prior to deployment.
- Simulations may be beneficial for designing density surveys for low-density species
- Breeding in DPKY reinforces the global importance of this tiger population

1. Introduction

Management of threatened species populations requires regular and robust monitoring to assess their status and evaluate the efficacy of conservation interventions (Karanth et al. 2017). Capture-recapture analyses are widely used population assessment methods that estimate state variables such as population size and vital parameters like survival, immigration, growth rates (Karanth et al. 2006; Harmsen et al. 2017) and are thus, preferred to understand population dynamics and evaluate conservation actions (Duangchantrasiri et al. 2016). Camera-traps, as passive detectors, have become a popular tool to non-invasively identify individuals from photo-captures (Karanth and Nichols 1998), a method particularly useful to study large felids such as tigers (*Panthera tigris;* Karanth et al. 2006). More recently, this approach, combined with a spatially explicit capture-recapture (SECR) framework (Efford 2004; Royle et al. 2014), is now a widely accepted method of estimating tiger densities and is used as a metric to monitor population change over time (Karanth et al. 2017; Royle et al. 2017).

Conducting capture-recapture surveys for large carnivores that are elusive and range over large areas of, what is often, difficult and remote terrain, can be challenging (Karanth and Nichols 2010). In order to reliably estimate population parameters, study designs must generate a sufficient sample of detections in a short enough time period to meet the assumption of population closure. However, for low-density populations, achieving a sufficient sample size can be difficult (White et al. 1982; Karanth and Nichols 1998), with low numbers of detections leading to a broad range of error and potentially limiting its utility as a reliable monitoring tool. Furthermore, surveys must also have a sufficient spatial extent to ensure presence of an individual and detection probability greater than zero. Such survey designs can be notably time and resource intensive (Karanth et al. 2017) and spatial arrangements of detectors can significantly influence the reliability of survey results (Royle et al. 2014). A review of jaguar (*P. onca*) density estimates highlighted that a majority of studies did not meet requirements necessary to produce unbiased estimates (Tobler and Powell 2013); in particular, reliability of estimates were undermined by sampling design and survey effort that were unsuitable for the target species, which occur at low densities. In light of these challenges, researchers must take great care in developing a robust survey design capable of meeting assumptions and achieving study objectives while ensuring resources are sufficient to carry out the survey effectively (Foster and Harmsen 2012). Such decision-making can be aided by simulations, where previous survey data can be used to determine which spatial arrangement of detectors can generate reliable estimates of population parameters (Obbard et al. 2010; Tobler and Powell 2013).

In this study, we (1) use simulations to investigate trap layout and evaluate study design prior to survey deployment, and (2) generate a reliable estimate of density for a population of tigers in the Dong Phayayen-Khao Yai (DPKY) forest complex in Eastern Thailand. Camera-trap surveys, following a primarily opportunistic study design, have been in place in this landscape since 2008 (Ash et al. 2020). However, sampling has been highly variable in terms of spatial and temporal regularity, precluding the use of capture-recapture analysis. Drawing on past data sources for parameter estimates (Ash et al. 2020; DNP et al. 2014, *unpublished*), we use simulations to assess the suitability of different trap arrays and survey lengths to develop a robust study design and, in turn, generate a reliable density estimate for this population. DPKY's conservation importance (Pisdamkam et al. 2010; Ash et al. 2020) necessitates reliable indicators of population status such as population density. Through this study, we present an estimate of tiger density in DPKY and evaluate simulations as a tool for developing effective SECR designs to reliably estimate low-density tiger populations.

2. Materials and methods

2.1 Study site

Recent reports confirm the presence of a small, but critical Indochinese tiger population (*P. t. corbetti* under current taxonomic designations in the IUCN Red List; Goodrich et al. 2015) within Thailand's DPKY forest complex, an area for which more information is required (Pisdamkam et al. 2010; Ash et al. 2020). This study was conducted in the Thap Lan-Pang Sida Tiger Conservation Landscape (TCL) of DPKY. This TCL spans 4,445km^2 and is expected to have sufficient habitat to support ~50 adult tigers (Sanderson et al. 2006). Camera-trap surveys across the TCL have detected ~17 adult tigers from 2008 to 2017, with most individuals detected within Thap Lan National Park (TLNP) and Pang Sida National Park (PSNP; Ash et al. 2020). These results have merited additional investigation to estimate population density, particularly in areas of suspected importance for tigers in this landscape. For the purpose of this study, we define our spatial sampling frame as a 567km^2 area of south-central TLNP and northern PSNP (Fig. 1).

2.2 Collating existing information to identify ideal camera-trapping locations

In order to identify suitable camera-trapping locations, we collated geographic location data from previous photographic captures of tigers within our sampling frame. We then reviewed ranger-based patrol data of tiger signs from at least 1,120 patrol man days, covering 1,307km^2 (58.46%) of TLNP, and tiger survey records from 2008 to 2015. From this, we collated geographic records on tiger and prey signs (e.g., tracks, faecal deposits, and territorial markings). Given that tigers are known to use topographic features such as ridgelines, valley bottoms, river beds and forest paths (Karanth 1995; Karanth and Nichols 1998), we also identified potential trap locations using topographic maps of the study area.

We identified 90 prospective trap locations for our survey. These were prioritized by locations where tigers were previously detected on camera-traps, followed by locations with records of tiger and prey sign. These locations covered approximately 306km^2 of our survey area, leaving a few notable gaps, one as large as 135km^2. To fill these survey gaps, we identified prominent topographic features such as ridgelines, valleys, and riverbeds for camera placement.

Given that estimated home range size of tigers, from elsewhere in Thailand, was assessed to be 70–84km^2 for females and 267–294km^2 for males (Simcharoen et al. 2014), it is safe to assume these trap locations ensured spatial coverage of the 567km^2 sampling frame that had no gaps that were sufficiently large to contain a tiger's movements during the sampling period and within which resident tigers had a capture probability greater than zero.

2.3 Simulating trapping data to evaluate survey design

Prior to conducting the survey, we evaluated our survey design to ensure that sampling would result in estimates of population density ($\hat{D}$) with low error and bias (i.e., relative standard error [RSE; equivalent to coefficient of variation] and relative bias [RB] respectively). If the estimated relative bias produced by our survey design was greater than a mean of 10% (Efford and Fewster 2012) or significantly different from that estimated from a trapping array of regular spacing (e.g., O'Brien and Kinnaird 2011; Borah et al. 2014; Brassine and Parker 2015), given the constraints of sampling (i.e., maximum of 90 trap locations), it would necessitate us to alter our trapping locations to minimize the bias. To generate this comparison, we simulated a regular trapping array of 75 trap locations within the sampling frame (Fig. 2a). Simulations were carried out in March and April 2016.

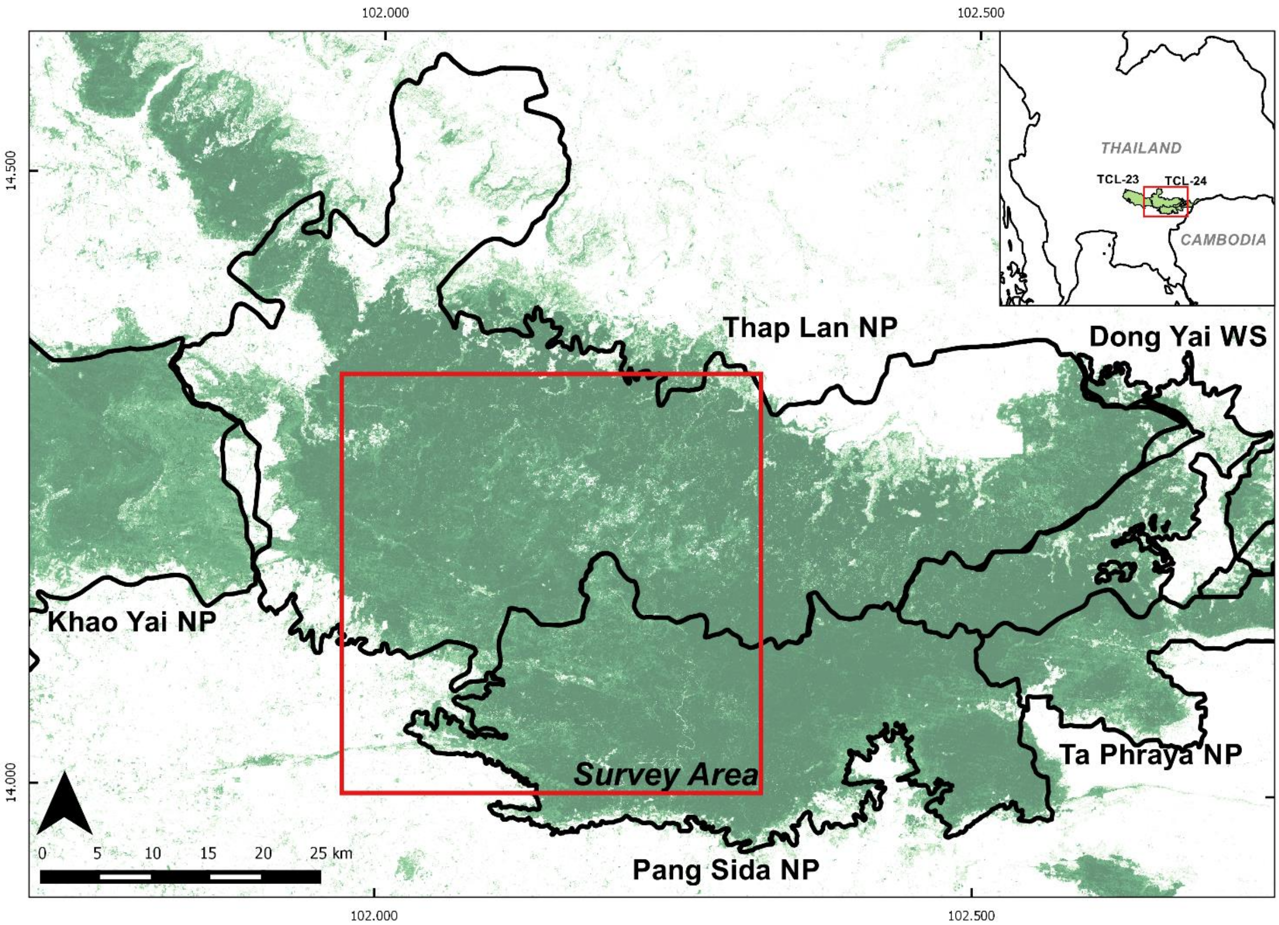

Fig. 1 The Dong Phayayen-Khao Yai forest complex (DPKY) and the survey area (square) for estimating tiger population density. Forest cover derived from Hansen et al. (2013).

As there had been no prior tiger population density surveys conducted within our sampling frame, no site-specific estimates of density were available to carry out the simulation. Although Ngoprasert and Gale (2019) conducted a survey in the region, the estimated density was derived from by-catch tiger data using baited trap stations. Hence, estimates of parameters required to simulate data were borrowed from a 2013 study conducted across 457km^2 of PSNP, south of our sampling frame (DNP et al. 2014, *unpublished*). This previous study provided data from a trap array of 26 trapping locations placed at a mean inter-trap distance of 3.35km. The density of tigers estimated during the study was 0.34 (± SE 0.17) individuals/100km^2 and the half-normal detection function was defined by an intercept (*g0*) of 0.034 (± SE 0.015) and spatial scale parameter (σ) of 9,623 (± SE 2425) meters. Although existing data suggest that more tigers inhabit TLNP in comparison to PSNP (Ash et al. 2020), and that tiger densities could be higher within our sampling frame, we simulated data using estimates of the mean, ± 1 and ± 2 SE for each of the parameters ($\hat{D}$, *g0* and σ) in the PSNP study to evaluate our survey design. Next, to satisfy the assumption of temporal closure in generating a population density estimate (Karanth and Nichols 2002, 2017), all scenarios were evaluated with 45- and 60-day sampling occasions in our simulations.

To evaluate the survey design, all simulations were carried out using the R package *'secrdesign'* (Efford 2017) within R v3.4.2 First, we generated a habitat mask around the spatial sampling frame with a buffer distance of 60km (i.e., around the recommended 4× the maximum simulated σ of 14,500m; Efford 2017). The mask was created to represent the available habitat within DPKY for the specified buffer distance. We then created scenarios that accounted for a range of five values (mean and ± 1 and ± 2 SE) for each of *g0* and σ (in all permutations and combinations) simulated for two sampling durations (45 and 60 days) and two trapping arrays (proposed and regular). This resulted in the creation of 500 unique scenarios for which we also generated 500 spatial capture-recapture datasets (or replicates) each. The simulated datasets were generated assuming a uniform (homogeneous) Poisson distribution. From these data, we summarized the simulated number of individuals (*n*) and captures (*ndet*). We then fit spatially explicit capture-recapture models for each of the datasets using the half-normal detection function. Given that several of our scenarios simulated small datasets (low *n* and *ndet*), we used the 'validate' function in the '*secrdesign*' package (Efford 2017) to remove estimates when a simulation failed. Finally, from the fitted models, we summarized the estimated population density across the replicates and assessed the RSE and RB of each of the scenarios.

2.4 Surveying for tigers and estimating population density

An examination of the RB from the simulations highlighted that our proposed trapping array performed comparably to the regular trapping array across the scenarios (see results and Appendix A for further details). Hence, camera trap placement on-site followed the proposed trap array without modifications. Seven teams, with an average team strength of nine personnel from both DNP and Freeland, were tasked with deploying the cameras at the 88 identified locations.

Cameras were placed at the predetermined trap locations based on previous camera-trap detections, tiger and prey sign, and topographic features likely to be used as travel routes for resident tigers in order to maximize detection probabilities. Paired stations, using two cameras, were used in order to photograph both flanks of a tiger passing in front of cameras. Cameras were placed approximately 50 cm above the ground and 1–2 m from the center of the trail. Areas in front of cameras were cleared of vegetation that may induce false triggers. All cameras were placed in protective housing to prevent theft or damage. Camera models included PantheraCam (white incandescent flash; V5, Panthera, New York,), Bushnell (infrared flash; Bushnell Corporation, Overland Park, USA) and Moultrie (incandescent flash; Moultrie Feeders, Birmingham, USA) trail cameras. Cameras were programmed to be active for 24-h with photos triggered at the shortest interval (1 to 15 s between photos) in order to minimize the potential for non-detection. Sampling was conducted from June 1st to August 16th, 2016. All cameras were checked at least once prior to their removal in August 2016.

Individual tigers and their sex were identified from their unique stripe patterns based on visual comparisons (confirmed by at least two authors). These unique tiger identities were then used to generate individual capture histories. For the purposes of analysis, we considered each day (24-h period) to be an individual sampling occasion. The capture histories specifically indexed the location (trap identity) and daily sampling occasions of each individual capture. Multiple captures of the same individual at the same location on a single sampling occasion were discarded. Given low capture rates and non-independence in captures of cubs, all analyses only pertained to individuals > 1 year of age.

Spatially explicit population density ($\hat{D}$), was estimated using a maximum likelihood-based inference implemented in the R package '*secr*' (Efford 2015). For the analysis, a state-space of 3400km^2 was created to represent the available habitat within DPKY at a buffer distance of 25km. This corresponded to 4 × σ of ~6,000m (Maffei and Noss 2008; Efford 2017) following the recommendation of the 'suggest buffer' function and rounding up from the 4,750m sigma from simulation results. Through our analysis, we accounted for sex-specific variability in the two detection parameters *g0* and σ. We constructed four candidate models that held parameters as either constant (.) or varying by sex. Models were ranked based on their Akaike's

Information Criterion (AIC; Akaike 1974) value and parameters of interest were derived from the most parsimonious model, as ranked by AIC. In addition, we also estimated spatially explicit population density ($\hat{D}$) using a Bayesian inference implemented in the R package '*SPACECAP*' (Gopalaswamy et al. 2012). We then compared the results of the survey (null model estimates from both a maximum likelihood and Bayesian inference) to simulated output for our trapping array and a regular trapping array (Table 2).

3. Results

3.1 Selecting camera-trapping locations

By collating photo-capture records of tigers from previous camera-trapping in the region, tiger and prey sign data from reconnaissance surveys and law enforcement patrols, and selecting prospective trap locations based on topographic features, we listed 102 potential trap locations. Given that we had sufficient cameras to sample at 88 locations, we chose 45 locations where tigers had been detected previously, 16 locations where tiger or prey sign were previously recorded, and 27 locations based on prominent topographic or local features (primarily selected to fill 'holes' in the trapping array; Fig. 2b).

3.2 Evaluating the survey design

Given that we were expecting tigers to occur at low densities, it was critical for us to first evaluate the performance of our trap array against a range of potential tiger densities. Our evaluation was primarily based on assessing the RSE and RB of the estimates of population density. We structured our comparisons to assess the performance of the irregular trapping design against a regular trap array. Karanth et al. (2017) recommend a short survey length (< 45 days) to ensure population closure, though longer durations have been used (Rayan and Linkie 2015). Given our population was likely at very low densities, we elected to test a 45-day and a slightly longer 60-day sampling duration to account for low detections. We present the results of our evaluation separately for 45- and 60-day sampling durations (see Supplementary Materials).

From our simulation of 250,000 datasets (500 scenarios ∗ 500 datasets each) the minimum number of individuals (n) detected ranged from 1 (± SE 0.09) to 77 (± SE 0.77). The lowest n (1) was simulated in the *a*

b

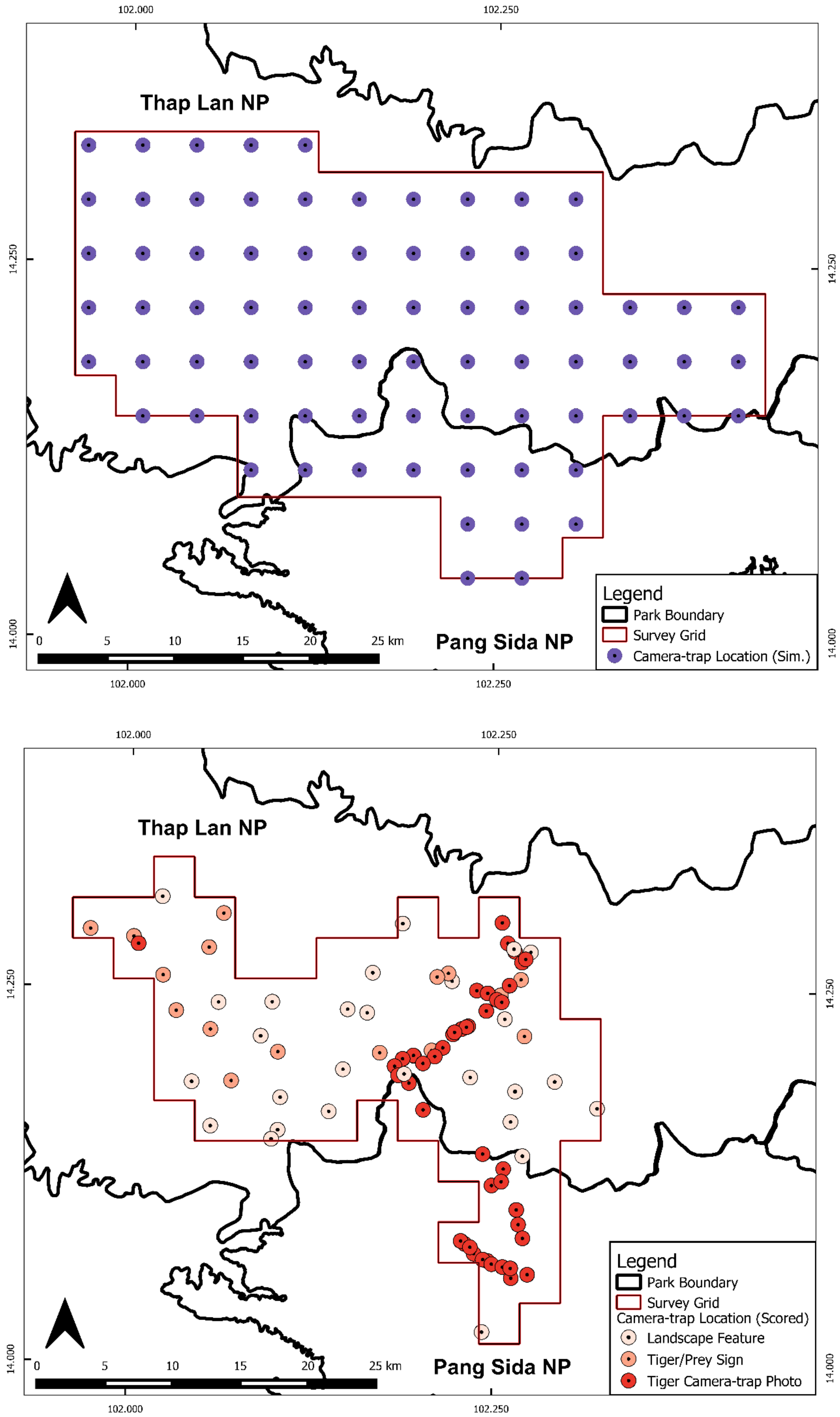

Fig. 2. (a) Survey grid and locations of camera-traps simulated in a regular array.; (b) Survey grid (3km × 3km) and locations of camera-traps (n = 88) for our trap array. Cameras were placed from June to August 2016. Locations were determined from previous tiger camera-trap detection (n = 45; darkest shade), previous record of tiger/prey sign (n = 16; medium shade), and landscape features (n = 27; lightest shade).

scenario where our trapping array sampled the site for 45 days when $\hat{D}$ was 0.1 individuals/100km^2, *g0* was 0.003 and σ was 4,750m. The highest *n* (77) was simulated in the scenario where the regular array sampled the site for 60 days when $\hat{D}$ was 0.7 individuals/100km^2, *g0* was 0.066 and σ was 14,500m. In general, simulated *n* from the regular array versus our trap array varied significantly (i.e., non-overlapping 95% CIs), with our trap array consistently detecting fewer *n* (Figs. A.1 & A.2). Irrespective of the simulated $\hat{D}$, *n* increased as σ and *g0* increased (Figs. A.1 & A.2).

In examining the number of independent detections (*ndet*), we observed a similar pattern as with *n*, where, irrespective of the simulated $\hat{D}$, *ndet* increased as σ and g_0 increased (Fig. A.3 & A.4). The minimum *ndet* of 1.6 (± SE 0.15) was produced when our trapping array sampled the site for 45 days when $\hat{D}$ was 0.1 individuals/100km^2, *g0* was 0.003 and σ was 4,750m. The highest *ndet* of 1,472.9 (± SE 19.72) was achieved where the regular array sampled the site for 60 days when $\hat{D}$ was 0.7 individuals/100km^2, *g0* was 0.066 and σ was 14,500m. Simulated *ndet* from the regular array versus our trap array varied, but the differences were less distinct in comparison to *n* (Figs. A.3 & A.4).

We fit spatially-explicit capture-recapture models to these simulated datasets. In general, we had a slightly greater rate of simulation failure when simulations were run for 45 (~22.8% failure in simulations) instead of 60 days (21.2%), irrespective of the trapping array. However, it is critical to note that these simulation failures occurred when $\hat{D}$ was low (either 0.1 or 0.2 individuals/100km^2) and σ was small (either 7,200m or 4,750m), irrespective of the simulated *g0*, sampling duration, or trap array (Figs. A.5 & A.6). Based on these results, we decided to employ a 60-day sampling duration for our survey of tigers in DPKY in 2016.
From our simulations, we noticed there was a high degree of variation in the RSE. The highest RSE from our simulations was 77.6% for a scenario when our trapping array sampled the site for 60 days when $\hat{D}$ was 0.2 individuals/100km^2, *g0* was 0.003 and σ was 12,000m. The lowest RSE from our simulations was 12.6% where the regular trapping array sampled the site for 60 days when $\hat{D}$ was 0.7 individuals/ 100km^2, *g0* was 0.066 and σ was 14,500m. Although RSE was lower with an increase in $\hat{D}$, RSE from the regular array versus our trap array varied significantly (i.e., non-overlapping 95% CIs), with our trap array consistently resulting in higher RSE (Figs. A.5 & A.6).

Table 1 Estimates of density ($\hat{D}$) and related parameters for four models, including lower (LCI) and upper (UCI) confidence interval values. For models where sex was included as a covariate, values are distinguished between males (m) and females (f).

Model	ΔAIC	$\hat{D}$	LCI	UCI	Pop	Pop(LCI)	Pop(UCI)	g_0 null	σ null	g_0 f	g_0 m	σ f	σ m
g_0SEX,sigmaSEX	0	0.63	0.32	1.21	19.92	13.88	33.46	-	-	0.043	0.017	2905.05	6117.84
F	-	0.42	0.18	0.97	-	-	-	-	-	-	-	-	-
M	-	0.21	0.08	0.53	-	-	-	-	-	-	-	-	-
sigmaSEX	8	0.62	0.32	1.19	19.49	13.64	32.71	0.0271	-	-	-	3305.18	5482.01
Null	25	0.54	0.28	1.02	15.75	11.59	26.60	0.0235	4850.74	-	-	-	-
g_0SEX	27	0.53	0.28	1.02	15.74	11.58	26.60	-	4851.64	0.0236	0.0234	-	-

Despite significant variation in RSE between the two trapping arrays, the RB was comparable across all scenarios (Figs. A.7 & A.8). The RB varied from 0.002% (± SE 1.83) in a scenario where our trapping array sampled the site for 45 days when $\hat{D}$ was 0.5 individuals/ 100km^2, *g0* was 0.066 and σ was 12,000m to 35.5% (± SE 16.43) where our trapping array sampled the site for 60 days when $\hat{D}$ was 0.1 individuals/100km^2, *g0* was 0.019 and σ was 9,750m. In general, RB was low when $\hat{D}$ was higher (Figs. A.7 & A.8).

Although the simulations indicated that our trapping array would result in fewer *n* and higher RSE compared to a regular trap array, RB produced from the model fits were similar for both trapping arrays. Given that we expected our sampling frame to support a higher tiger density than PSNP (from where we derived the simulation parameters), it was safe to assume that we would be able to accumulate a sufficient number of captures and recaptures to estimate $\hat{D}$ with low RB (<10%; Efford and Fewster 2012). These results indicated that our trapping array was valid and likely to generate a reliable density estimate. We proceeded to implement our trapping array unaltered and planned for a 60-day survey deployment.

3.3 Estimating tiger population density

Our field sampling effort with 88 camera stations for 61 days resulted in a trap effort of 4,793 trap nights (out of a potential 5,280 trap nights). This shortfall was due to camera theft, damage, and displacement by elephants/poachers, camera failure, battery depletion, and other factors. Through the sampling period we documented 108 independent detections of tigers from 338 photographs. However,

Table 2 Survey results and resulting secr and SPACECAP estimates from the null model in comparison with simulated results for our and regular trap arrays.

	Survey Results		Simulated Results	
	Maximum likelihood inference (secr)	**Bayesian inference (SPACECAP)**	**Our Trap Array**	**Regular Trap Array**
Mt+1	9		9 (8-9)	12 (11-13)
Ndet	107		63 (58-68)	59 (56-63)
$\hat{D}$	0.54 (0.28 – 1.02)	0.56 (0.34 - 0.78)	0.5	0.5
g_0	0.0235 (0.018-0.031)	0.0231 (0.0167-0.0293)	0.019	0.019
σ	4850.74 (4258-5526)	4894.08 (4304.63-5545.09)	4750	4750
RSE	-	-	37 (34-40)	30 (29-32)
RB	-	-	6 (-7 - 18)	7 (-2 - 16)

there was one detection where the tiger could not be reliably identified, which was dropped from analysis. The remaining 107 detections were included in the analysis, obtained from 38 trap locations. Of these successful trap sites, 69% were obtained from trap locations where tigers had previously been photographed, 8% from locations based on previous tiger or prey sign, and 23% where trap locations were chosen based on prominent topographic or local features. From these images, we identified 9 adult tigers, consisting of 4 males and 5 females. In addition, we also detected 4 cubs from 3 litters, though cubs were not included in our analysis.

Based on these data of 9 adults and 107 detections, we fit four spatially explicit capture-recapture models that incorporated the effect of sex on the two detection parameters. The results of the analysis indicated that the model with the best fit was one that incorporated variation in sex for both *g0* (0.043 for females, 0.017 for males) and σ (2,905 for females, 6,118 for males; Table 1). Based on this analysis, the resulting density estimate was 0.63 tigers per 100km^2 (95% CI 0.32 -1.21 tigers per 100km^2) and the population estimate for this area was 20 (14–33) individuals.

4. Discussion

In this study, we estimated a density of 0.63 tigers per 100km^2 (0.32–1.21) in DPKY. Although it is a small population (20 [14–33]), the presence of breeding individuals highlights the importance of this population of Indochinese tigers. Our study utilized simulations and previous data to aid in the design, validation, and implementation of an effective survey design suitable for generating a robust density estimate for a low-density population of tigers. Simulations provided validation of our trap array, which benefited from field-derived data and ease of implementation in comparison to a more traditional, regularly-spaced design.

4.1 Evaluation of simulations

A key component of our study was the evaluation of simulations as a tool for developing an effective SECR survey design in order to reliably estimate tiger population density. Our results suggest simulations may be beneficial for areas with low species density where the need for a sufficient number of detections for a robust estimate is particularly challenging. Further, our study demonstrates the utility of simulations in evaluating the potential effectiveness of non-uniform trapping arrays, consistent with findings from Wilton et al. (2014). Our simulations resulted in slightly higher failure rates under 45-day scenarios, particularly when $\hat{D}$ was low and σ small. Given that we predicted a relatively low population density, these results helped us determine the 60-day sampling period used during surveys, which allowed us to collate a sufficient number of detections to generate our density estimate. Further, a comparable RB between our trapping array and the regular array indicated we could proceed with our study design with reasonable confidence, despite a slightly higher RSE.

Overall, our simulations produced scenarios that closely reflected actual results under the null model (Table 2). Values for *n*, $\hat{D}$, *g0*, and σ for both our trapping array and the regular trapping array differed only slightly from actual results; however, simulation estimates for *ndet* in these scenarios - 59 and 63 for regular and our arrays, respectively - were much lower when compared to the results from our survey (107). This disparity was likely due to our trapping array design which prioritized camera locations by higher detection probabilities, based on prior knowledge. Potentially inflated probability of detection was not accounted for in our simulations. This may also explain why simulations for the regular trapping configuration predicted higher *n* values compared to our design. Specifically, simulations applied a circular home-range defined by σ and *g0* values for individuals in the population. As a result, given that a detector placed anywhere within a home range could detect an individual, the uniform configuration of detectors in the regular design may have resulted in slightly better predicted performance in our simulations. Relatively analogous performance of our simulations to survey results reflect findings from Wilton et al. (2014), which reinforce the utility of simulations in evaluating survey design.

SECR surveys to generate tiger density and population estimates may be reasonably flexible in their design and implementation provided that locations of traps are selected to maximize detections (Royle et al. 2017). Our trapping array utilized clustered detectors in areas of known tiger presence to increase detections while incorporating more spatially-dispersed detectors for increased spatial coverage and to fill gaps in the survey area. This design performed reasonably well, enabling us to generate both a sufficient number of detections while also identifying individuals ranging outside more intensively trapped survey areas. Further, this design was relatively easy to implement. This strong performance and ease of implementation of non-uniform survey designs has also been demonstrated in previous studies (Efford and Fewster 2012; Sun et al. 2014; Wilton et al. 2014). Central-clustered and spatially-dispersed types of design may be beneficial for suspected low-density populations (Sun et al. 2014; Wilton et al. 2014) or studies with limited resources where consideration for generating sufficient detections must be reconciled with maintaining spatial coverage due to large home ranges. This design may also be advantageous given that densities are likely to be variable across landscapes, particularly for areas with clear patterns of habitat preference and disturbance (Drewry et al. 2012; Fuller et al. 2016).

As was the case in Wilton et al. (2014), our use of a more intensive trap array was well-served by prior knowledge of species locations, which was considerably valuable in guiding placement of cameras to improve detections and, in turn, reliability of density estimates. More than 51% of our stations were at points where tigers had previously been photographed, which disproportionately generated > 69% of tiger detections during our survey period. Poor knowledge of species distribution may represent a challenge to employing such a survey design. However, it may be possible to utilize our approach using data from similar or nearby habitats to aid in parameterizing simulations prior to full surveys, as was the case for our simulations using a density estimate from DNP et al. (*unpublished*).

While the regular trap array had slightly higher predicted *n* and lower RSE, we opted to utilize our non-regular trap array. A relatively high RSE (~30) was expected for both arrays, given an expected small population, thus, we focused primarily on comparing RB, which was reasonably low for our non-regular array (<10%; Efford and Fewster 2012) . Our simulations indicate that a regular trap array, in some regards, may perform better than a non-regular array depending on where traps are positioned in relation to simulated home ranges (see Efford and Fewster 2012) despite likely increased detection probabilities for a non-regular array which utilizes travel routes, such as trails. We were unable to account for this in our simulations, but a streamlined framework for incorporating this variability into future simulations would be useful. Overall, simulations can act as a useful guide, though results in the real world, which is subject to considerable variability and chance, can differ. Simulations are not a replacement for informed study design and are best implemented in concert with expert interpretation and sound judgement.

4.2 Tiger population density estimate

In line with our predictions, our density estimate of 0.63 (0.32–1.21) tigers per 100km^2 was higher than the 0.34 tigers per 100km^2 in PSNP (DNP et al. 2014, *unpublished*). We note, however, that the density estimate from PSNP was generated from a Bayesian inference of a null model implemented in SPACECAP (Gopalaswamy et al. 2012). For comparison, similar analysis of our dataset resulted in a density estimate of 0.56 tigers (0.34–0.78) per 100km^2 (Table 2). Nevertheless, the stronger performance of models with sex as a covariate reinforces the importance of accounting for sex in density studies (Sollmann et al. 2011; Foster and Harmsen 2012; Efford and Mowat 2014). This is particularly relevant for tigers and other big cats, which can exhibit strong differences in movement patterns, territoriality, and home range depending on sex, which in turn, are likely to influence σ and *g0* estimates (Harihar et al. 2009; Goodrich et al. 2010; Sollmann et al. 2011; Gray and Prum 2012).

A previous study conducted by Ngoprasert and Gale (2019), estimated a density of 2.1 ± 1.4 tigers per 100km^2 (95% CI 0.5–5.3) in DPKY from by-catch of tigers during a camera-trap study on bears from 2012 to 2014. While our density estimate is notably lower than this estimate, we note there are factors in the study by Ngoprasert and Gale (2019) that make comparisons difficult. Notably, this previous study was not designed specifically for tigers and, while authors use similar camera-spacing as in a previous tiger study elsewhere in Thailand, the study ultimately had an extremely low sample size of tiger detections. This produced an exceedingly wide 95% confidence interval (0.5–5.3) and population estimate ranges (16 to 186 tigers), a result that limits its utility in comparison with other estimates or to reliably monitor changes in population over time. This reinforces the importance of generating a clear study design likely to generate a robust density estimate prior to survey deployment in low-density tiger populations.

Our density estimate is also considerably lower than estimates from Huai Kha Khaeng Wildlife Sanctuary in Thailand's Western Forest Complex (WEFCOM). Duangchantrasiri et al. (2016) estimated a population density ranging from 1.27 to 2.09 tigers/100km^2 from 2005 to 2012, generated with *SPACECAP*. Relative to other sites, our density estimate is comparable to some of the lowest estimates in the tiger's global range (Harihar et al. 2018). We speculate that there may be a few reasons for this. Hunting of both tigers and prey was historically common in DPKY though there is a paucity of information to quantify its intensity and extent (Lynam et al. 2006; Ash 2015, *unpublished*). This may have been exacerbated by anthropogenic pressures, such as human habitation in core areas, communist insurgency in the 1970s, an influx of transboundary refugees and concurrent poaching in the 1970s and 1980s and historical logging concessions (Lynam et al. 2006; Ash 2015, *unpublished*). It is possible that tigers and prey are still recovering from these pressures which may have limited their abundance and extent. Prey is a critical determinant of tiger densities throughout their range (Karanth et al. 2004) and it is possible that prey densities may currently be a major constraining factor on tiger abundance in our study site. Historically, tiger densities in Thailand would have likely been highest in lowland forest mosaics (Rabinowitz 1993) which, over the past 150 years, have all but disappeared. Remaining populations in Thailand, including DPKY, are largely restricted to protected areas in mountainous habitat that may not be conducive to supporting high densities of tigers (Rabinowitz 1993).

4.3 Scope and limitations

Capture-recapture methods and SECR, in particular, require adherence to a number of assumptions in order to generate reliable estimates of density (Foster and Harmsen 2012; Royle et al. 2014). While it is not possible for us to quantify potential demographic changes that would violate population closure, our sampling period was relatively short, contained within a single climatic season, and we did not observe patterns of detection that would indicate significant changes in activity centers. Further, our trapping configuration was unlikely to leave gaps within which a resident tiger had a detection probability of zero, given evidence of relatively large home ranges. All individual tigers were identified by two researchers to minimize errors in identification (Kelly et al. 2008).

We acknowledge several potential violations of assumptions in our study. Some evidence suggests that home ranges are unlikely to be circular and that SECR may not perform as well with complex home range configurations (Efford 2004; Foster and Harmsen 2012; Ivan et al. 2013). Results from other studies demonstrate that tiger ranges are influenced by a myriad of complex ecological and anthropogenic factors (Karanth et al. 2004, 2011; Ivan et al. 2013). Efford (2019) suggests that estimates may be robust to non-circular home-ranges, though bias may arise when elongated home ranges are aligned with linear detector arrays. Although some detectors were deployed in our trap array along linear features such as roads, valleys and ridgelines, detection patterns do not suggest home ranges were elongated and aligned with these features. Given SECR analysis also assumes that detection probability declines with distance from a home range center. This may be violated somewhat if an individual has more than one activity center within their home range (Foster and Harmsen 2012) though this may be mitigated through aggregation of $g0$ and σ across individuals to solve for a single activity center within SECR analysis. It is possible that, in some cases, detections of individuals were not independent given that movement of wide-ranging mammals like tigers introduces complex temporal patterns of auto-correlation (Cushman 2010). However, given that there were few records of re-detection of the same individuals at single detectors across consecutive occasions, the effect of these patterns may be minimal in our study. Violation of these assumptions may introduce overdispersion and bias density or variance estimates. These are common challenges when estimating density for species such as tigers (Karanth and Nichols 1998; Foster and Harmsen 2012) which merits additional investigation.

4.4 Conservation implications

The survey was a valuable step toward improving understanding of tigers in this landscape and has revealed information of global conservation importance. Confirmed breeding, cub-rearing, and possible dispersal of cubs in this population establishes this landscape as a breeding population for the Indochinese tiger (*Panthera tigris corbetti*). At this time, this likely represents the only confirmed breeding population in Thailand outside of its Western Forest Complex and the greater Dawna-Tenasserim landscape (Pisdamkam et al. 2010; DNP 2016; Ash et al. 2020). With a lack of recent breeding records from other parts of the Indochinese tiger's range (Lynam and Nowell 2011), this reinforces the critical importance of this population. We have also revealed that this population has much lower population density - 0.63 (0.32–1.21) tigers per 100km^2 - relative to other habitats in the tiger’s current range (Duangchantrasiri et al. 2016; Harihar et al. 2018). Concerted efforts must be made if this population is to be saved from extirpation. Baseline metrics generated from this survey are, therefore, a valuable reference with which to evaluate the impact of conservation interventions at the site in the future.

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Appendix A. Supplementary data

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References

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Automat Contr 19:716–723

Ash E (2015) Thap Lan National Park - Threat and Needs Assessment (Unpublished). Freeland Foundation, Bangkok

Ash E, Kaszta Ż, Noochdumrong A, et al (2020) Opportunity for Thailand's Forgotten Tigers: Assessment of Indochinese tiger Panthera tigris corbetti and prey from camera-trap surveys in Eastern Thailand. Oryx 55:204–211. https://doi.org/10.1017/S0030605319000589

Borah J, Sharma T, Das D, et al (2014) Abundance and density estimates for common leopard Panthera pardus and clouded leopard Neofelis nebulosa in Manas National Park, Assam, India. Oryx 48:149–155. https://doi.org/DOI: 10.1017/S0030605312000373

Brassine E, Parker D (2015) Trapping Elusive Cats: Using Intensive Camera Trapping to Estimate the Density of a Rare African Felid. PLoS One 10:e0142508. https://doi.org/10.1371/journal.pone.0142508

Cushman SA (2010) Animal Movement Data: GPS Telemetry, Autocorrelation and the Need for Path-Level Analysis. In: Spatial Complexity, Informatics, and Wildlife Conservation. Springer Japan, Tokyo, pp 131–149

DNP (2016) Practical Plan to Improve Tiger Population 2015-2035 (20 Years). Department of National Parks, Wildlife and Plant Conservation (DNP), Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

Drewry JM, Van Manen FT, Ruth DM (2012) Density and genetic structure of black bears in coastal South Carolina. J Wildl Manage 77:153–164. https://doi.org/10.1002/jwmg.443

Duangchantrasiri S, Umponjan M, Simcharoen S, et al (2016) Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. Conserv Biol 30:639–648. https://doi.org/10.1111/cobi.12655

Efford M (2004) Density estimation in live-trapping studies. Oikos 106:598–610. https://doi.org/10.1111/j.0030-1299.2004.13043.x

Efford MG (2017) secrdesign: Sampling Design for Spatially Explicit Capture-Recapture. R Package Version 2.5.4.

Efford MG (2015) secr: Spatially Explicit Capture-Recapture. R package version 2.9.5

Efford MG (2019) Non-circular home ranges and the estimation of population density. Ecology 100:e02580. https://doi.org/10.1002/ecy.2580

Efford MG, Fewster RM (2012) Estimating population size by spatially explicit capture–recapture. Oikos 122:918–928. https://doi.org/10.1111/j.1600-0706.2012.20440.x

Efford MG, Mowat G (2014) Compensatory heterogeneity in spatially explicit capture–recapture data. Ecology 95:1341–1348. https://doi.org/10.1890/13-1497.1

Foster RJ, Harmsen BJ (2012) A critique of density estimation from camera-trap data. J Wildl Manage 76:224–236. https://doi.org/10.1002/jwmg.275

Fuller AK, Sutherland CS, Royle JA, Hare MP (2016) Estimating population density and connectivity of American mink using spatial capture-recapture. Ecol Appl 26:1125–1135. https://doi.org/10.2352/ISSN.2470-1173.2016.3.VSTIA-512

Goodrich JM, Lynam A, Miquelle DG, et al (2015) Panthera tigris. IUCN Red List Threat. Species 2015 e.T15955A50659951

Goodrich JM, Miquelle DG, Smirnov EN, et al (2010) Spatial structure of Amur (Siberian) tigers (Panthera tigris altaica) on Sikhote-Alin Biosphere Zapovednik, Russia. J Mammal 91:737–748. https://doi.org/10.1644/09-MAMM-A-293.1

Gopalaswamy AM, Royle JA, Hines JE, et al (2012) Program SPACECAP: software for estimating animal density using spatially explicit capture-recapture models. Methods Ecol Evol 3:1067–1072. https://doi.org/10.1111/j.2041-210X.2012.00241.x

Gray TNE, Prum S (2012) Leopard density in post-conflict landscape, Cambodia: Evidence from spatially explicit capture-recapture. J Wildl Manage 76:163–169. https://doi.org/10.1002/jwmg.230

Hansen MC, Potapov P V., Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science (80-) 342:850–853. https://doi.org/10.1126/science.1244693

Harihar A, Chanchani P, Borah J, et al (2018) Recovery planning towards doubling wild tiger Panthera tigris numbers: Detailing 18 recovery sites from across the range. PLoS One 13:e0207114. https://doi.org/10.1371/journal.pone.0207114

Harihar A, Pandav B, Goyal SP (2009) Subsampling photographic capture-recapture data of tigers (Panthera tigris) to minimize closure violation and improve estimate precision: a case study. Popul Ecol 51:471–479. https://doi.org/10.1007/s10144-009-0138-4

Harmsen BJ, Foster RJ, Sanchez E, et al (2017) Long term monitoring of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize; Implications for camera trap studies of carnivores. PLoS One 12:e0179505. https://doi.org/10.1371/journal.pone.0179505

Ivan JS, White GC, Shenk TM (2013) Using simulation to compare methods for estimating density from capture-recapture data. Ecology 94:817–826. https://doi.org/10.1890/12-0102.1

Karanth K., Nichols JD (2010) Non-invasive Survey Methods for Assessing Tiger Populations. In: Tilson R, Nyhus PJ (eds) Tigers of the World, Second Edition. Elsevier Inc., New York, pp 241–261

Karanth KU (1995) Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture models. Biol Conserv 71:333–338. https://doi.org/10.1016/0006-3207(94)00057-W

Karanth KU, Gopalaswamy AM, Kumar NS, et al (2011) Monitoring carnivore populations at the landscape scale: Occupancy modelling of tigers from sign surveys. J Appl Ecol 48:1048–1056. https://doi.org/10.1111/j.1365-2664.2011.02002.x

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862. https://doi.org/10.2307/176521

Karanth KU, Nichols JD (2002) Monitoring Tigers and Their Prey: A manual for researchers, managers and conservationists in tropical Asia. Centre for Wildlife Studies, Bangalore, India

Karanth KU, Nichols JD (eds) (2017) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore

Karanth KU, Nichols JD, Harihar A, et al (2017) Field practices: Assessing tiger population dynamics using photographic captures. In: Karanth KU, Nichols JD (eds) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore, pp 191–224

Karanth KU, Nichols JD, Kumar NS, et al (2004) Tigers and their prey: Predicting carnivore densities from prey abundance. Proc Natl Acad Sci U S A 101:4854–4858. https://doi.org/10.1073/pnas.0306210101

Karanth KU, Nichols JD, Kumar NS, Hines JE (2006) Assessing tiger population dynamics using photographic capture-recapture sampling. Ecology 87:2925–2937. https://doi.org/10.1890/0012-9658(2006)87[2925:ATPDUP]2.0.CO;2

Kelly MJ, Noss AJ, Di Bitetti MS, et al (2008) Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. J Mammal 89:408–418. https://doi.org/10.1644/06-MAMM-A-424R.1

Lynam A, Nowell K (2011) Panthera tigris ssp. corbetti. IUCN Red List Threat. Species 2011 e.T136853A4346984

Lynam A, Round P, Brockelman W (2006) Status of Birds and Large Mammals in Thailand's Dong Phayayen - Khao Yai Forest Complex. Wildlife Conservation Society and Biodiversity Research Training (BRT) Programme, Bangkok

Maffei L, Noss AJ (2008) How Small is too Small? Camera Trap Survey Areas and Density Estimates for Ocelots in the Bolivian Chaco. Biotropica 40:71–75. https://doi.org/10.1111/j.1744-7429.2007.00341.x

Ngoprasert D, Gale GA (2019) Tiger density, dhole occupancy, and prey occupancy in the human disturbed Dong Phayayen – Khao Yai Forest Complex, Thailand. Mamm Biol 95:51–58. https://doi.org/10.1016/j.mambio.2019.02.003

O'Brien TG, Kinnaird MF (2011) Density estimation of sympatric carnivores using spatially explicit capture–recapture methods and standard trapping grid. Ecol Appl 21:2908–2916. https://doi.org/10.1890/10-2284.1

Obbard ME, Howe EJ, Kyle CJ (2010) Empirical comparison of density estimators for large carnivores. J Appl Ecol 47:76–84. https://doi.org/10.1111/j.1365-2664.2009.01758.x

Pisdamkam C, Prayurasiddhi T, Kanchanasaka B, et al (2010) Thailand Tiger Action Plan - 2010-2012. Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

Rabinowitz A (1993) Estimating the Indochinese tiger (Panthera tigris corbetti) population in Thailand. Biol Conserv 65:213–217. https://doi.org/10.1016/0006-3207(93)90055-6

Rayan DM, Linkie M (2015) Conserving tigers in Malaysia: A science-driven approach for eliciting conservation policy change. Biol Conserv 184:18–26. https://doi.org/10.1016/j.biocon.2014.12.024

Royle J, Chandler RB, Sollmann R, Gardner B (2014) Spatial Capture-Recapture. Elsevier, Oxford

Royle JA, Gopalaswamy AM, Dorazio RM, et al (2017) Concepts: Assessing Tiger Population Dynamics Using Capture–Recapture Sampling. In: Karanth KU, Nichols JD (eds) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore, pp 163–189

Sanderson E, Forrest J, Loucks C, et al (2006) Setting Priorities for the Conservation and Recovery of Wild Tigers: 2005-2015 - The Technical Assessment. WCS, WWF, Smithsonian, and NFWF-STF, New York - Washington, DC

Simcharoen A, Savini T, Gale GA, et al (2014) Female tiger Panthera tigris home range size and prey abundance: important metrics for management. Oryx 48:370–377. https://doi.org/10.1017/S0030605312001408

Sollmann R, Furtado MM, Gardner B, et al (2011) Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. Biol Conserv 144:1017–1024. https://doi.org/10.1016/j.biocon.2010.12.011

Sun CC, Fuller AK, Royle JA (2014) Trap Configuration and Spacing Influences Parameter Estimates in Spatial Capture-Recapture Models. PLoS One 9:e88025. https://doi.org/10.1371/journal.pone.0088025

Tobler MW, Powell GVN (2013) Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. Biol Conserv 159:109–118. https://doi.org/10.1016/j.biocon.2012.12.009

White GC, Anderson DR, Burnham KP, Otis DL (1982) Capture-Recapture and Removal Methods for Sampling Closed Populations. Los Alamos National Laboratory, LA 8787-NERP, Los Alamos

Wilton CM, Puckett EE, Beringer J, et al (2014) Trap Array Configuration Influences Estimates and Precision of Black Bear Density and Abundance. PLoS One 9:e111257. https://doi.org/10.1371/journal.pone.0111257

Glossary

AIC: Akaike's Information Criterion

$\hat{D}$: Estimate of population density (individuals/100km^2)

DPKY: Dong Phayayen-Khao Yai Forest Complex

g0: intercept, probability of detection at home range centre

n: number of individuals detected

ndet: Number of detections

RSE: Relative standard error (equivalent to coefficient of variation)

RB: Relative bias

SECR: Spatially explicit capture-recapture

TCL: Tiger Conservation Landscape

σ: spatial scale parameter, distance from home range centre

Supplementary Materials 1

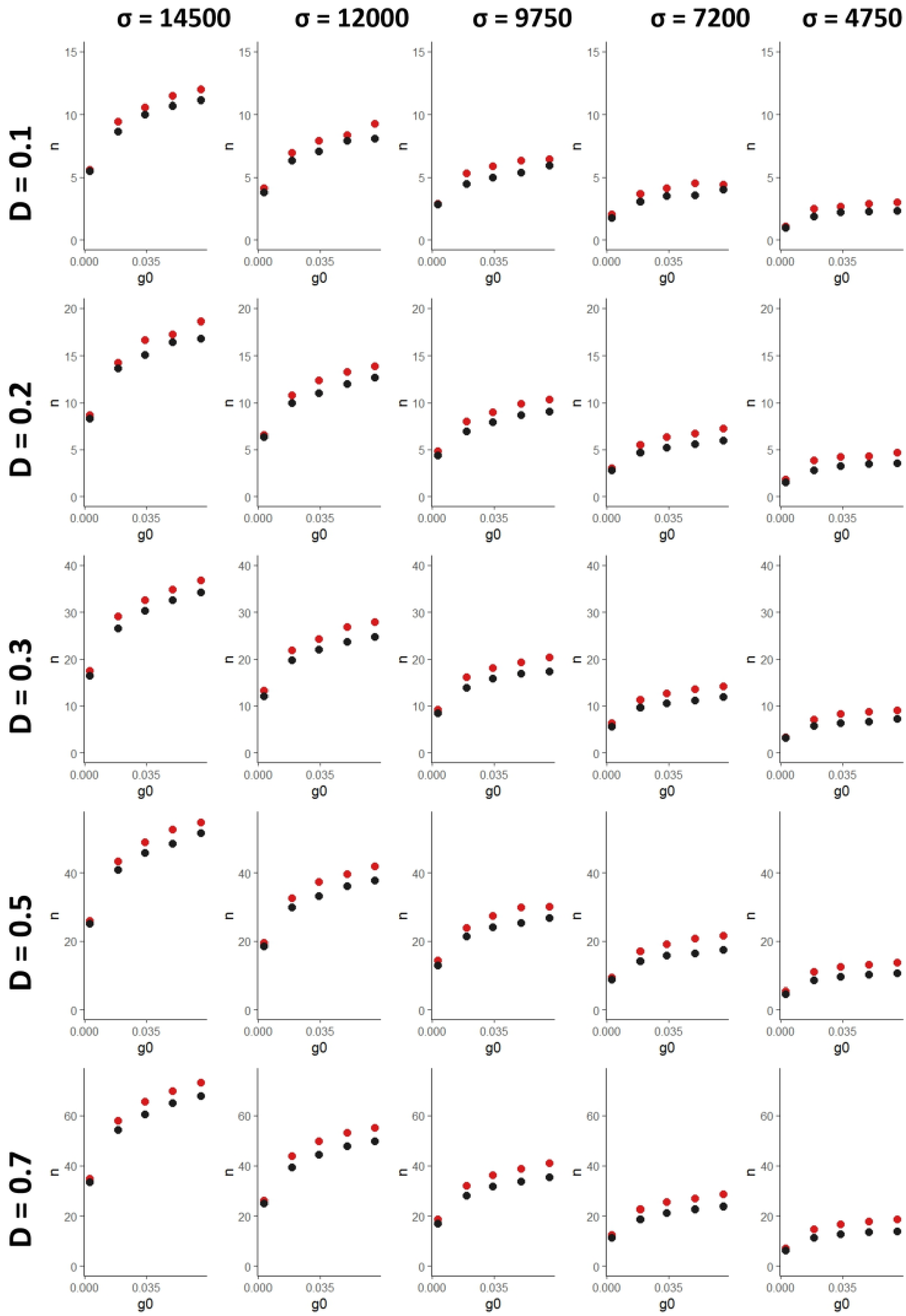

Fig. 1 Simulated *n* across $\hat{D}$, g0, and σ values for a 45-day sampling duration. Red symbols denote values for the regular trapping array while black symbols denote values for our trapping array.

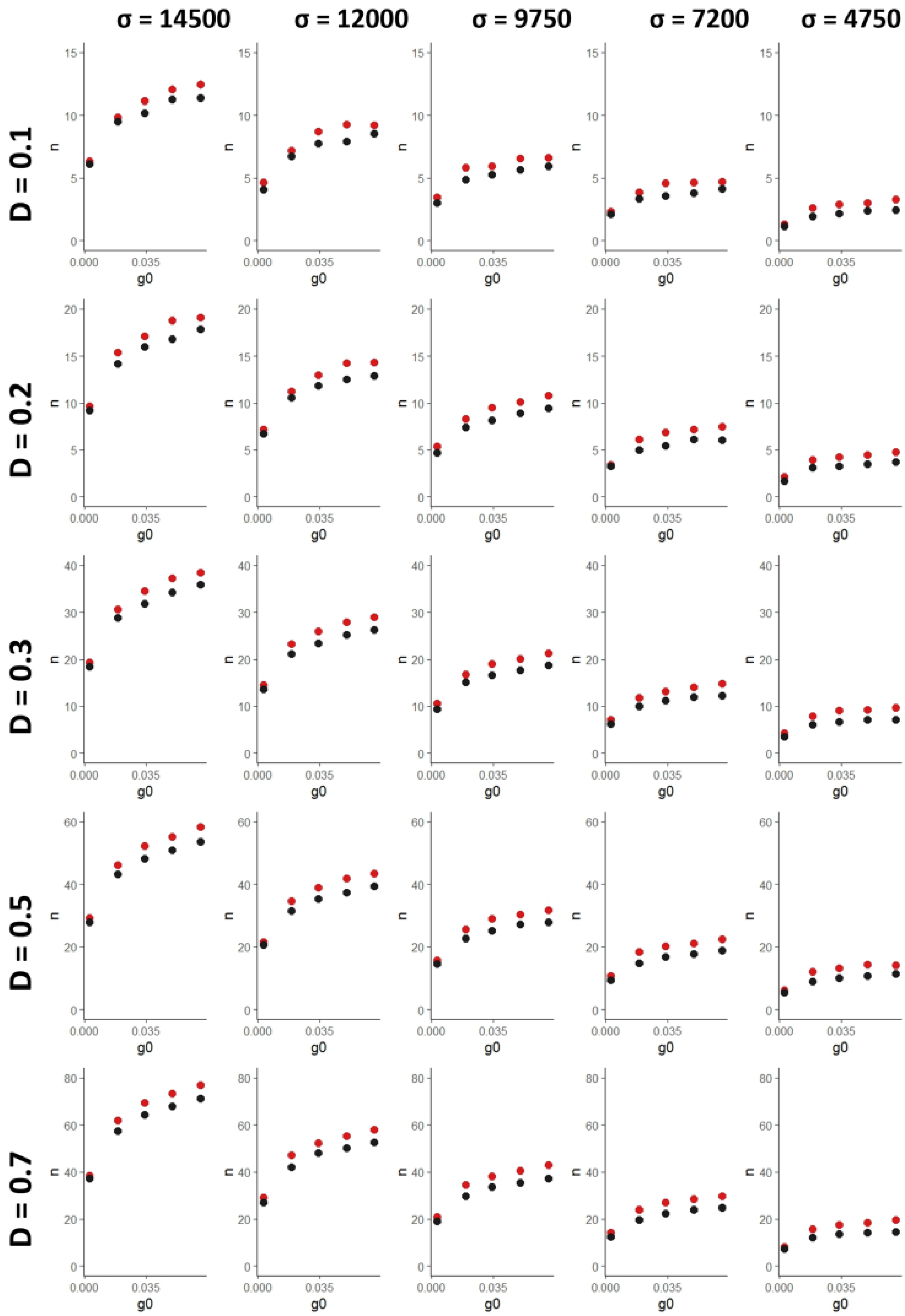

Fig. 2 Simulated *n* across $\hat{D}$, g0, and σ values for a 60-day sampling duration. Red symbols denote values for the regular trapping array while black symbols denote values for our trapping array.

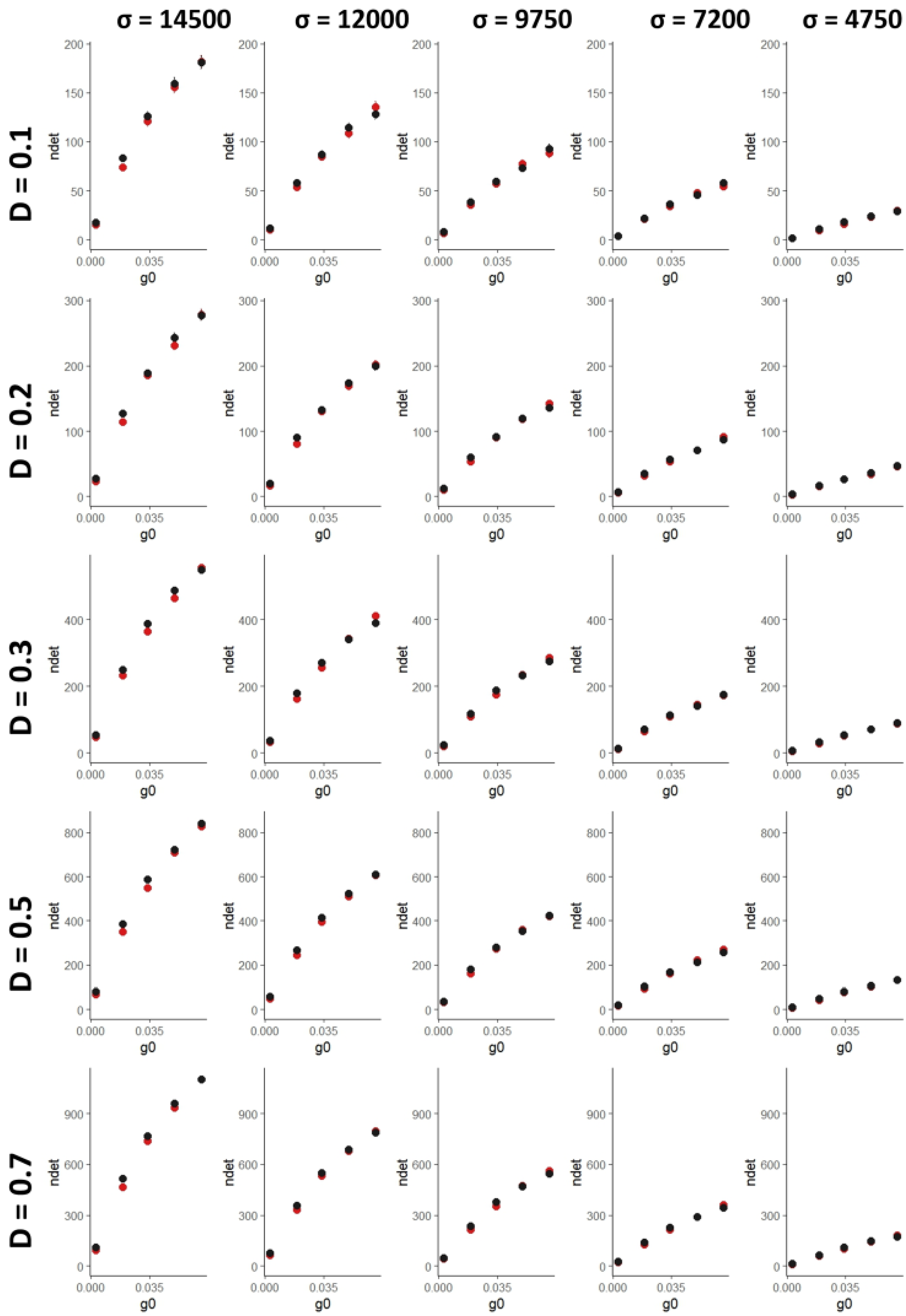

Fig. 3 Simulated *ndet* across $\hat{D}$, g0, and σ values for a 45-day sampling duration. Red symbols denote values for the regular trapping array while black symbols denote values for our trapping array.

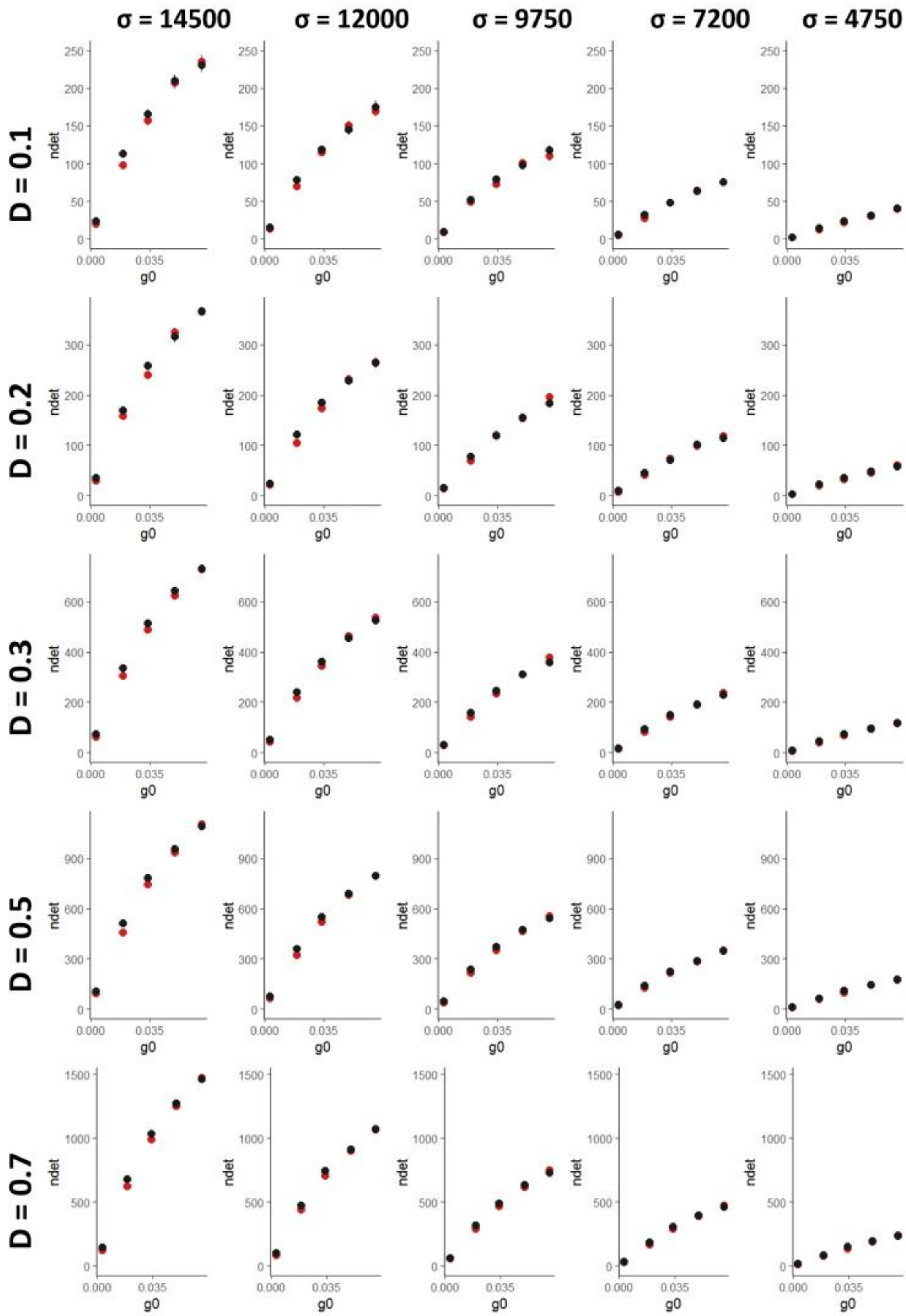

Fig. 4 Simulated *ndet* across $\hat{D}$, g0, and σ values for a 60-day sampling duration. Red symbols denote values for the regular trapping array while black symbols denote values for our trapping array.

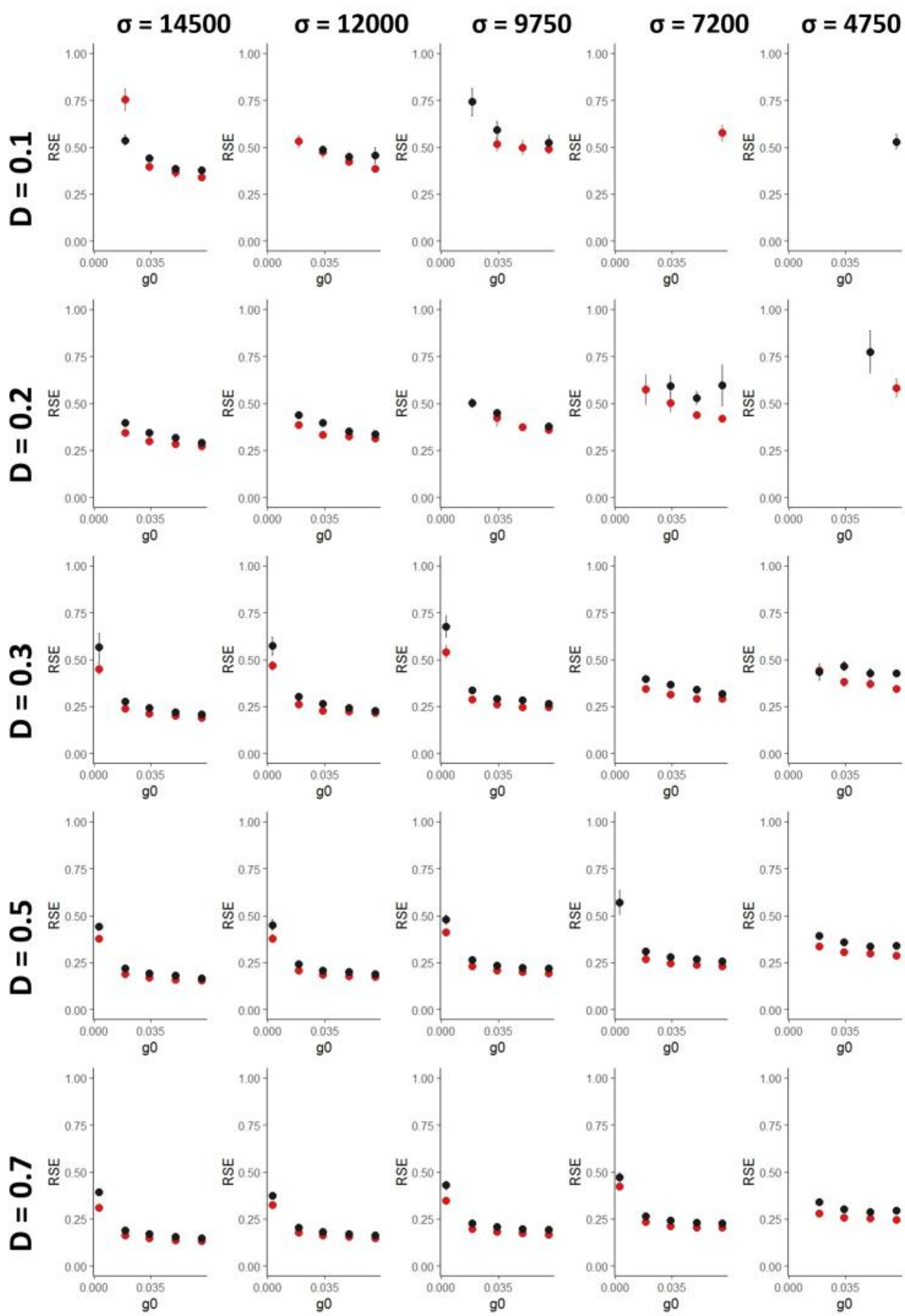

Fig. 5 Simulated relative standard error (RSE) across $\hat{D}$, g0, and σ values for a 45-day sampling duration. Red symbols denote values for the regular trapping array while black symbols denote values for our trapping array.

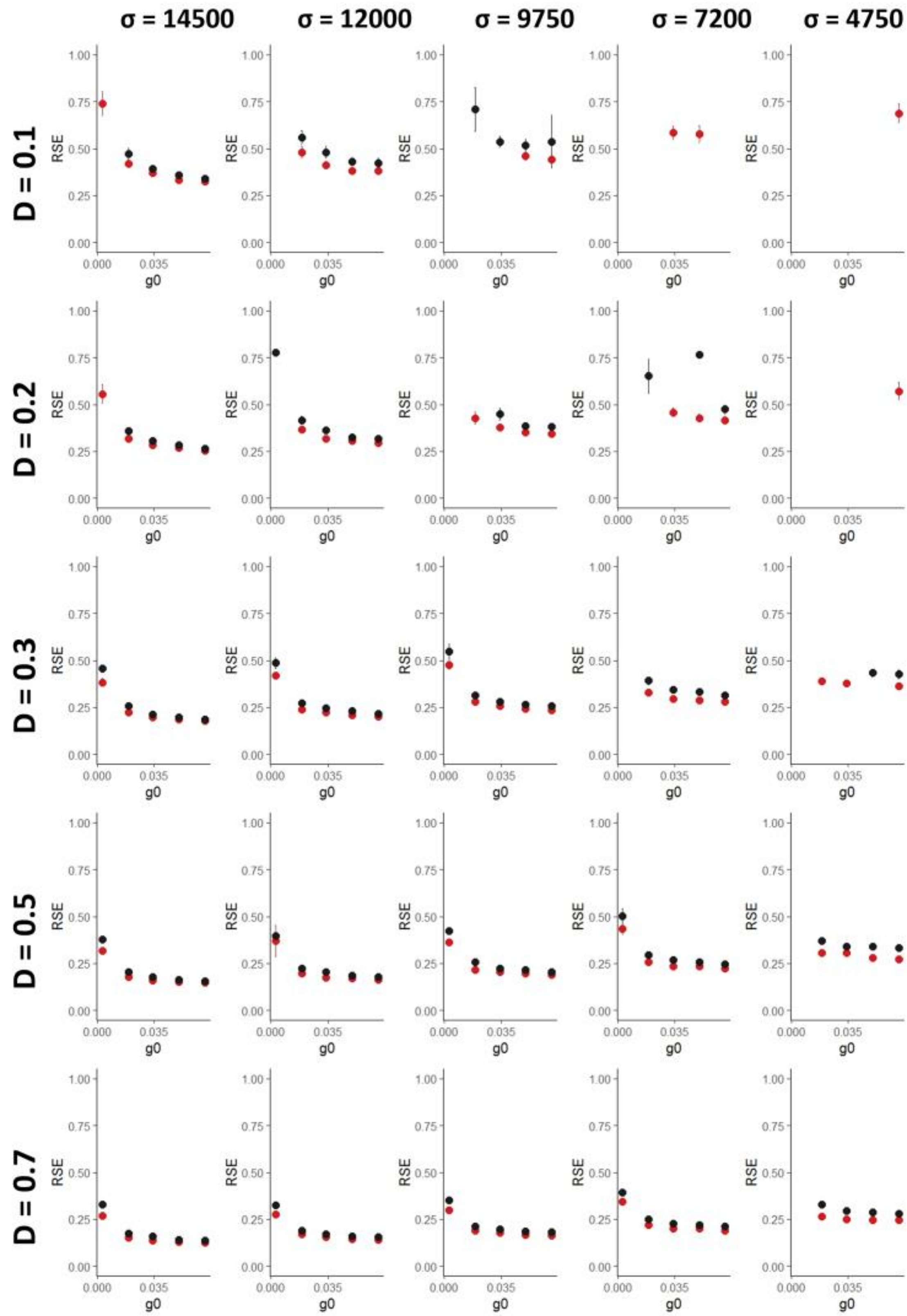

Fig. 6 Simulated relative standard error (RSE) across $\hat{D}$, g0, and σ values for a 60-day sampling duration. Red symbols denote values for the regular trapping array while black symbols denote values for our trapping array.

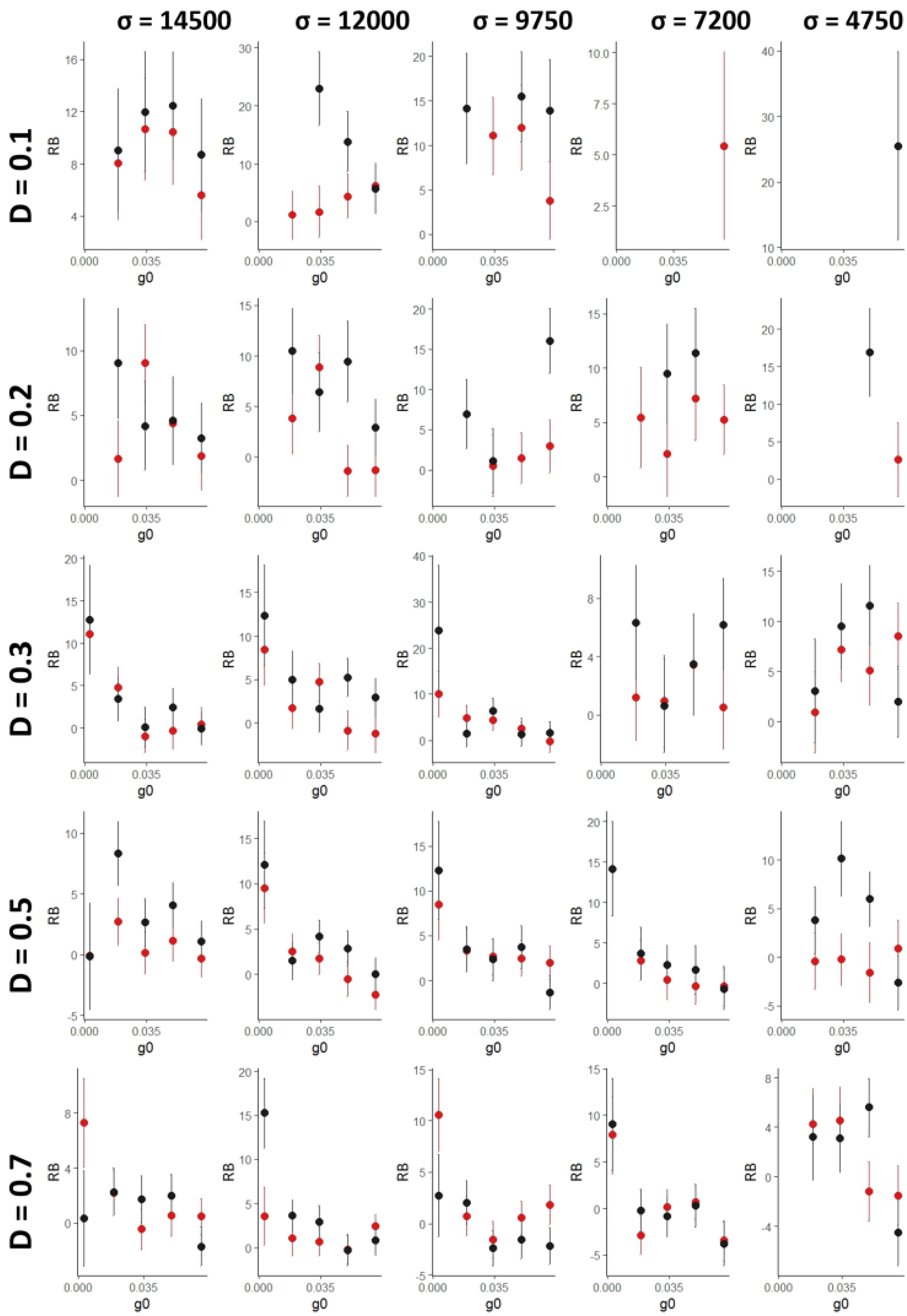

Fig. 7 Simulated relative bias (RB) across $\hat{D}$, g0, and σ values for a 45-day sampling duration. Red symbols denote values for the regular trapping array while black symbols denote values for our trapping array.

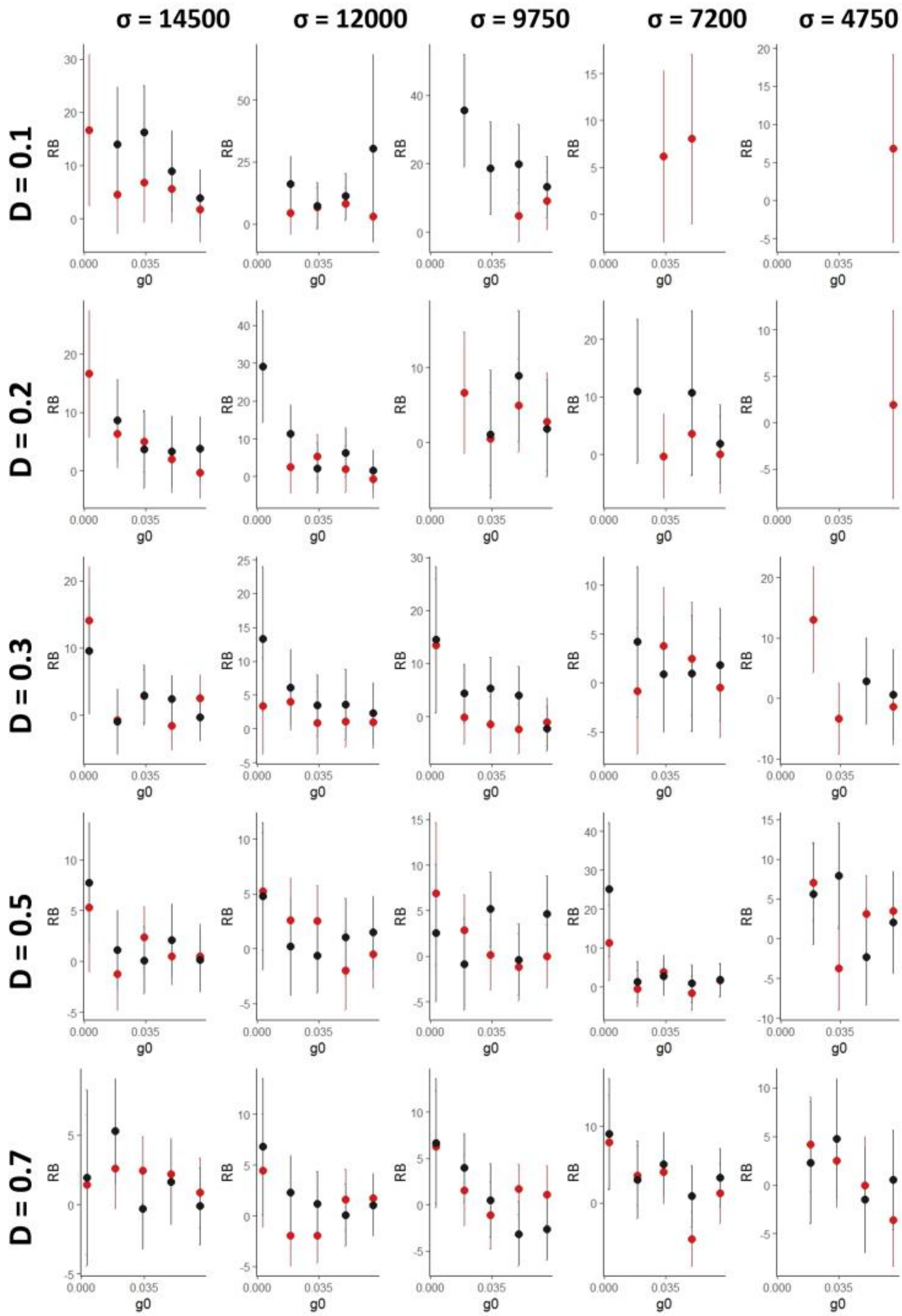

Fig. 8 Simulated relative bias (RB) across $\hat{D}$, g0, and σ values for a 60-day sampling duration. Red symbols denote values for the regular trapping array while black symbols denote values for our trapping array.

Supplementary Materials 2

Table 1 Estimates of density ($\hat{D}$) and related parameters for four models for a 45-day survey period, including lower (LCI) and upper (UCI) confidence interval values. For models where sex was included as a covariate, values are distinguished between males (m) and females (f).

Model	ΔAIC	$\hat{D}$	LCI	UCI	Pop	Pop(LCI)	Pop(UCI)	g_0 null	σ null	g_0 f	g_0 m	σ f	σ m
g_0SEX,sigmaSEX	0	0.60	0.28	1.26	17.54	8.29	37.14	-	-	0.061	0.024	2228.18	5235.84
F	-	0.42	0.16	1.08	-	-	-	-	-	-	-	-	-
M	-	0.18	0.06	0.50	-	-	-	-	-	-	-	-	-
sigmaSEX	5	0.62	0.32	1.19	17.31	8.17	36.65	0.0360	-	-	-	2567.54	4781.55
Null	21	0.47	0.23	0.97	13.84	6.71	28.55	0.0313	4212.20	-	-	-	-
g_0SEX	23	0.47	0.23	0.97	13.84	6.71	28.56	-	4211.96	0.0312	0.0314	-	-

Table 2 Model rankings for (a) 45-day and (b) 61-day survey periods.

(a)

Model	detectfn	npar	logLik	AIC	AICc	dAICc	AICcwt
g0~1 sigma~SEX	halfnormal	3	-402.921	811.842	819.842	0	0.9651
g0~SEX sigma~SEX	halfnormal	4	-399.2397	806.479	826.479	6.637	0.0349
g0~1 sigma~1	halfnormal	2	-411.9079	827.816	830.816	10.974	0
g0~SEX sigma~1	halfnormal	3	-411.9077	829.815	837.815	17.973	0

(b)

Model	detectfn	npar	logLik	AIC	AICc	dAICc	AICcwt
g0~SEX sigma~SEX	halfnormal	4	-602.6237	1213.247	1223.247	0	0.807
g0~1 sigma~SEX	halfnormal	3	-607.6541	1221.308	1226.108	2.861	0.193
g0~1 sigma~1	halfnormal	2	-617.2707	1238.541	1240.541	17.294	0
g0~SEX sigma~1	halfnormal	3	-617.2695	1240.539	1245.339	22.092	0

Chapter 6

How Important Are Resistance, Dispersal Ability, Population Density and Mortality in Temporally Dynamic Simulations of Population Connectivity? A Case Study of Tigers in Southeast Asia

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Title

How Important Are Resistance, Dispersal Ability, Population Density and Mortality in Temporally Dynamic Simulations of Population Connectivity? A Case Study of Tigers in Southeast Asia

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Abstract

Development of landscape connectivity and spatial population models is challenging, given the uncertainty of parameters and the sensitivity of models to factors and their interactions over time. Using spatially- and temporally-explicit simulations, we evaluate the sensitivity of population distribution, abundance and connectivity of tigers in Southeast Asia to variations of resistance surface, dispersal ability, population density, and mortality. Utilizing a temporally dynamic cumulative resistant kernel approach, we tested (1) effects and interactions of parameters on predicted population size, distribution, and connectivity, and (2) displacement and divergence in scenarios across timesteps. We evaluated the effect of varying levels of factors on simulated population, cumulative resistance kernel extent, and kernel sum across nine timesteps, producing 24,300 simulations. We demonstrate that predicted population, range shifts, and landscape connectivity are highly sensitive to parameter values with significant interactions and relative strength of effects varying by timestep. Dispersal ability, mortality risk, and their interaction dominated predictions. Further, population density had intermediate effects, landscape resistance had relatively low impacts, and mitigation of linear barriers (highways) via lowered resistance had little relative effect. Results are relevant to regional, long-term tiger population management, providing insight into potential population growth and range expansion across a landscape of global conservation priority.

Keywords landscape connectivity; cumulative resistant kernels; sensitivity analysis; mortality risk; resistance surface; *Panthera tigris*; dispersal; divergence; displacement; Dong Phayayen-Khao Yai Forest Complex

1. Introduction

Population dynamics are the result of the interplay between birth, death, immigration, and emigration. Classic population models assume well-mixed populations with no spatial structure (e.g., Volterra 1928; Lotka 1932). Spatially explicit population models typically have adopted a metapopulation framework (Levins 1970) in which a network of populations interact through dispersal. However, in many cases, populations are better characterized as gradient systems of differential density, mortality, dispersal, and other factors across heterogeneous landscapes (Cushman et al. 2015). In real landscapes, populations grow, shrink, spread, and contract through space and time in response to spatially varying habitat quality gradients, patterns of mortality risk, and how landscape features drive movement and dispersal. Accounting for temporally dynamic interactions among spatially explicit patterns of habitat quality, mortality rates, and dispersal is a deeply challenging task (Cushman 2015; Barros et al. 2019).

Dispersal, range expansion, population viability, and other processes of research and management interest emerge from complex interactions between a species' life-history traits, landscape configuration, and anthropogenic influence (Diffendorfer 1998; Walters 2007; Cushman et al. 2010). Researchers developing models of population dynamics in complex landscapes face the challenging prospect of capturing these influential factors sufficiently to produce reliable outputs. At a fundamental level, population dynamics are influenced considerably by landscape heterogeneity at multiple scales and ecological patterns affecting biological processes, such as population connectivity. Specifically, connectivity emerges as a function of the ability of organisms to move across the landscape in response to three factors: distribution and density of the source population, resistance of the landscape, and dispersal ability of the organism (Cushman et al. 2013). Perhaps most important, and usually unaccounted for, spatially-heterogeneous mortality risk can dominate trajectories of population dynamics through space and time (Kramer-Schadt et al. 2004; Kaszta et al. 2019). To reliably predict population dynamics and connectivity, it is therefore essential to integrate distribution, abundance, resistance, dispersal ability and mortality risk explicitly into integrated spatial models (e.g., Cushman 2015; Barros et al. 2019).

Variation in these parameters may drastically influence results. For example, a number of studies have shown a high degree of sensitivity and complex interactions among factors affecting population size, distribution, and connectivity (Cushman et al. 2010, 2014; Elliot et al. 2014; Cushman 2015; Barros et al. 2019; Kaszta et al. 2019, 2020). Empirical data necessary for accurate parameterization of models may be difficult to obtain (Zeller et al. 2012). Thus, if researchers develop models via a narrowly or vaguely-defined set of parameters, as is often the case (Spear et al. 2010), they may be limited in their ability to ascertain if model predictions reflect what is likely to occur in reality. In addition, it is essential to understand the relative sensitivity of models to variation in critical parameters, to assess how reliable they are, given parametric uncertainty, and to guide where empirical or theoretical research should focus to improve the precision of parameter estimates.

There are several key factors in the development of connectivity models used in spatially explicit modeling of population dynamics that merit investigations into their effect. Such models are often highly reliant on resistance surfaces, which define step-wise cost to movement and can aid in determining paths for dispersal, and have received a high degree of focus (e.g., Zeller et al. 2012). However, there has been comparatively less attention on investigating the potential effect of non-linear relationships between landscape configuration and cost to movement (Cushman et al. 2010; Carroll et al. 2020). Importantly, while resistance surfaces may implicitly incorporate mortality as a constraint to movement (Diniz et al. 2020), they may be a poor correlate for elevated mortality risk (e.g., hunting/poaching, road collisions, etc.) during dispersal, that can otherwise drastically affect conclusions on functional connectivity in a landscape (Kramer-Schadt et al. 2004; Cushman 2006; Cushman et al. 2016). In reality, mortality risk across landscapes can be highly spatially heterogeneous and models may not explicitly incorporate or investigate its effects (Thatte et al. 2018; Kaszta et al. 2019). Predictions of landscape configuration and connectivity can also be extremely sensitive to species dispersal ability or related parameters dictating movement thresholds (Kanagaraj et al. 2013; Moqanaki and Cushman 2017). This reinforces the need for investigations into model sensitivity to dispersal ability, particularly given that empirical movement data is rarely available to inform model development (Zeller et al. 2012). Lastly, investigations into the degree to which thresholds of population density or size interact with these and other factors are less common than investigations into the effect of these factors on population metrics (Cushman et al. 2010; Carmona and Franco 2015).

Simulation modeling has emerged as a critical investigation tool to understand and predict spatially explicit population dynamics. Simulations can enable researchers to test hypotheses on the effect of varying parameter values on predicted population distributions, abundance and landscape connectivity (Cushman 2015; Barros et al. 2019; Kaszta et al. 2019, 2020). However, somewhat neglected has been the use of simulations evaluating temporal dynamics in a spatially explicit framework (Cushman and McGarigal 2007). Incorporating time-sensitivity and temporal dynamism in analysis enables evaluation of the degree of displacement from initial conditions through time, divergence between scenarios at each timestep, and time-lags in species response to landscape configurations (Cushman and McGarigal 2007).

This study evaluates the degree to which simulations of population and connectivity dynamics in a spatially explicit context are sensitive to the variation of critical parameters. Specifically, we apply a dynamic spatial modeling approach, using cumulative resistance kernels (Cushman 2015; Barros et al. 2019) and spatially differential mortality risk to test: (1) the strength of effects and interactions of parameters on predicted population size, distribution, and connectivity, and (2) the degree of displacement and divergence among scenarios across timesteps. Concurrently, we evaluate the implications of these effects for the regional conservation of an endangered species, the Indochinese tiger (*Panthera tigris corbett*i). We utilized data from a population of tigers in the Dong Phayayen-Khao Yai forest complex (DPKY) in Eastern Thailand (Ash et al. 2020b). We consider this to be an ideal candidate species since tigers are wide-ranging, occur within metapopulations shaped considerably through dispersal and landscape configuration, and are a species of notable and urgent conservation concern (Vasudev et al. 2017; Thapa et al. 2017). Tigers have suffered severe range collapse throughout Southeast Asia, likely being extirpated from Cambodia, Lao PDR, and Viet Nam (Goodrich et al. 2015; Gray et al. 2017; Rasphone et al. 2019). Our focal landscape of DPKY is likely to be the eastern-most breeding population of tigers in Southeast Asia and may serve as a source population for recolonization of areas in which they were extirpated both within and beyond this landscape. Understanding the population dynamics of this landscape, its degree of connectivity with other potential habitats, and how these factors change over time will be critical for developing long-term management and conservation strategies.

2. Materials and Methods

2.1 Study area

Our study area (Figure 1) contains three tiger conservation landscapes (TCLs; Sanderson et al. 2006) with notable protected area and forest coverage: the Dong Phayayen-Khao Yai Forest Complex in Eastern Thailand (DPKY; TCLs-23/24), the Phnom-Dong Rak landscape in Eastern Thailand, and the Cambodian Northern Plains (TCL-26) landscape in Northern Cambodia. DPKY is of particular importance, given it currently supports an established breeding population of tigers (TCL-24; Ash et al. 2020b) which could potentially disperse to, and re-colonize, the other TCLs in which tigers have been extirpated (TCL-23/26). To account for potential habitat which may facilitate tiger movement between and beyond these protected area complexes, we generated a 45-km buffer from protected area borders in ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011). This distance was selected based on the maximum scale of analysis considered in Reddy et al. (2017) in their investigation of landscape-scale gene flow of tigers in central India. This produced a total study area of ~157,920km^2, including parts of Thailand, Cambodia, and a small section of southern Lao PDR. The area contains a heterogeneous mix of topography, forest, and anthropogenic land cover. Forest cover configuration in this area varies considerably, from small, relatively isolated patches to large contiguous forest blocks. Much of this forest cover occurs within protected areas, with most land use outside protected areas dominated by agriculture, villages, and urban areas.

2.2 Landscape connectivity simulations

To test the sensitivity of landscape connectivity models, we varied four sets of factors: (1) resistance surface ((i) highway mitigation scenario [SCEN]; (ii) resistance transformation [RES]); (2) dispersal ability (KERN); (3) population density (DENS); and (4) mortality function (MORT). Each factor set included several levels to evaluate the influence of adjusting these factors on resulting simulated population (*N*), cumulative resistance kernel extent (*kernext*), and kernel sum (*kernsum*), with kernels generated from the Universal Corridor Network Simulator (UNICOR) v2.0 (Landguth et al. 2012). A workflow diagram depicting these methods is presented in Figure 2.

2.2.1 Resistance surfaces

Our approach employs the use of resistance surfaces, a commonly-used foundation for applied connectivity and dispersal modeling (Spear et al. 2010; Graves et al. 2014). In resistance surfaces, pixels in a landscape are assigned values reflecting step-wise cost to individual movement, with low values representing areas of relatively little resistance and high values representing strong resistance. Resistance surfaces assume that landscape-level movement of organisms is dictated by cost of movement and that pixel values in the resistance surface accurately reflect that cost.

Resistance surfaces provide the foundation for connectivity analysis (Zeller et al. 2012), but do not

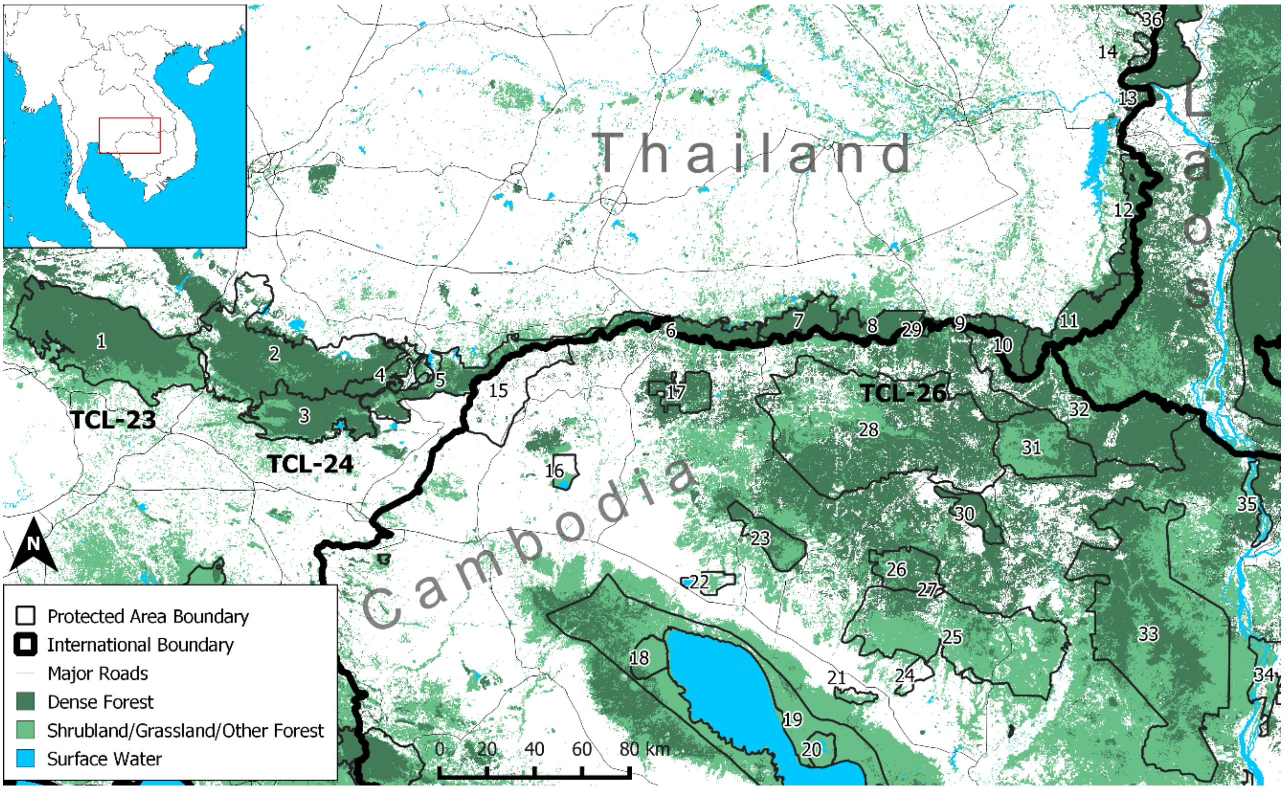

Fig. 1 Study area for connectivity analysis. Protected areas were generated from UNEP-WCMC and IUCN (2019); a full listing of names can be found in Supplementary Materials 1. Forest cover was generated from 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018) reclassed into dense forest (including Forest, Evergreen Forest, Flooded Forest, and Mixed Forest), and Shrubland/Grassland/Other Forest (including Shrubland, Grassland, Wetlands and Orchard/Plantation). Major roads were derived from OpenStreetMap (2019). The eastern section (TCL-24) of the Dong Phayayen-Khao Yai forest complex (2-5) acts as the source site for our simulations.

reflect connectivity itself. Specifically, resistance is point specific, but connectivity is path or route specific, governed by source population distribution and density, resistance of the landscape, and dispersal ability of the organism (Cushman et al. 2013). We employed resistant kernel modeling (Compton et al. 2007) to simulate the effects of different levels of dispersal ability, mortality, and resistance in predicting the dynamic spread of the tiger population over time. The resistant kernel method is particularly suitable for this application given that it produces a spatial incidence function of the expected rate of movement through each cell in the landscape as a function of source population distribution, resistance, and dispersal ability.

Thus, this is an ideal method for predicting rates and patterns of dispersal (e.g., Cushman et al. 2016) and population spread (e.g., Cushman 2015; Barros et al. 2019).

We tested potential resistance maps generated from Indian connectivity and tiger dispersal models (Krishnamurthy et al. 2016; Reddy et al. 2017), an inversed locally-generated habitat suitability model (Ash et al. 2021), and an expert-derived resistance surface (Supplementary Materials 1). Model predictions varied considerably. Empirical models developed outside our study area either overpredicted resistance of relatively intact lowland forest or overpredicted resistance along potentially important forest ridgelines likely to be used by tigers (Karanth 1995; Karanth and Nichols 1998). Further, the inversed locally-generated habitat-suitability model (Ash et al. 2021) predicted unusually high resistance in areas outside DPKY even in large areas of intact forest cover, potentially owing to third order sampling for the model and a lack of representation of certain habitats occurring outside this landscape. The expert model appeared to reflect patterns of likely tiger presence in DPKY from the empirically-developed habitat-suitability model and predicted low resistance along forested ridgelines and large blocks of forest, while appropriately scaling up resistance in human-dominated areas. Expert-based approaches to parametrize resistance surfaces are often criticized as inaccurately reflecting landscape effects on actual movement (Zeller et al. 2012). However, given the empirical models tested did not reflect the particular context and limitations of our system and the expert-model reflected behavioral patterns observed in the literature, the expert-derived resistance surface was identified as the most suitable. Additional details can be found in Supplementary Materials 1.

The expert-based approach utilized land cover data from the 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018). Land cover was reclassified into five resistance values: Dense forest (1), Scrub forest (20), Agriculture-village matrix (50), Reservoirs/Surface water (80), and Urban

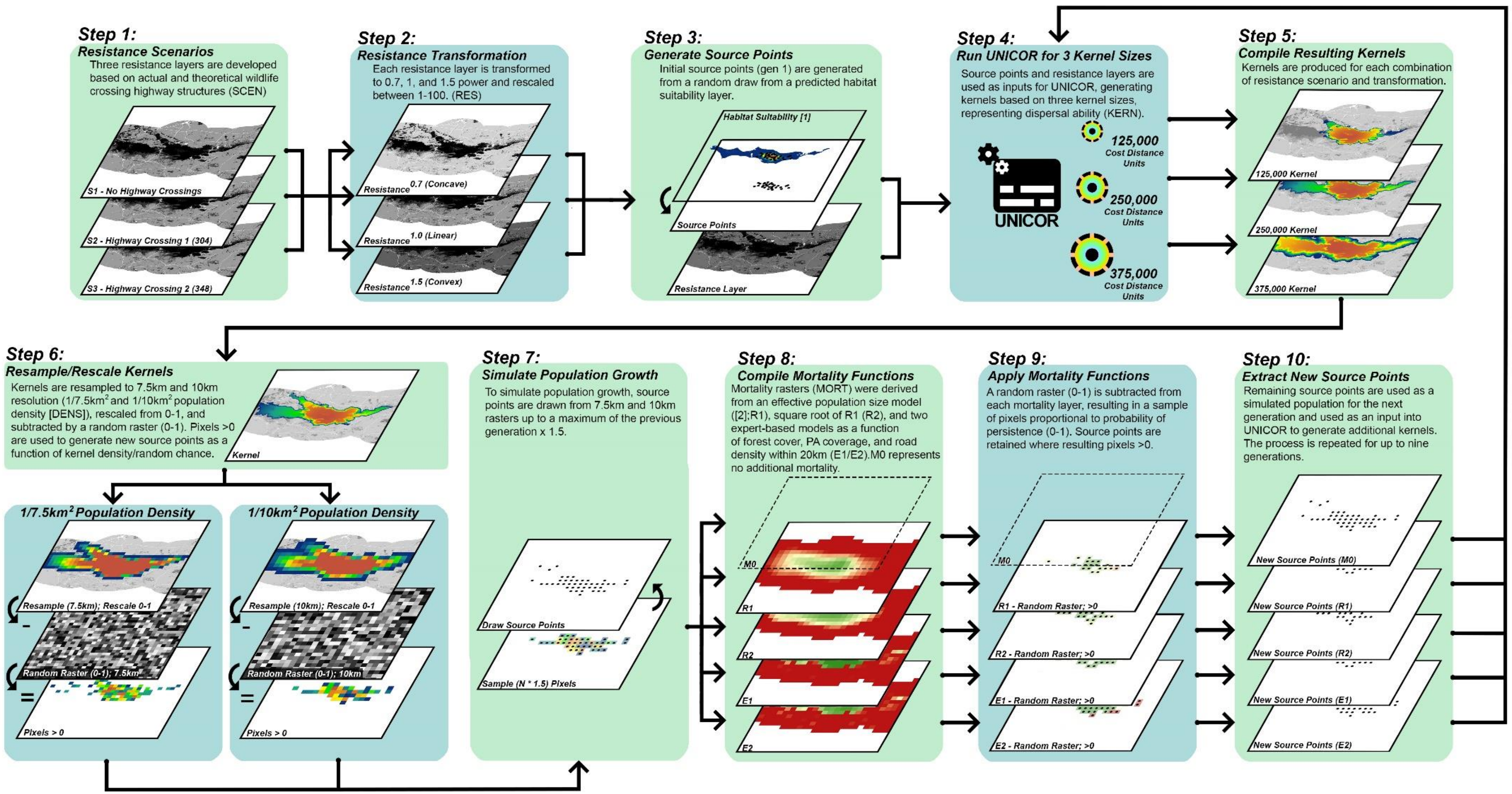

Fig. 2 Diagram depicting methods workflow, including development of highway crossing resistance scenarios (SCEN), resistance transformation (RES), adjusting dispersal ability (KERN), adjusting population density (DENS), and developing and applying mortality functions (MORT). [1] Ash et al.(2021); [2] Reddy et al. (2017)).

areas (100). Minor and major roads (OpenStreetMap 2019) were assigned resistance values of 30 and 100, respectively, where overlapping land-cover values were lower.

Using this resistance layer, we developed three highway mitigation scenarios to test the effect of highway crossing structures (SCEN). Scenarios included: S1 - no mitigation of highways (resistance layer as described above); S2 – mitigation of local highway route 304 through wildlife crossing structures with lower resistance (20) for pixels representing their present locations; and S3 – mitigation of route 304 (S2) and hypothetical mitigation of another local highway, route 348. Further details can be found in Supplementary Materials 1.

To account for resistance uncertainty and evaluate sensitivity to resistance values, we further modified resistance layers to test for three power functions (RES). In addition to the base resistance layer (r10), we also calculated resistance layers to the 0.7 power (r07) and the 1.5 (r15) power which were then rescaled from 1 to 100 and resampled to 250m resolution. These functions transform the linear shape of the resistance function of landcover into concave (0.7 power) or convex (1.5 power) forms, reflecting different hypotheses about the relative resistance of landcover classes (e.g., Reddy et al. 2017).

2.2.2 Population source points

To simulate tiger dispersal from DPKY, we derived a set of source points, representing individual animals, which were distributed probabilistically and proportional to tiger habitat suitability (*sensu* Cushman et al. 2016; Kaszta et al. 2020). First, we rescaled a multi-scale- and shape-optimized tiger habitat suitability model developed by Ash et al. (2021) for DPKY, in which values were proportional to predicted presence on a scale from 0 to 1. Second, we calculated the difference between this layer and a uniform random raster with values ranging from 0 to 1, extracting resulting pixels with positive values as potential source points. Third, we drew a random sample of 30 points from these pixels, representing the upper range of recent population estimates (Ash et al. 2020a). Source points were generated based on evidence that no tigers currently occur in our study area outside of DPKY (Lynam and Nowell 2011; Gray et al. 2017; Rasphone et al. 2019).

2.2.3 Dispersal ability

To evaluate potential dispersal from source points, we utilized UNICOR v2.0 (Landguth et al. 2012) to generate cumulative resistance kernels. These represent the sum of resistance kernels from each source point as a function of total cost distance within the resistance layer and defined kernel width, reflecting predicted density of dispersing individuals for each pixel (Compton et al. 2007; Cushman et al. 2014). We tested a range of dispersal abilities (KERN) by applying kernel widths of 125,000 (125k), 250,000 (250k), and 375,000 (375k) cost-distance units (cu) for each scenario (S1, S2, and S3) and resistance transformation (r07, r10, and r15). These kernel widths correspond to potential dispersal distances of 125km, 250km, and 375km in ideal habitat (resistance value of 1), respectively. While reliable dispersal data for tigers is rare, tigers are known to disperse within this range of distances (Sunquist 2010; Sarkar et al. 2016; Joshi et al. 2016). This enables evaluation of the effect of different dispersal abilities on predicted connectivity (e.g., Cushman et al. 2014, 2016) and population spread (Barros et al. 2019).

2.2.4 Population density and growth

We used a dynamic kernel spread modeling approach first described by Cushman (2015) and recently applied in a similar way in Barros et al. (2019) which models changes in population distribution across a temporally dynamic framework. Specifically, we modeled population spread across nine discrete timesteps, representing non-overlapping generations. At each timestep, new source points were generated based on kernel layers generated by UNICOR in the previous timestep. To test for the effects of different densities of the tiger population (DENS, area-specific carrying capacity) these source points were generated at one of two maximum densities. For each factor combination, kernel surfaces were resampled by bilinear interpolation either to 7,500m (7.5km) or 10,000m (10km) resolution. This resulted in two different densities of source points (maximum of 1/56.26km^2 or 1/100km^2), reflecting potential differences in simulated territory spacing and carrying capacity of tigers in the study area. These resampled kernel layers were rescaled between 0 and 1, which were then subtracted by a uniform random raster (0-1). These difference rasters produced probabilistic layers for the generation of new source points at both densities for the next timestep, proportional to predicted dispersal density.

To determine the number of source points generated at each timestep and to evaluate simulated population spread, we used a maximum population growth rate of 1.5 per generation timestep (previous generation x 1.5). This assumes half a given population are breeding females with a relatively conservative mean lifetime fecundity of three (see Smith and McDougal 1991; Karanth and Stith 1999; Linkie et al. 2006). These source points were then used as an input to run UNICOR for the next generational timestep. This was repeated for each subsequent timestep (up to 9). In effect, the population (N) and distribution of source points for each timestep and factor combination were based on probabilistic sampling of kernels at one of two densities, a maximum potential population growth rate of 50% per timestep, and random chance.

2.2.5 Mortality

To investigate the potential effect of mortality on the simulated population (MORT), at each timestep we filtered source points based on one of five mortality functions, representing spatially differential probability of survival (pixel values ranging 0 to 1).

Function M0 represents the base scenario described above wherein source points for each timestep were determined by a combination of kernel density, maximum potential population growth rate, and random chance, with no additional modifications.

Functions R1 and R2 were based on a tiger effective population size model from Reddy et al. (2017), applied with locally generated spatial layers to predict the potential effective population size of tigers in our study area. The model predicts tiger effective population size as a function of the focal mean of protected area coverage within a 45-km radius, mean forest cover within a 45-km radius, and mean landscape resistance within a 42.5km radius. In contrast to the resistance model derived from Reddy et al (2017), which defined resistance via specific habitat patterns not reflected in our study landscape, the effective population size model parsimoniously generated predictions broadly applicable to tigers throughout their range (i.e., broad extents of forest cover and protected area presence; Walston et al. 2010; Sunarto et al. 2012; Goodrich et al. 2015; Kafley et al. 2016). This model produced predictions reflecting reasonable and consistent patterns of high and low potential presence, and by extension, potential survivability across our landscape. This model, rescaled between 0 and 1, was used to predict mortality risk (R1), representing high mortality risk where predicted potential effective population size is low. To account for uncertainty and investigate the sensitivity of simulations to variation in spatial mortality risk, we calculated the square root of R1, reducing mortality risk in moderate to high suitability areas (R2).

For comparison of approaches and to further test model sensitivity, we also tested two additional expert-based mortality functions with spatially differential probability of mortality (E1 and E2). Evidence suggests that survival probability of dispersing tigers, particularly outside protected areas, can be moderately to extremely low (Smith 1993; Goodrich et al. 2008). To account for this, we generated a simplified spatially differential mortality risk layer in which survival is a function of available tree cover, protected area coverage, and presence of roads. This layer of spatial probability of survival was capped at 0.8 in protected areas with 100% forest cover and no roads within a 20km radius, declining in probability as forest cover decreases and road density within 20km increases, lower by a factor of 10 outside protected areas. To account for uncertainty and to test the sensitivity of results to this mortality function, we also produced a modified expert-derived mortality scenario (E2) following the approach of E1 but modifying the maximum survivability outside protected areas from 10% to 50%. Formulas for these functions are depicted in Supplementary Materials 1.

Mortality functions were applied following the generation of source points for each timestep and parameter combination. At each timestep, mortality layers (values representing low [0] to high [1] probability of survival) were subtracted by a random raster with values from 0 to 1. Source points overlapping with pixels in the difference raster < 0 were simulated mortalities and were removed. In effect, mortality-corrected source points were a function of kernel value (expected dispersers arriving at a location in that time step), modeled likelihood of a disperser surviving at that location, and random chance. Resulting source points were then used for the next generation, up to nine generations in total for all combinations of parameters.

Additional details on mortality functions and their development are expanded upon in Supplementary Materials 1.

2.3 Evaluation of simulated scenarios

Variations in resistance scenarios (SCEN - S1, S2, and S3), non-linear resistance transformation (RES - r07, r10, and r15), dispersal ability (KERN - 125kcu, 250kcu, and 375kcu), population density (DENS - 7.5km and 10km), and mortality function (MORT - M0, R1, R2, E1, and E2) allowed us to simulate a total of 270 tiger population growth and connectivity scenarios across nine generations. To improve the sample size for our evaluation and account for stochastic processes, we ran 10 iterations of each of these scenarios (2,700 scenarios with nine generations/timesteps), resulting in a total of 24,300 simulations. Each simulation produced outputs of simulated population size (*N*), total cumulative kernel extent (*kernext*), and sum of resistant kernel surface (*kernsum*, as a total measure of synoptic connectivity).

Simulated population size (*N*) was defined as the number of source points retained at the end of a given timestep. Kernel extent (*kernext*) was defined as the count of pixels with values greater than the fiftieth percentile of the distribution of values in the originating cumulative kernel surface at generation 1, for each kernel width (125kcu, 250kcu, and 375kcu). Lastly, kernel sum (*kernsum*) was calculated as the sum of all pixel values within a cumulative resistance kernel layer. *N* gives a direct measure of the simulated size of the tiger population, extent presents the extent of occupied tiger habitat, and kernel sum represents the total area-weighted density of tigers as a function of population size and connectivity.

To evaluate variation in population and connectivity among simulations, we summarized the frequencies of population trajectories above the baseline population of *N*=30, below the baseline, and those in which the population had become extinct (*N=0* by timestep 9). For the purposes of evaluating dispersal from the source population in DPKY, we summarized the frequency of simulations in which source points were generated in Khao Yai National Park (KYNP) in the western section of DPKY, Cambodia, and Lao PDR. We considered these areas successfully colonized if populations persisted to timestep 9.

To test for significant differences between *N*, kernel extent, and kernel sum across the four investigated factors - resistance surface (SCEN and RES), dispersal ability (KERN), population density (DENS), and mortality function (MORT) - we conducted a factorial analysis of variance (ANOVA), considering differences significant if $p < 0.05$. To investigate the strength and form of multivariate interactions, we produced time-series maps, surface plots via Matlab (version 18c, MathWorks, Inc., Natick, Massachusetts, United States), and multivariate trajectory analysis (Cushman and McGarigal 2007), plotting predicted connectivity values across the nine timesteps/generations for the mean of all replications for each combination of factors. We used Mantel tests (Mantel 1967) to evaluate the effect size and interactions among factors. We evaluated two distance-based response variables, divergence among scenarios, and displacement of scenarios from initial conditions (Cushman and McGarigal 2007). The Mantel analysis quantifies the effect size (as measured by Mantel *r* value) of the correlation between the response (divergence or displacement) and whether scenarios had the same or different levels of each factor (SCEN, RES, KERN, DENS, and MORT).

3. Results

Our simulations produced clear and significant differences in simulated population size, kernel extent, and kernel sum trajectories with evidence of strong interactions among factors. These factors drive varying degrees of divergence and displacement from initial states, with implications for patterns of dispersal, colonization, and population persistence. We describe these results in detail below.

3.1 Population trajectory and colonization

The majority of simulations (~73%; 1,965), by timestep 9, had population values lower than the baseline (*N=30;* Table 1; Supplementary Materials 2, Table S1). In simulations where population values increased, 72% (507) were those with no additional mortality (M0) and higher population density (7.5km - 62% of runs where *N*>30). Conversely, population declines were associated primarily with elevated spatially differential mortality functions with little difference among population density, resistance transformation, or dispersal ability. However, the frequency of extinction (population declines to 0 by timestep 9) increased with resistance transformation from concave to convex (19% to 49% of extinctions) and higher dispersal ability (2% of simulated extinctions were with a dispersal ability of 125kcu, up to 74% with a dispersal ability of 375kcu).

A large majority of simulations (93%, 2,510) resulted in dispersal to KYNP in at least one timestep. However, colonization of KYNP (presence at timestep 9) was considerably lower (53%, 1,425; Table 1; Supplementary Materials 2, Table S2). Simulations tended to have a lower frequency of dispersal to KYNP when dispersal ability was lower (79% [712] of simulations with dispersal ability of 125kcu vs. 100% for 250kcu and 375kcu simulations), with much lower rates of successful colonization (41% [371] for 125kcu, 68% [609] for 250kcu, and 49% [445] for 375kcu). Dispersal to this area was also slightly lower for simulations with concave resistance (85% [765] of r07 simulations vs 95% and 99% for r10 and r15, respectively), and those with larger territory spacing (90% [1,217] in simulations with 10km spacing vs 96% [1,293] with 7.5km spacing). These trends also hold when considering rates of successful colonization with varying resistance (49% [438] of r07 simulations, 53% [473] of r10 and 57% [514] of r15). Approximately 20% (547) of all simulations resulted in dispersal to areas in Cambodia in at least one timestep, largely attributed to scenarios with no additional mortality (78% [425] of instances). Successful colonization of areas in Cambodia was only observed in 9% (243) of simulations, of which 97% (235) were in scenarios with no additional mortality (M0). There was generally a higher rate of dispersal to and colonization of areas in Cambodia as resistance shifted from concave (r07) to convex (r15) forms and as dispersal ability increased (125kcu to 375kcu). Only 2% (41) of simulations resulted in dispersal to Lao PDR in any timestep, with only 1% (38) of simulations resulting in colonization. All of these cases were in simulations with no additional mortality (M0) and maximum dispersal ability (375kcu), with almost all cases when resistance was convex (r15). Dispersal to and colonization of areas outside the source site did not appear substantially affected by highway mitigation scenario (SCEN).

3.2 Analysis of variance

The factorial analysis of variance of the effects of factors on predicted population size (*N*), extent of connected population (*kernext*), and sum of kernel density (*kernsum*) showed clear and consistent patterns across all three response variables. All main effects, with the exception of highway mitigation scenario (SCEN) and resistance transformation (RES; *N* at timestep 4), were very highly significant across timesteps for all three response variables (Supplementary Materials 2, Tables S3-S29). In contrast, SCEN was only significant for timesteps 2-5 for *kernsum*. Two-way interactions of population density with mortality function (DENS:MORT), mortality function with resistance transformation (MORT:RES), and mortality function with dispersal ability (MORT:KERN) were very highly significant for all timesteps for all three response variables. Two-way interactions of highway mitigation scenario and mortality (SCEN:MORT) were significant for timesteps 2-6 for *kernsum* and timesteps 5-7 for *N*. Among three-way interactions, DENS:MORT:KERN was significant in all timesteps across response variables, MORT:RES:KERN was significant for all timesteps and response variables with the exception of two timesteps for *N*, and DENS:RES:KERN was significant in 75% of time steps for all response variables. The three-way interaction DENS:MORT:RES was significant in 88% of timesteps for *N* and *kernsum*, but only 50% of timesteps for *kernext*. Three-way interactions involving SCEN (SCEN:MORT:RES and SCEN:MORT:KERN) were only significant at timestep 5 for *kernsum*. None of the other three-way interactions were significant for any timestep for any response variable. The four-way interaction of DENS:MORT:RES:KERN was significant across 75% of timesteps for *N*, 88% of timesteps for *kernsum*, and 50% for *kernext*, and the four-way interaction of SCEN:DENS:MORT:RES was only significant at timestep 3. The ANOVA results underscore two main outcomes. First, there are strong multivariate interactions, particularly between dispersal ability (KERN), resistance transformation (RES), mortality function (MORT), and territory spacing (DENS). Second, highway mitigation scenario (SCEN) and its interactions did not affect response variables as significantly compared to other factors in our modeling experiment. Given it is difficult to interpret the main effects in the presence of strong interactions, further analysis focused on deconstructing these interactions.

3.3 Multivariate interactions

Time-series maps (Figure 3; Supplementary Materials 3, Figures S1-S6) and surface plots (Figure 4; Supplementary Materials 3, Figures S7-S12) demonstrated a number of strong interactions between factors.

Table 1 Summary of simulation results within factor groups by parameter at timestep 9 out of 2,700 simulations. Results are summarized by (a) simulated population (*N*) at timestep 9 and (b) number of simulations in which source points were generated in Khao Yai National Park (NP), Cambodia, or Lao PDR at timestep 9 (e.g., successful colonization). This reflects a summary of all simulation results specific to each factor group - resistance surface (highway mitigation scenario [SCEN] and resistance transformation, [RES]), dispersal ability (KERN), population density (DENS), and mortality function (MORT) - amalgamating all other factors and parameters. A detailed breakdown of simulation results can be found in Supplementary Materials 2; Tables S1-S2.

		(a)				**(b)**		
Factor	**Parameter**	**N>30**	**N=30**	**N= 1 to 30**	**N = 0**	**Khao Yai NP**	**Cambodia**	**Lao PDR**
SCEN	S1	233	7	500	160	455	79	16
	S2	238	11	508	143	498	76	9
	S3	235	11	499	155	472	88	13
DENS	10km	268	18	812	252	641	99	18
	7.5km	438	11	695	206	784	144	20
MORT	M0	507	5	28	-	474	235	38
	E1	4	3	363	170	169	1	-
	E2	21	5	393	121	220	1	-
	R1	-	-	373	167	124	-	-
	R2	174	16	350	-	438	6	-
RES	r07	243	17	555	85	438	64	-
	r10	240	5	508	147	473	69	1
	r15	223	7	444	226	514	110	37
KERN	125kcu	264	17	608	11	371	12	-
	250kcu	256	10	525	109	609	92	-
	375kcu	186	2	374	338	445	139	38
	All	706	29	1507	458	1425	243	38

First, mortality function interacts strongly with dispersal ability. In the absence of spatially elevated mortality risk (M0), all three response variables increase dramatically at later timesteps, particularly for simulations with greater dispersal ability and higher potential population density (7.5km). In contrast, simulations with elevated mortality risk (R1, R2, E1, and E2) show no large increase in any of the three response variables across timesteps, and, in simulations with the highest dispersal ability (375kcu), populations frequently declined to extinction as a result of dispersal mortality exceeding replacement.

Generally, *N* and *kernsum* values increased in simulations with higher maximum potential tiger density (7.5km), especially in scenarios with higher dispersal and (relatively) lower mortality risk. *Kernext* increases are greatest in scenarios with low mortality, high dispersal, and lower maximum potential tiger density, as this forces the population to spread more rapidly across a greater extent as available territories fill faster at lower density. The different resistance scenarios interact with mortality, density, and dispersal such that *N* and *kernsum* variables greatly increase, especially in later timesteps. This is the case when there is low mortality risk, high dispersal, high potential maximum density, and when resistance is convex and does not highly penalize marginal habitat. In this combination of parameters, the rate of population growth is maximized.

3.4 Multivariate trajectory analysis

Multivariate trajectory analysis plots (Figure 5; Supplementary Materials 3, Figures S13-S18), show trajectories over time of simulations corresponding to all combinations of dispersal ability, territory density, resistance transformation, and mortality scenario in a three-dimensional space defined by *kernext*, *kernsum* and *N*. These trajectories show that the major differences are related to mortality risk (MORT) interacting with dispersal ability (KERN), with additional, but lesser effects, from resistance transformation (RES) and population density (DENS). Specifically, most scenarios that have elevated mortality risk as an inverse function of habitat quality do not result in large increases in any of the three connectivity measures (*kernext*, *kernsum*, or *N*) over the simulated time frame. In contrast, scenarios in which there is no elevated mortality risk (red spheres in Figure 5) show large increases over time, especially for scenarios in which population density is higher (up to 1/7.5km^2), with substantially lesser effects for different resistance surfaces. Figure 5 shows one view of this three-dimensional space at timestep 6 and readers are encouraged to view the full 3D dynamic visualizations in Supplementary Materials 3.

3.5 Analysis of effect size and interactions among factors using mantel tests

The full table of all Mantel results sorted by effect size is shown in Supplementary Materials 2 (Tables S30-S37) for divergence and displacement, respectively. The main results are most easily presented as line graphs (Figures 6 and 7). For divergence of scenarios from each other over time, mortality function (MORT) had the dominant effect. For each response variable (*kernext*, *kernsum*, *N*, and the multivariate combination of these) the mortality model matrix in which all mortality scenarios are coded as 1 and the non-mortality scenarios as 0 was most supported across all timesteps, followed by the ordinal mortality model in which scenarios were ordered from lowest to highest mortality risk (MORT2). Dispersal ability (KERN) and the interaction of dispersal distance and ordinal mortality (KERN-MORT2) had moderate relative effect size, which was nearly equal to mortality in the first few timesteps but dropped to low relative support, comparatively, in later timesteps (Figure 6). For displacement of response variable values from initial condition, there was a different, but even clearer pattern (Figure 7). For all response variables (*kernext*, *kernsum*, *N* and the multivariate combination of these), the interaction between dispersal ability (KERN) and mortality (MORT and MORT2) had the highest Mantel correlation across all timesteps. There was similar support for mortality effects alone (MORT), and mortality interacting with resistance transformation (MORT-RES).

There were consistent relationships in terms of the relative effect size of the correlation between the best model and the four response variables over timesteps (Figure 8). Across all timesteps, the best Mantel model had the largest correlation with predicted *N*, followed by *kernext* and the multivariate combination of the three response variables. *Kernsum* had the lowest correlation with divergence or displacement across all timesteps.

4. Discussion

The ability of models to produce reliable and meaningful predictions of population distribution, abundance and connectivity is governed by the interactive and temporally dynamic effects of several factors such as landscape resistance, population density, dispersal ability, and mortality. Using a spatially- and temporally-explicit simulation approach, we investigated the impacts of these factors on population

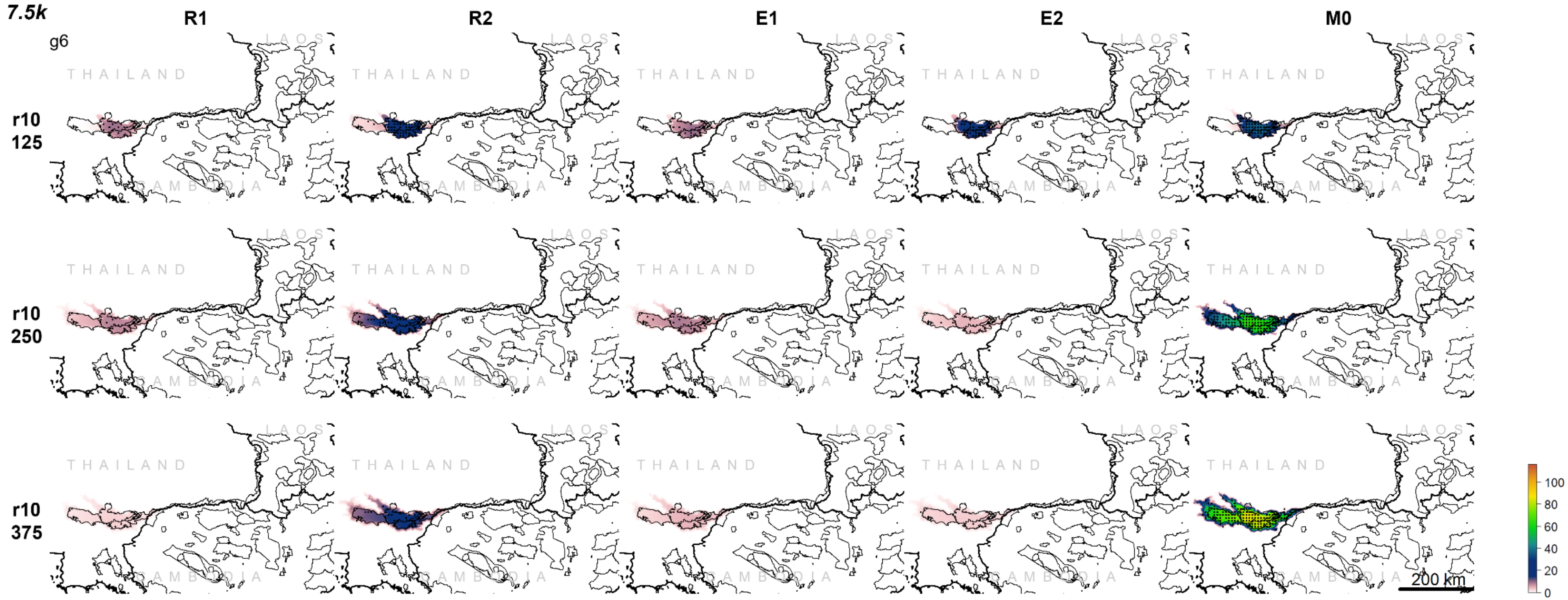

Fig. 3 Sample maps demonstrating divergence in cumulative resistance kernels and populations between combinations of mortality function (MORT – R1, R2, E1, E2, and M0) and dispersal ability (KERN – 125kcu, 250kcu, and 375kcu) at timestep 6, holding highway mitigation scenario (SCEN - S3), territory spacing (DENS - 7.5km), and resistance transformation (RES - r10) constant. Values reflect the expected cumulative density of dispersing individuals from each source point. Additional maps and timestep animations can be found in Supplementary Materials 3, Tables S1-S6.

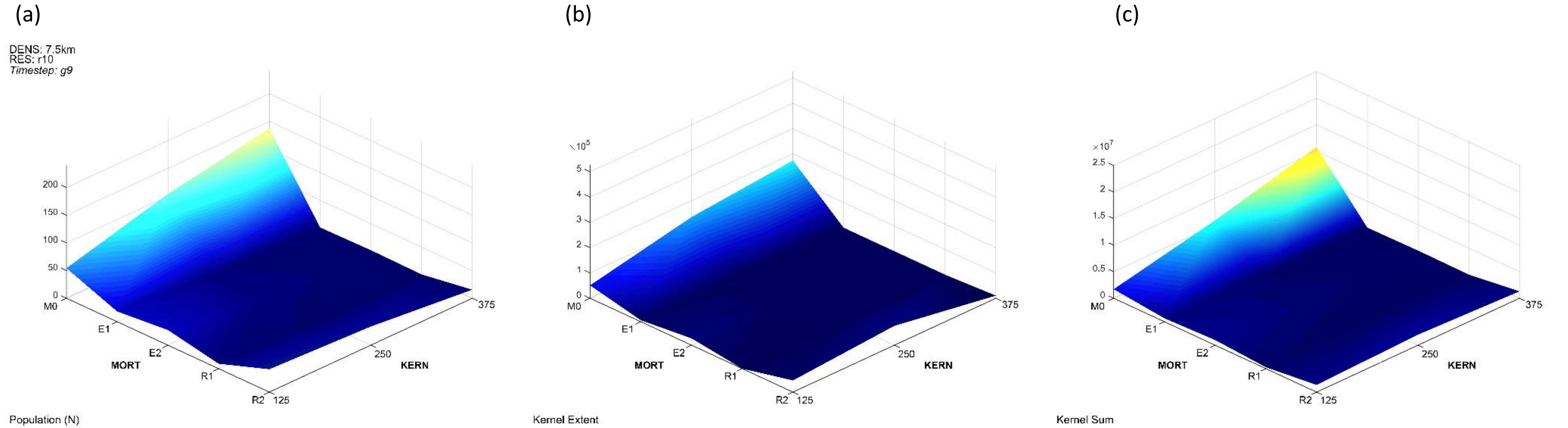

Fig. 4 Surface plots showing variation in predicted (a) population size (*N*), (b) kernel extent, and (c) sum of kernel value for the 15 combinations of dispersal ability (KERN - 3 levels) and mortality risk (MORT - 5 levels) for resistance transformation 1.0 (RES – r10) and maximum population density 1/7.5km^2 (DENS – 7.5km) at timestep 9. The figure shows a strong interaction between dispersal ability and mortality risk, with the predicted values of all three variables remaining low for all scenarios involving elevated mortality risk, across all dispersal abilities, while all three variables increase linearly with dispersal ability when there is no differential mortality risk across the landscape. Animations of these and other plots can be viewed in Supplementary Materials 3, Tables S7-S12.

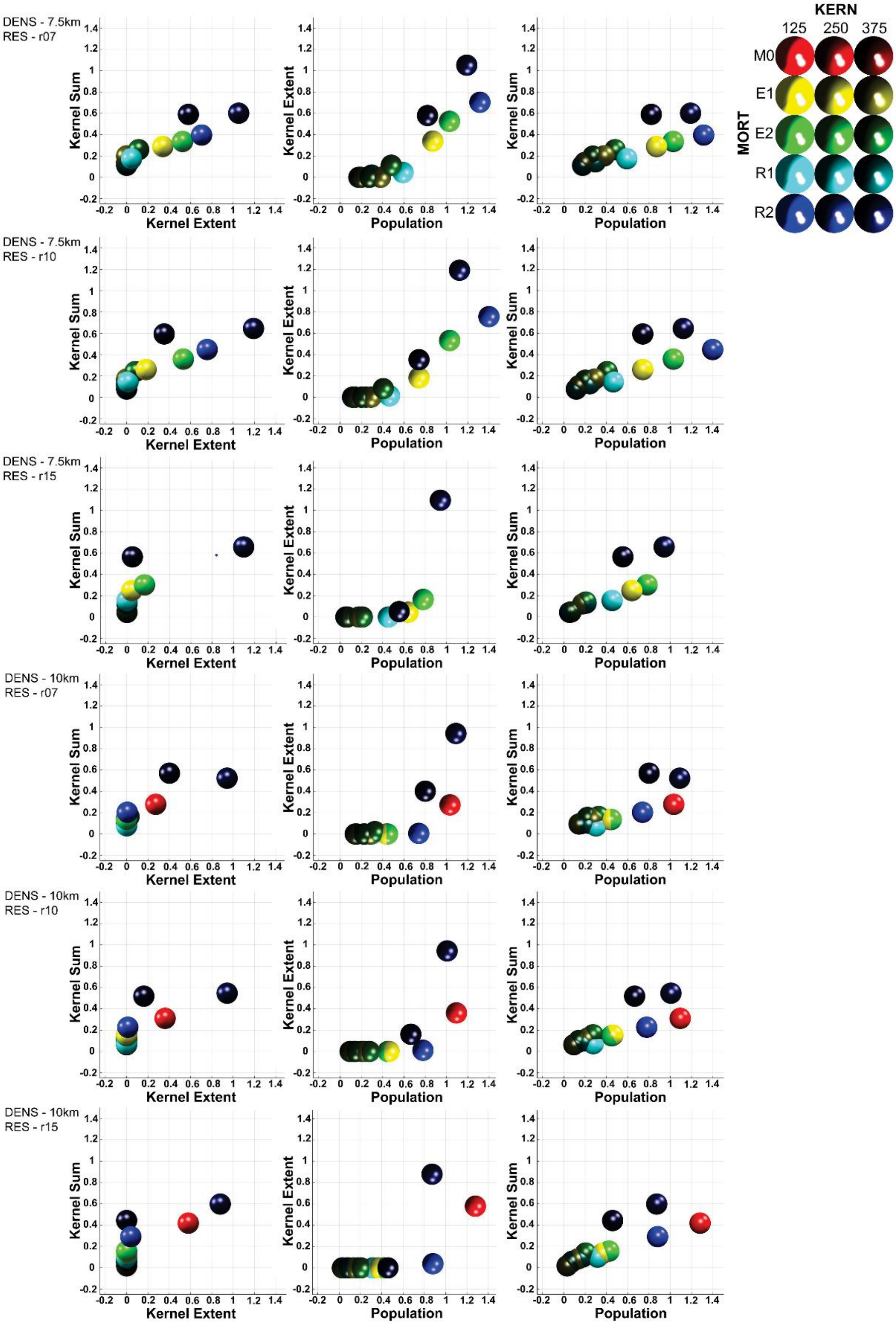

Fig. 5 Three orthogonal views of the three-dimensional trajectory of scenarios in a space defined by kernel extent, sum kernel value, and population size, at timestep 6 across population density (DENS) and resistance transformations (RES). Sphere color indicates different combinations of dispersal ability (KERN) and mortality risk (MORT). The figure shows that scenarios with low mortality risk (M0; red spheres), in which population density is high, have much greater predicted kernel extent, kernel sum, and higher simulated population size (extreme values extending outside axis limits). Animations of these and other plots can be viewed in Supplementary Materials 3, Tables S13-S18.

connectivity and population size of tigers in Eastern Thailand. Our study demonstrated a high degree of sensitivity of simulated population size, extent and connectivity to parameter values and, in particular, evidence of strong interactions between factors which may drastically affect results. Dispersal ability and spatially differential mortality risk dominated predictions of connectivity and population size, and these factors strongly interacted to affect predictions. While similar dominant effects of dispersal ability on connectivity predictions were previously reported by several studies (e.g., Cushman et al. 2010, 2013, 2016), less attention has been directed to the effect of spatially differential mortality risk on population size and connectivity (Kramer-Schadt et al. 2004; Kaszta et al. 2019, 2020).

This is among the first studies to explicitly evaluate the interaction of dispersal ability and mortality on population size, distribution, and connectivity in a spatially- and temporally-explicit dynamic framework. Distribution and density of individuals in the population had intermediate effects on predictions, landscape resistance overall had relatively low impacts on predicted connectivity, and small-scale mitigation of linear barriers had limited measurable impact. Importantly, there was a high degree of variation in the relative importance of factors depending on whether the assessment was based on divergence among scenarios or displacement of scenarios from initial conditions. Furthermore, results differed depending on whether the assessment was based on extent of connected kernel, sum of kernel value, or population size. Our study also documented temporal variation in the relative effects of different factors on connectivity. These results are of particular relevance to the development of connectivity and species dispersal modeling and for conservation planning. We elaborate and discuss each of these main results in the paragraphs that follow.

First, for both displacement (change of a single scenario from initial condition) and divergence (difference between scenarios at a given timestep) of scenarios, we found that spatially heterogeneous mortality risk and dispersal ability dominated predictions of connectivity and population size. Main effects for these factors had very highly significant differences in population and connectivity metrics across all timesteps and exhibited the strongest effects when comparing Mantel correlations. Spatially heterogeneous mortality risk is frequently not accounted for in dispersal and population connectivity modeling studies

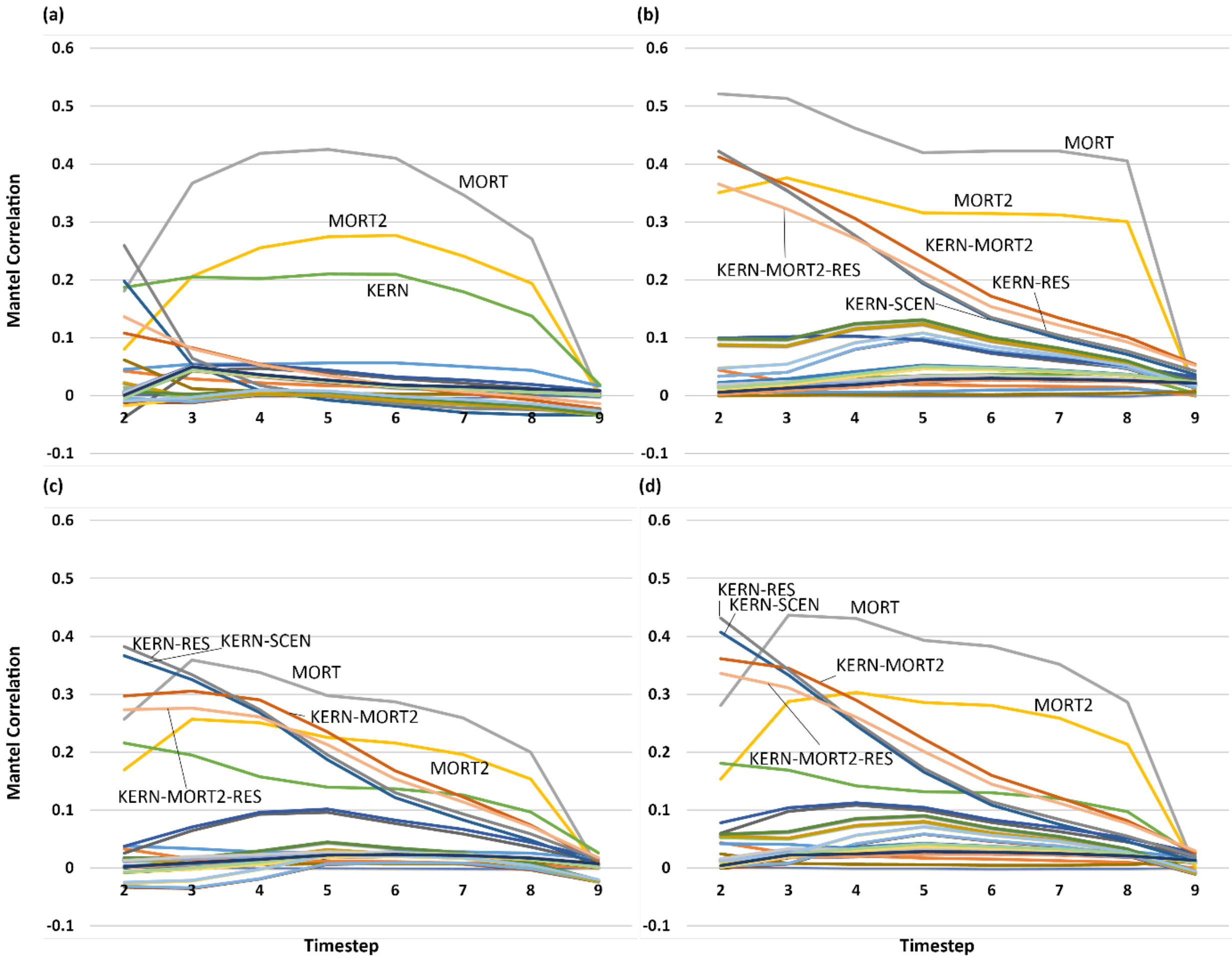

Fig. 6 Mantel correlations between response variables (a) Kernel Extent, (b) Population Size, (c) Kernel Sum, and (d) multivariate distance between these response variables and divergence among scenarios over timesteps. Timestep is depicted on the x-axis with Mantel correlation on the y-axis. The highest correlating factors are labeled: MORT – mortality model matrix with all mortality scenarios coded 1 and non-mortality 0; MORT2 – mortality model matrix with scenarios coded ordinally from highest to lowest degree of mortality risk; KERN – dispersal distance varying with kernel bandwidth; KERN-MORT2 – model matrix combining KERN and MORT2 by addition; KERN-RES – model matrix combining KERN and resistance model matrices by addition; KERN-SCEN – model matrix combining KERN and highway mitigation model matrices by addition; and KERN-MORT2-RES – model matrix combining KERN, MORT2 and RES model matrices by addition.

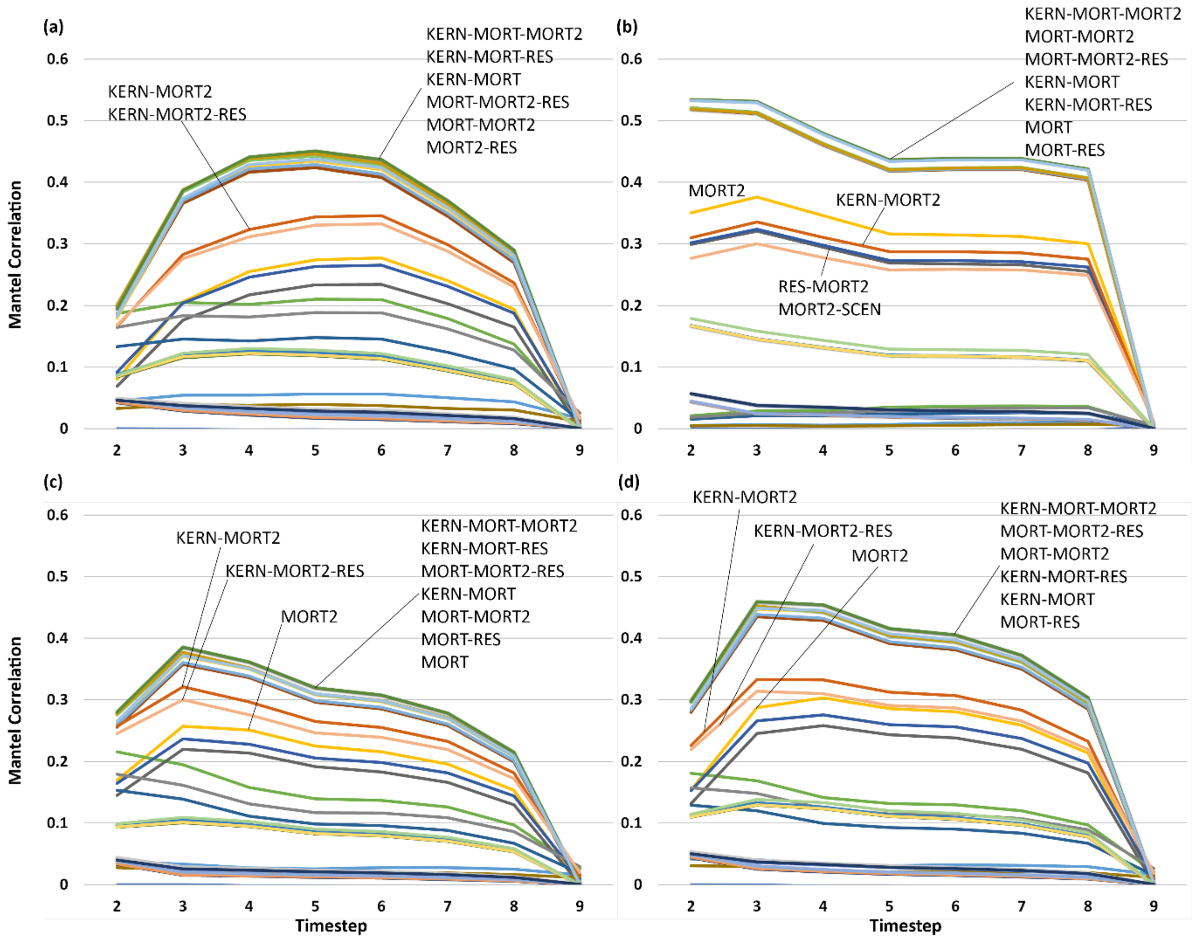

Fig. 7 Mantel correlations between response variables (a) Kernel Extent, (b) Population Size, (c) Kernel Sum, and (d) multivariate distance between these response variables and displacement of scenarios from initial value over timesteps. Timestep is depicted on the x-axis with Mantel correlation on the y-axis. The highest correlating factors are labeled: MORT – mortality model matrix with all mortality scenarios coded 1 and non-mortality 0; MORT2 – mortality model matrix with scenarios coded ordinally from highest to lowest degree of mortality risk; KERN – dispersal distance varying with kernel bandwidth; KERN-MORT2 – model matrix combining KERN and MORT2 by addition; KERN-RES – model matrix combining KERN and resistance model matrices by addition; MORT2-SCEN – model matrix combining MORT2 and highway mitigation model matrices by addition and KERN-MORT2-RES – model matrix combining KERN, MORT2 and RES model matrices by addition.

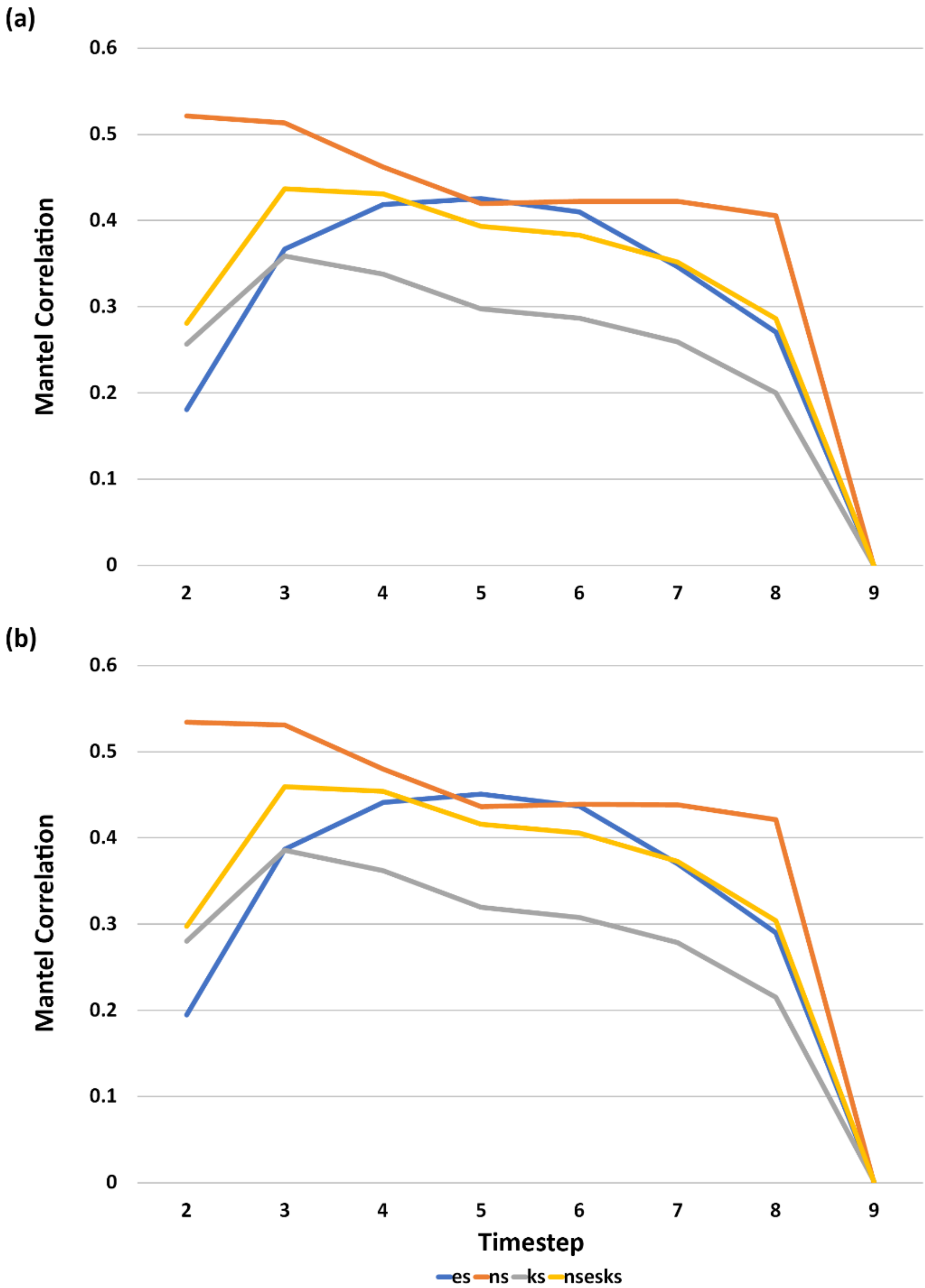

Fig. 8 Plot of Mantel correlation of the best model for (a) divergence and (b) displacement over timesteps for each of the response variables: es – kernel extent, ns – population size, ks – kernel sum, and nsesks – multivariate combination of kernel extent, population size, and kernel sum. In both cases, population size had the strongest correlation with the best scenario model matrix over nearly all timesteps, equaled only by kernel extent in timestep 5.

(Thatte et al. 2018; Kaszta et al. 2019), despite evidence that dispersal- or hostile matrix-related mortality can exert a considerable influence on species populations and lead to greater vulnerability to demographic stochasticity (Carroll and Miquelle 2006; Thapa 2014; Naude et al. 2020). Resistance surfaces, which are widely used, may indirectly account for mortality as a function of a more generalized resistance to dispersal (Cushman et al. 2010; Zeller et al. 2012; Kaszta et al. 2019, 2020; Diniz et al. 2020), though this relationship may be tenuous and lack transparency. Its entanglement with other factors affecting distribution and movement precludes the ability to discern how mortality influences connectivity via realized dispersal, potentially leading to overestimates of the degree of connectivity within a landscape from the perspective of the organism in question (Diniz et al. 2020). Our results suggest that the application of an additional function of mortality in connectivity modeling can produce highly divergent conclusions on the degree of connectivity within a landscape and trajectory of the population of study. These results are similar to the findings of Kaszta et al. (2019) and Kramer-Schadt et al. (2004) in which the introduction of mortality risk via infrastructure resulted in isolation and declines of populations of wide-ranging felids that would have otherwise been predicted to be highly connected based on habitat quality and resistance alone.

Similarly, our results were particularly sensitive to dispersal ability, which exerted a relatively disproportionate effect on population and connectivity trajectories. This is consistent with a number of other studies in which predictions of landscape configuration and connectivity were extremely sensitive to parameters associated with dispersal ability or related parameters dictating movement thresholds (Kanagaraj et al. 2013; Moqanaki and Cushman 2017). While some models may be relatively insensitive to dispersal ability (Puyravaud et al. 2017), this nonetheless underscores the need for particular care in developing these parameters. Ideally, dispersal models should be parameterized with reliable, empirically-derived movement data, though this can be considerably difficult to obtain and are rarely applied in dispersal modeling studies (Cushman 2006; Zeller et al. 2012; Vasudev et al. 2017). This presents a particular challenge to those investigating landscape connectivity where the dispersal ability of target species is poorly understood. Studies in which the latter situation applies may benefit from testing a range of dispersal ability values to account for this uncertainty and potential sensitivity in such parameters.

Second, dispersal ability and mortality risk strongly interacted to affect connectivity predictions, with very high predicted connectivity and population size when dispersal ability is high and mortality risk is low. Importantly, however, when dispersal ability and mortality risk are both high, these factors interacted to produce high mortality rates as dispersing individuals encountered high-risk locations with greater frequency, leading to elevated mortality and declining populations. In these scenarios, overall connectivity and population size remained low and, in some cases, the population declined to extinction even though dispersal ability was high. When mortality risk is high, lower connectivity, due to lower dispersal ability or higher landscape isolation, can produce more viable and larger populations than when dispersal is high (Cushman 2006). These kinds of interactions were also a key finding of Cushman et al. (2010) in which the effects of fragmentation on simulated populations and connectivity became stronger with increasing dispersal ability. Dispersal is a highly costly and risky process (Bonte et al. 2012), and such patterns may emerge when species disperse into hostile, human-dominated matrices. Species with high vagilities are more likely to encounter barriers or sources of mortality during the dispersal process compared to less vagile species (Carr and Fahrig 2001; Carr et al. 2002) which may undermine population viability if mortality rates become unsustainably high (Kramer-Schadt et al. 2004). In effect, elevated mortality risk in highly fragmented landscapes may result in selection pressure for lower dispersal ability (Ewers and Didham 2006). Gibbs (1998) documented greater persistence of organisms in landscapes with low habitat area when dispersal rates were low, a pattern further demonstrated by Cushman et al. (2010) through resistant kernel simulation modeling. These patterns are reflective of connectivity being governed by complex interactions of physiological traits, animal behavior, and landscape structure (Goodwin and Fahrig 2002). Given the strong effects of these interactions, it is possible that, without explicitly testing for these in connectivity modeling studies, their effects may remain obfuscated and poorly understood.

Third, we found that mitigating linear barriers, namely major highways, by reducing local resistance in one location, such as through single overpass structures and tunnels, had very limited impact on kernel extent, kernel sum, or population size. There is strong, consistent evidence of the negative effects of roads on connectivity and population persistence (Kerley et al. 2002; Kramer-Schadt et al. 2004; Coffin 2007; Jackson and Fahrig 2011; Thatte et al. 2018). Wide-ranging carnivores with long dispersal abilities can be particularly sensitive to fragmentation caused by roads (Trombulak and Frissell 2000; Carroll et al. 2001). Roads are known to be a source of significant risk for large felids (Schwab and Zandbergen 2011; Moqanaki and Cushman 2017), potentially leading to isolation of populations when incorporated into movement or genetic models (Kramer-Schadt et al. 2004; Thatte et al. 2018). Other factors, particularly mortality and dispersal ability, were more important in our study and dominated patterns of divergence and displacement in our metrics. The literature suggests that one of the critical effects of roads is direct mortality, in some cases, more so compared to their effects as barriers to movement (Jackson and Fahrig 2011). Such risks were incorporated in our mortality functions which had a large effect, but investigation of finer-scale impacts of roads on individuals was not possible in our study. For studies utilizing cumulative resistance kernels, incorporating the effects of roads by modifying resistance in a small area may result in similar patterns where other factors dominate predictions of connectivity in comparison. The dominating effects of other factors in our study, particularly mortality, reinforces the fact that modeling studies investigating the potential effects of small-scale individual highway mitigation structures must incorporate these factors. Further, costly efforts to mitigate the effects of linear barriers such as highways may be of little benefit if mortality risk and resistance across the landscape as a whole remain high.

Fourth, patterns and degrees of landscape resistance independently had relatively low impacts on predicted connectivity in comparison with dispersal ability and mortality risk. Our results are consistent with evidence from studies utilizing similar methods in which cumulative resistance kernels were found to be relatively insensitive to differences or error in resistance surfaces (Compton et al. 2007; Cushman et al. 2014; Moqanaki and Cushman 2017; Kaszta et al. 2020). Our findings are also aligned with studies in which resistance emerges with weaker effects relative to dispersal ability (Cushman et al. 2010, 2016; Moqanaki and Cushman 2017), which was comparatively stronger in its effect in our study. These results may contribute to evidence that understanding the spatial patterns of mortality risk, dispersal ability of the species, and species distribution and abundance in the landscape may be more important than optimal parameterization of resistance surfaces. This is important because a large amount of research has been dedicated to methods of estimating landscape resistance from habitat (Zeller et al. 2012; Keeley et al. 2016), movement (Elliot et al. 2014; Zeller et al. 2017), and genetic (Zeller et al. 2017; Reddy et al. 2017; Winiarski et al. 2020) methods. These are often extremely challenging studies that are logistically difficult to implement and highly costly. If landscape resistance is generally of low impact relative to other major factors influencing connectivity and population dynamics, then future investment in research and management application might better be focused on understanding spatial patterns of mortality risk, documenting distribution and abundance of source populations, and quantifying movement and dispersal distances with greater precision.

Fifth, distribution and density of individuals in the population had intermediate effects on connectivity predictions, more than resistance, but less than dispersal ability or mortality risk. Similar studies commonly examine how connectivity influences population metrics such as size or density, but there is a dearth of evaluations of how thresholds of population density interact with other factors to influence connectivity (Carmona and Franco 2015). Our results seem consistent with available evidence suggesting models may be sensitive to parameters governing source population size and density (e.g., Cushman et al. 2013). Population size, along with dispersal ability were strong factors influencing connectivity in simulations conducted by Cushman et al. (2010, 2013) which found dramatic differences in predicted connectivity and core areas depending on how source locations were modeled (e.g., based on potential vs. actually occupied habitat). This shows that the extant distribution and population size of a focal species has a large influence on the functional connectivity and subsequent changes in population size and connectivity over time. In territorial species, increased density can necessitate dispersal (Matthysen 2005). With larger territory sizes, high-quality habitat may be limited, forcing dispersers to marginal habitat. These patterns are reflected in our study in which higher population density simulations allowed for utilization of available habitat more than those simulating populations at lower density. This resulted in significant differences in population and connectivity metrics.

Sixth, we found variation in the relative importance of factors depending on whether the assessment was based on divergence among scenarios or displacement of scenarios from initial conditions. For divergence between scenarios at the same timestep, mortality risk was predominant, while the interaction between mortality risk and dispersal ability primarily affected displacement of scenarios from initial conditions. Populations are dynamic, and explicitly measuring spatio-temporal dynamism within populations may improve models of ecological change and their interpretation, which may augment the development of management and conservation interventions. Cushman and McGarigal (2007) demonstrated this, quantifying important interactions and differences in the magnitude of the effect of timber cutting patterns and intensity on marten habitat over time. Understanding the rate of divergence and displacement in a multivariate response space and quantifying the factors that drive differences in these measures is critical to quantitative and rigorous evaluation of the effects of varied and potentially nuanced factors on population size and connectivity in a temporally dynamic context (Cushman and McGarigal 2007).

Seventh, we saw differences in results depending on whether the assessment was based on kernel extent, kernel sum, or population size. Generally, there were higher correlations between factors and population size than with kernel extent or kernel sum, notably with MORT/MORT2 at earlier timesteps. Kernel extent generally had somewhat higher correlations with factors than kernel sum. Both kernel metrics were highly correlated with predicted population size suggesting they may be reliable indicators of effects on population connectivity and viability. These metrics could also, in some cases, be used as a surrogate for population size, which is often harder to estimate or predict. However, population size had a stronger overall relationship than either kernel measures, and, importantly we note that this simulation of population size was built on a kernel model of spread, which makes an objective and independent assessment of the utility of kernel density as a surrogate for population size and density difficult. Nonetheless, past empirical studies (Puyravaud et al. 2017; Reddy et al. 2017) found strong positive relationships between kernel density predictions and observed species distribution and density. Furthermore, individual-based spatially explicit simulation modeling has shown a strong positive correlation between resistant kernel connectivity predictions and population density (Puyravaud et al. 2017).

Eighth, we observed considerable temporal variation in the relative effects of different factors on connectivity across our simulation time period. Specifically, we found the impacts of mortality risk peaked at different timesteps for different response metrics. For population size, the correlation was highest in the second timestep, for kernel extent in the fifth, and for kernel sum in the third. This suggests that the effects of different factors on populations and their connectivity are dependent on the context of the population in terms of whether it is expanding from a small initial extent and size or reaching equilibrium with existing landscape conditions. These results reflect evidence of time-dependence in landscape connectivity, an important implication given that connectivity studies often do not account for time in their models (Kramer-Schadt et al. 2004). Simulations by Cushman and McGarigal (2007) on the effects of forest cutting regimes on marten habitat responses resulted in considerable time-lags in observed effects, occurring decades after anthropogenic disturbance. The potential for these delayed effects has important management implications for a number of species as, in many cases, processes of landscape fragmentation have occurred relatively recently or are ongoing, suggesting their full effects may yet to be realized (Ewers and Didham 2006; Kaszta et al. 2020). Being able to discern these effects further reinforces the utility of incorporating timesteps and multivariate trajectory analysis into connectivity modeling.

4.1 Implications for tiger management and conservation

Our study focused primarily on investigating the sensitivity of population and connectivity models to parameterization decisions, using tigers as a case study. Incorporating movement and other empirical data into such models is necessary for generating reliable conclusions (Cushman 2006; Vasudev et al. 2017). The use of such data in connectivity modeling is rare, often resulting from lack of availability, and is a considerable challenge for understudied or endangered species that nonetheless require urgent intervention (Zeller et al. 2012). In these circumstances, such as for our study population, it is advisable to test a range of parameters to account for this uncertainty and to discern potentially important patterns.

In our study, a number of strong patterns emerged that may have important implications for the conservation of tigers in this landscape. A majority of simulations resulted in dispersal to KYNP, though successful colonization was less frequent. There was a low frequency of dispersal to areas of Cambodia and successful colonization was extremely rare in our study. These cases were primarily simulations with extremely high dispersal ability and convex resistance, and virtually all were with no additional mortality, which is unlikely to be biologically realistic. Mortality was a key factor in our study and would potentially act as a considerable obstacle for long-range dispersal and re-colonization. Further, dispersing tigers tend to have disproportionately higher rates of mortality than established residents in protected areas (Gurung et al. 2006; Goodrich et al. 2008). While male tigers have been known to disperse considerably long distances, female tigers have a tendency for philopatry and shorter dispersal (Sunquist et al. 1999; Singh et al. 2013; Gour et al. 2013). This may preclude natural recolonization and recovery in Cambodia and Lao PDR even with low mortality rates.

4.2 Limitations

While our study contributes a number of important insights, simulations are inherently limited, given that models cannot account for the entirety of potential factors that dictate population spread over long time periods, and require empirical validation (Cushman 2006; Zeller et al. 2012). Our study did not account for dynamic processes of landscape and climate change which may exert considerable influence on our study population over the next several decades. Cambodia, for example, has experienced considerable rates of deforestation and limited protected area security (Rostro-García et al. 2016; Lohani et al. 2020), which would undermine efforts to support population persistence and maintain broad-scale connectivity. Conversely, we did not test scenarios of habitat restoration which may otherwise augment movement through our study landscape (e.g., Kaszta et al. 2019). Our framework simplifies processes of population spread that may be further influenced by complex demographic, behavioral, and life-history traits. These may include differential fecundity and variable mortality by age or sex class, or distinguishing between residents and dispersers, which may have drastically different perceptions of the landscape (Elliot et al. 2014). Further, evidence from other studies suggests a strong relationship between tiger densities and prey abundance, which are likely to influence population persistence and range expansion (Karanth and Stith 1999; Karanth et al. 2004).

Ultimately, incorporating these factors would have introduced additional layers of complexity, further entangling confounding factors and making interpretation challenging. While empirical validation is ideal for population connectivity modeling, this is notably challenging for long-term simulation studies such as ours. Nonetheless, given the conservation urgency of many species, it is important to evaluate potential scenarios affecting population size and connectivity before they unfold (Kaszta et al. 2020). We believe our analysis was sufficient for achieving our study objectives, particularly for investigating the sensitivity of models to some of the most central factors that influence connectivity and population spread. Our flexible and powerful framework may prove useful for explicitly testing these additional factors in future studies.

We note that there are a number of potential fine-scale effects that may also influence population dynamics but were only partially addressed by our study. Mortality, as an effect, is incorporated through mortality functions, though these are introduced at the end of each timestep based on kernel density and random chance. This represents a more explicit process of mortality than is typically inferred via resistance surfaces (Zeller et al. 2012; Diniz et al. 2020). However, this does not capture finer-scale elevated mortality during dispersal events, such as when simulated individuals cross roads or are poached, which could be a limiting factor in population connectivity (Kramer-Schadt et al. 2004; Thatte et al. 2018).

Further, mortality in our study was higher outside of protected areas, owing to evidence that dispersal outside these areas is typically associated with a higher risk of mortality (Smith 1993; Goodrich et al. 2008). However, the effectiveness of protection may vary considerably across formally gazetted protected areas, some of which may lack sufficient deterrents to poaching that may otherwise differentiate these parks from a hostile matrix. We did not test scenarios reflecting high rates of mortality, typical of increased poaching pressure within protected areas or in areas with poor enforcement and high poaching pressure. However, given the strong effect of mortality in our study, this would have likely dramatically increased rates of extinction, reinforcing the importance of reducing mortality at a landscape scale.

Incorporating green infrastructure along highways has been recommended to help mitigate the effects of an expanding network of roads on Southeast Asian wildlife (Clements et al. 2014). While we did not document strong effects of individual highway mitigations in our study, we recommend further, dedicated research at finer scales to determine the local effect of existing structures on wildlife in the area. There has been a paucity of studies formally investigating the effect of highway crossing structures on tiger population connectivity. However, studies on other wide-ranging carnivores have documented the use of such structures which could facilitate movement at a landscape scale (Gloyne and Clevenger 2001; Ford et al. 2017; González-Gallina et al. 2018). Nonetheless, the types and locations of wildlife crossing structures along linear barriers such as highways should be considered carefully given that use of these structures may vary due to a number of complex factors and by species (Clevenger and Waltho 2000; Caldwell and Klip 2020). Purported benefits of wildlife crossing structures included in infrastructure development planning may not sufficiently justify the construction of new roads in areas of wildlife conservation importance. We echo the sentiment of Ash et al. (2020c) recommending limited development of infrastructure that could fragment habitat or facilitate access in DPKY, such as roads, particularly given the strong effects of mortality in our study.

5. Conclusions

Our study provides a number of insights that may be informative for future applications of spatially explicit modeling in dynamic population and landscape connectivity assessments, particularly for rare or threatened species. This study demonstrates that spatial population and connectivity models can be highly sensitive to model parameters, producing highly divergent patterns of connectivity and population trajectories. Notably, ours is one of the first studies to explicitly evaluate the interaction of dispersal ability and mortality on population size, distribution, and connectivity in a spatially explicit dynamic framework. These factors were dominant in our study and we recommend that future studies explicitly account for spatially differential mortality and potential interactions with dispersal ability. Our study also underscores the importance of incorporating a temporally-explicit framework into models, given the potential for strong differences in the effect of factors across timesteps that may affect interpretation. Explicitly quantifying patterns of divergence between factors and displacement from initial conditions is crucial for reliably evaluating changes in connectivity over time. In the absence of empirical data to parameterize dispersal and connectivity models more reliably, our approach of evaluating model sensitivity via cumulative resistance kernels is particularly useful to investigate the differential effects of a range of factors. Our study identifies potential population growth and range expansion scenarios for tigers along with key factors relevant to their long-term management across a landscape of global conservation priority.

Supplementary Materials: The following are available online at https://www.mdpi.com/2073-445X/9/11/415/s1, Supplementary Materials 1—Additional Methods Information, Supplementary Materials 2—Additional Results Tables, Supplementary Materials 3—Supplementary Figures and Figure Animations.

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References

Ash E, Hallam C, Chanteap P, et al (2020a) Estimating the density of a globally important tiger (Panthera tigris) population: Using simulations to evaluate survey design in Eastern Thailand. Biol Conserv 241:108349. https://doi.org/10.1016/j.biocon.2019.108349

Ash E, Kaszta Ż, Noochdumrong A, et al (2020b) Opportunity for Thailand's Forgotten Tigers: Assessment of Indochinese tiger Panthera tigris corbetti and prey from camera-trap surveys in Eastern Thailand. Oryx 55:204–211. https://doi.org/10.1017/S0030605319000589

Ash E, Kaszta Ż, Redford T, et al (2020c) Environmental factors, human presence, and prey interact to explain patterns of tiger presence in Eastern Thailand. Anim Conserv 24:268–279. https://doi.org/10.1111/acv.12631

Ash E, Macdonald DW, Cushman SA, et al (2021) Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: A case study of tigers (Panthera tigris) in Thailand. Landsc Ecol 36:455–474. https://doi.org/10.1007/s10980-020-01105-6

Barros T, Carvalho J, Fonseca C, Cushman SA (2019) Assessing the complex relationship between landscape, gene flow, and range expansion of a Mediterranean carnivore. Eur J Wildl Res 65:44. https://doi.org/10.1007/s10344-019-1274-6

Bonte D, Van Dyck H, Bullock JM, et al (2012) Costs of dispersal. Biol Rev 87:290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

Caldwell MR, Klip JMK (2020) Wildlife Interactions within Highway Underpasses. J Wildl Manage 84:227–236. https://doi.org/10.1002/jwmg.21801

Carmona P, Franco D (2015) Impact of Dispersal on the Total Population Size, Constancy and Persistence of Two-patch Spatially-separated Populations. Math Model Nat Phenom 10:45–55. https://doi.org/10.1051/mmnp/201510204

Carr LW, Fahrig L (2001) Effect of Road Traffic on Two Amphibian Species of Differing Vagility. Conserv Biol 15:1071–1078. https://doi.org/10.1046/j.1523-1739.2001.0150041071.x

Carr LW, Fahrig L, Pope SE (2002) Impacts of Landscape Transformation by Roads. In: Gutzwiller KJ (ed) Applying Landscape Ecology in Biological Conservation. Springer New York, New York, NY, pp 225–243

Carroll C, Miquelle DG (2006) Spatial viability analysis of Amur tiger Panthera tigris altaica in the Russian Far East: The role of protected areas and landscape matrix in population persistence. J Appl Ecol 43:1056–1068. https://doi.org/10.1111/j.1365-2664.2006.01237.x

Carroll C, Noss RF, Paquet PC (2001) Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecol Appl 11:961–980. https://doi.org/10.1890/1051-0761(2001)011[0961:CAFSFC]2.0.CO;2

Carroll KA, Hansen AJ, Inman RM, et al (2020) Testing landscape resistance layers and modeling connectivity for wolverines in the western United States. Glob Ecol Conserv 23:e01125. https://doi.org/10.1016/j.gecco.2020.e01125

Clements GR, Lynam AJ, Gaveau D, et al (2014) Where and how are roads endangering mammals in Southeast Asia's forests? PLoS One 9:e115376. https://doi.org/10.1371/journal.pone.0115376

Clevenger AP, Waltho N (2000) Factors Influencing the Effectiveness of Wildlife Underpasses in Banff National Park, Alberta, Canada. Conserv Biol 14:47–56. https://doi.org/10.1046/j.1523-1739.2000.00099-085.x

Coffin AW (2007) From roadkill to road ecology: a review of the ecological effects of roads. J Transp Geogr 15:396–406. https://doi.org/10.1016/j.jtrangeo.2006.11.006

Compton BW, McGarigal K, Cushman SA, Gamble LR (2007) A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conserv Biol 21:788–799. https://doi.org/10.1111/j.1523-1739.2007.00674.x

Cushman AS, Lewis SJ, Landguth LE (2014) Why Did the Bear Cross the Road? Comparing the Performance of Multiple Resistance Surfaces and Connectivity Modeling Methods. Diversity 6:844–854. https://doi.org/10.3390/d6040844

Cushman SA (2015) Pushing the envelope in genetic analysis of species invasion. Mol Ecol 24:259–262

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biol Conserv 128:231–240. https://doi.org/10.1016/j.biocon.2005.09.031

Cushman SA, Compton BW, McGarigal K (2010) Habitat Fragmentation Effects Depend on Complex Interactions Between Population Size and Dispersal Ability: Modeling Influences of Roads, Agriculture and Residential Development Across a Range of Life-History Characteristics. In: Cushman SA, Huettmann F (eds) Spatial Complexity, Informatics, and Wildlife Conservation. Springer Japan, Tokyo, pp 369–385

Cushman SA, Elliot NB, Macdonald DW, Loveridge AJ (2016) A multi-scale assessment of population connectivity in African lions (Panthera leo) in response to landscape change. Landsc Ecol 31:1337–1353. https://doi.org/10.1007/s10980-015-0292-3

Cushman SA, H. McRae B, McGarigal K (2015) Basics of Landscape Ecology: An Introduction to Landscapes and Population Processes for Landscape Geneticists. In: Balkenhol N, Cushman SA, Storfer AT, Waits LP (eds) Landscape Genetics. John Wiley & Sons, Ltd, Chichester, UK, pp 9–34

Cushman SA, Landguth EL, Flather CH (2013) Evaluating population connectivity for species of conservation concern in the American Great Plains. Biodivers Conserv 22:2583–2605. https://doi.org/10.1007/s10531-013-0541-1

Cushman SA, McGarigal K (2007) Multivariate Landscape Trajectory Analysis. In: Bissonette JA, Storch I (eds) Temporal Dimensions of Landscape Ecology: Wildlife Responses to Variable Resources. Springer US, Boston, MA, pp 119–140

Diffendorfer JE (1998) Testing Models of Source-Sink Dynamics and Balanced Dispersal. Oikos 81:417–433. https://doi.org/10.2307/3546763

Diniz MF, Cushman SA, Machado RB, De Marco Júnior P (2020) Landscape connectivity modeling from the perspective of animal dispersal. Landsc Ecol 35:41–58. https://doi.org/10.1007/s10980-019-00935-3

Elliot N, Cushman S, Macdonald DW, Loveridge A (2014) The devil is in the dispersers: the metrics of landscape connectivity change with demography. J Appl Ecol 51:1169–1178. https://doi.org/10.1111/1365-2664.12282

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117–142. https://doi.org/10.1017/S1464793105006949

Ford AT, Barrueto M, Clevenger AP (2017) Road mitigation is a demographic filter for grizzly bears. Wildl Soc Bull 41:712–719. https://doi.org/10.1002/wsb.828

Gibbs JP (1998) Amphibian Movements in Response to Forest Edges, Roads, and Streambeds in Southern New England. J Wildl Manage 62:584–589. https://doi.org/10.2307/3802333

Gloyne CC, Clevenger AP (2001) Cougar Puma concolor use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. Wildlife Biol 7:117–124. https://doi.org/10.2981/wlb.2001.009

González-Gallina A, Hidalgo-Mihart MG, Castelazo-Calva V (2018) Conservation implications for jaguars and other neotropical mammals using highway underpasses. PLoS One 13:e0206614. https://doi.org/10.1371/journal.pone.0206614

Goodrich JM, Kerley LL, Smirnov EN, et al (2008) Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. J Zool 276:323–329. https://doi.org/10.1111/j.1469-7998.2008.00458.x

Goodrich JM, Lynam A, Miquelle DG, et al (2015) Panthera tigris. IUCN Red List Threat. Species 2015 e.T15955A50659951

Goodwin BJ, Fahrig L (2002) How does landscape structure influence landscape connectivity? Oikos 99:552–570. https://doi.org/10.1034/j.1600-0706.2002.11824.x

Gour DS, Bhagavatula J, Bhavanishankar M, et al (2013) Philopatry and Dispersal Patterns in Tiger (Panthera tigris). PLoS One 8:e66956. https://doi.org/10.1371/journal.pone.0066956

Graves T, Chandler RB, Royle JA, et al (2014) Estimating landscape resistance to dispersal. Landsc Ecol 29:1201–1211. https://doi.org/10.1007/s10980-014-0056-5

Gray TNE, Crouthers R, Ramesh K, et al (2017) A framework for assessing readiness for tiger Panthera tigris reintroduction: a case study from eastern Cambodia. Biodivers Conserv 26:2383–2399. https://doi.org/10.1007/s10531-017-1365-1

Gurung B, Smith JLD, McDougal C, Karki JB (2006) Tiger Human Conflicts: Investigating Ecological and Sociological Issues of Tiger Conservation in the Buffer Zone of Chitwan National Park, Nepal. WWF-Nepal Program, Kathmandu, Nepal

Jackson ND, Fahrig L (2011) Relative effects of road mortality and decreased connectivity on population genetic diversity. Biol Conserv 144:3143–3148. https://doi.org/10.1016/j.biocon.2011.09.010

Joshi AR, Dinerstein E, Wikramanayake E, et al (2016) Tracking changes and preventing loss in critical tiger habitat. Sci Adv 2:e1501675–e1501675. https://doi.org/10.1126/sciadv.1501675

Kafley H, Gompper ME, Sharma M, et al (2016) Tigers (Panthera tigris) respond to fine spatial-scale habitat factors: occupancy-based habitat association of tigers in Chitwan National Park, Nepal. Wildl Res 43:398–410. https://doi.org/10.1071/WR16012

Kanagaraj R, Wiegand T, Kramer-Schadt S, Goyal SP (2013) Using individual-based movement models to assess inter-patch connectivity for large carnivores in fragmented landscapes. Biol Conserv 167:298–309. https://doi.org/10.1016/j.biocon.2013.08.030

Karanth KU (1995) Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture models. Biol Conserv 71:333–338. https://doi.org/10.1016/0006-3207(94)00057-W

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862. https://doi.org/10.2307/176521

Karanth KU, Nichols JD, Kumar NS, et al (2004) Tigers and their prey: Predicting carnivore densities from prey abundance. Proc Natl Acad Sci U S A 101:4854–4858. https://doi.org/10.1073/pnas.0306210101

Karanth KU, Stith BM (1999) Prey depletion as a critical determinant of tiger population viability. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 100–113

Kaszta Ż, Cushman SA, Hearn AJ, et al (2019) Integrating Sunda clouded leopard (Neofelis diardi) conservation into development and restoration planning in Sabah (Borneo). Biol Conserv 235:63–76. https://doi.org/10.1016/j.biocon.2019.04.001

Kaszta Ż, Cushman SA, Htun S, et al (2020) Simulating the impact of Belt and Road initiative and other major developments in Myanmar on an ambassador felid, the clouded leopard, Neofelis nebulosa. Landsc Ecol 35:727–746. https://doi.org/10.1007/s10980-020-00976-z

Keeley ATH, Beier P, Gagnon JW (2016) Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc Ecol 31:2151–2162. https://doi.org/10.1007/s10980-016-0387-5

Kerley LI, Goodrich JM, Miquelle DG, et al (2002) Effects of Roads and Human Disturbance on Amur Tigers. Conserv Biol 16:97–108. https://doi.org/10.1046/j.1523-1739.2002.99290.x

Kramer-Schadt S, Revilla E, Wiegand T, Breitenmoser U (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. J Appl Ecol 41:711–723. https://doi.org/10.1111/j.0021-8901.2004.00933.x

Krishnamurthy R, Cushman SA, Sarkar MS, et al (2016) Multi-scale prediction of landscape resistance for tiger dispersal in central India. Landsc Ecol 31:1355–1368. https://doi.org/10.1007/s10980-016-0363-0

Landguth EL, Hand BK, Glassy J, et al (2012) UNICOR: a species connectivity and corridor network simulator. Ecography (Cop) 35:9–14. https://doi.org/10.1111/j.1600-0587.2011.07149.x

Levins R (1970) Some mathematical problems in biology. In: Extinction. The American Mathematical Society, Providence, Rhode Island, pp 77–107

Linkie M, Chapron G, Martyr DJ, et al (2006) Assessing the viability of tiger subpopulations in a fragmented landscape. J Appl Ecol 43:576–586. https://doi.org/10.1111/j.1365-2664.2006.01153.x

Lohani S, Dilts TE, Weisberg PJ, et al (2020) Rapidly Accelerating Deforestation in Cambodia's Mekong River Basin: A Comparative Analysis of Spatial Patterns and Drivers. Water 12:2191. https://doi.org/10.3390/w12082191

Lotka AJ (1932) The growth of mixed populations: Two species competing for a common food supply. J Washingt Acad Sci 22:461–469

Lynam A, Nowell K (2011) Panthera tigris ssp. corbetti. IUCN Red List Threat. Species 2011 e.T136853A4346984

Mantel N (1967) The Detection of Disease Clustering and a Generalized Regression Approach. Cancer Res 27:209 LP – 220

Matthysen E (2005) Density-dependent dispersal in birds and mammals. Ecography (Cop) 28:403–416. https://doi.org/10.1111/j.0906-7590.2005.04073.x

Moqanaki EM, Cushman SA (2017) All roads lead to Iran: Predicting landscape connectivity of the last stronghold for the critically endangered Asiatic cheetah. Anim Conserv 20:29–41. https://doi.org/10.1111/acv.12281

Naude VN, Balme GA, O'Riain J, et al (2020) Unsustainable anthropogenic mortality disrupts natal dispersal and promotes inbreeding in leopards. Ecol Evol 10:3605–3619. https://doi.org/10.1002/ece3.6089

OpenStreetMap (2019) OpenStreetMap. www.openstreetmap.org. Accessed 10 Jun 2019

Puyravaud JP, Cushman SA, Davidar P, Madappa D (2017) Predicting landscape connectivity for the Asian elephant in its largest remaining subpopulation. Anim Conserv 20:225–234. https://doi.org/10.1111/acv.12314

Rasphone A, Kéry M, Kamler JF, Macdonald DW (2019) Documenting the demise of tiger and leopard, and the status of other carnivores and prey, in Lao PDR's most prized protected area: Nam Et - Phou Louey. Glob Ecol Conserv 20:e00766. https://doi.org/10.1016/j.gecco.2019.e00766

Reddy PA, Cushman SA, Srivastava A, et al (2017) Tiger abundance and gene flow in Central India are driven by disparate combinations of topography and land cover. Divers Distrib 23:863–874. https://doi.org/10.1111/ddi.12580

Rostro-García S, Kamler JF, Ash E, et al (2016) Endangered leopards: Range collapse of the Indochinese leopard (Panthera pardus delacouri) in Southeast Asia. Biol Conserv 201:293–300. https://doi.org/10.1016/j.biocon.2016.07.001

Sanderson E, Forrest J, Loucks C, et al (2006) Setting Priorities for the Conservation and Recovery of Wild Tigers: 2005-2015 - The Technical Assessment. WCS, WWF, Smithsonian, and NFWF-STF, New York - Washington, DC

Sarkar MS, Ramesh K, Johnson JA, et al (2016) Movement and home range characteristics of reintroduced tiger (Panthera tigris) population in Panna Tiger Reserve, central India. Eur J Wildl Res 62:537–547. https://doi.org/10.1007/s10344-016-1026-9

Schwab AC, Zandbergen PA (2011) Vehicle-related mortality and road crossing behavior of the Florida panther. Appl Geogr 31:859–870. https://doi.org/10.1016/j.apgeog.2010.10.015

SERVIR-Mekong (2018) SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS). SERVIR-Mekong/USAID/NASA/ADPC/ICIMOD, Asian Disaster Preparedness Center (ADPC), Bangkok, Thailand

Singh R, Qureshi Q, Sankar K, et al (2013) Use of camera traps to determine dispersal of tigers in semi-arid landscape, western India. J Arid Environ 98:105–108. https://doi.org/10.1016/j.jaridenv.2013.08.005

Smith JLD (1993) The Role of Dispersal in Structuring the Chitwan Tiger Population. Behaviour 124:165–195. https://doi.org/10.1163/156853993X00560

Smith JLD, McDougal C (1991) The Contribution of Variance in Lifetime Reproduction to Effective Population Size in Tigers. Conserv Biol 5:484–490. https://doi.org/10.1111/j.1523-1739.1991.tb00355.x

Spear SF, Balkenhol N, Fortin MJ, et al (2010) Use of resistance surfaces for landscape genetic studies: Considerations for parameterization and analysis. Mol Ecol 19:3576–3591. https://doi.org/10.1111/j.1365-294X.2010.04657.x

Sunarto S, Kelly MJ, Parakkasi K, et al (2012) Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS One 7:e30859. https://doi.org/10.1371/journal.pone.0030859

Sunquist M (2010) What is a Tiger? Ecology and Behavior. In: Tilson R, Nyhus P (eds) Tigers of the World, Second Edition. Elsevier, New York, pp 19–34

Sunquist M, Karanth UK, Sunquist F (1999) Ecology, behaviour and resilience of the tiger and its conservation needs. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 5–18

Thapa K, Wikramanayake E, Malla S, et al (2017) Tigers in the Terai: Strong evidence for meta-population dynamics contributing to tiger recovery and conservation in the Terai Arc Landscape. PLoS One 12:e0177548. https://doi.org/10.1371/journal.pone.0177548

Thapa TB (2014) Human caused mortality in the leopard (Panthera pardus) population of Nepal. J Inst Sci Technol 19:150–155. https://doi.org/10.3126/jist.v19i1.13842

Thatte P, Joshi A, Vaidyanathan S, et al (2018) Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations. Biol Conserv 218:181–191. https://doi.org/10.1016/j.biocon.2017.12.022

Trombulak SC, Frissell CA (2000) Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities. Conserv Biol 14:18–30. https://doi.org/10.1046/j.1523-1739.2000.99084.x

UNEP-WCMC, IUCN (2019) Protected Planet. The World Database on Protected Areas (WDPA), UNEP-WCMC, Cambridge, U.K., www.protectedplanet.net

Vasudev D, Nichols JD, Ramakrishnan U, et al (2017) Assessing Landscape Connectivity for Tigers and Prey Species: Concepts and Practice. In: Karanth KU, Nichols JD (eds) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore, pp 255–288

Volterra V (1928) Variations and fluctuations of the number of individuals in animal species living together. ICES J Mar Sci 3:3–51

Walston J, Robinson JG, Bennett EL, et al (2010) Bringing the tiger back from the brink-the six percent solution. PLoS Biol 8:6–9. https://doi.org/10.1371/journal.pbio.1000485

Walters S (2007) Modeling scale-dependent landscape pattern, dispersal, and connectivity from the perspective of the organism. Landsc Ecol 22:867–881. https://doi.org/10.1007/s10980-006-9065-3

Winiarski KJ, Peterman WE, Whiteley AR, McGarigal K (2020) Multiscale resistant kernel surfaces derived from inferred gene flow: An application with vernal pool breeding salamanders. Mol Ecol Resour 20:97–113. https://doi.org/10.1111/1755-0998.13089

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landsc Ecol 27:777–797. https://doi.org/10.1007/s10980-012-9737-0

Zeller KA, Vickers TW, Ernest HB, Boyce WM (2017) Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study. PLoS One 12:e0179570. https://doi.org/10.1371/journal.pone.0179570

Supplementary Materials 1

Additional Methods Information

1. Study Site

Table 1 Protected areas as depicted in Figure 1 of the main text.

ID	Protected Area	Country
1	Khao Yai National Park	Thailand
2	Thap Lan National Park	Thailand
3	Pang Sida National Park	Thailand
4	Dong Yai Wildlife Sanctuary	Thailand
5	Ta Phraya National Park	Thailand
6	Huai Thabthan-Had Samran Wildlife Sanctuary	Thailand
7	Huai Sala Wildlife Sanctuary	Thailand
8	Panom Dong Rak Wildlife Sanctuary	Thailand
9	Khao Phravihan National Park	Thailand
10	Yod Dom Wildlife Sanctuary	Thailand
11	Phu Chong - Na Yoi National Park	Thailand
12	Boon Trik - Yod Mon Wildlife Sanctuary	Thailand
13	Kaeng Tana National Park	Thailand
14	Pha Tam National Park	Thailand
15	Banteay Chhmar Protected Landscape	Cambodia
16	Ang Trapeng Thmor Protected Landscape	Cambodia
17	Sanghrukkhavan Wildlife Sanctuary	Cambodia
18	Prek Toal Core Area (Ramsar Site)	Cambodia
19	Tonle Sap Multiple Use Area	Cambodia
20	Boeng Chhmar Core Area (Ramsar Site, Wetland of International Importance)	Cambodia
21	Stung Sen Core Area (Ramsar Site) Multiple Use Area	Cambodia
22	Angkor Protected Landscape	Cambodia
23	Preah Jayavaraman-Norodom "Phnom Kulen" National Park	Cambodia
24	North Tonle Sap Protected Landscape	Cambodia
25	Boeng Paer Wildlife Sanctuary	Cambodia
26	Phnom Thnout-Phnom Pok Wildlife Sanctuary	Cambodia
27	Prasat Bakan (Preah Khan Kampong Svay) Protected Landscape	Cambodia
28	Kulen Promtep Wildlife Sanctuary	Cambodia
29	Preah Vihear Protected Landscape	Cambodia
30	Phnom Tbaeng Natural Heritage Park	Cambodia
31	Preah Roka Wildlife Sanctuary	Cambodia
32	Chhaeb Wildlife Sanctuary	Cambodia
33	Prey Lang Wildlife Sanctuary	Cambodia
34	Sambour Wildlife Sanctuary	Cambodia
35	Stung Treng Ramsar Site Wetland of International Importance	Cambodia
36	Phou Xiengthong National Biodiversity Conservation Area	Laos

2. Evaluating Potential Resistance Models

In order to investigate potential landscape connectivity in our study site, we developed four potential resistance surfaces. These were based on a scale-optimized habitat selection model for tigers in DPKY, two multivariate optimized India-based resistance models, and an expert-derived resistance model.

2.1 DPKY model

The DPKY model was derived from a multi-scale optimized (MSO) habitat-selection model developed by Ash et al. (2021; "Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: A case study of tigers (*Panthera tigris*)"). This model was developed in the study to help test the influence of spatial scale- and functional shape-optimization on the performance of habitat suitability models in comparison to non-optimized models, and to discern the influence of spatial scale on habitat selection. This model utilizes a considerably large, local camera trap-based data set (Ash et al. 2020a). Coefficients in the model include (Table 2): percentage of open forest (16km), percentage of bamboo forest (16km), correlation length of secondary forest (4km), standard deviation of compound topographic index (8km), camera effort, percentage of shrubland/grassland (8km), standard deviation of terrain roughness index (1km), and correlation length of open forest (8km). As this was a habitat-selection model, resulting predicted values were inverted and rescaled with a negative exponential transformation (Mateo-Sánchez et al. 2015; Wan et al. 2019) to reflect potential resistance to movement.

2.2 Reddy et al 2017 Indian resistance model

The second resistance map was based on a multivariate optimized resistance model developed by Reddy et al. (2017), describing the relationship between tiger genetic distance and land cover variables in central India. Covariates in this model were included with five potential max resistance values (R_{max}) and exponents of the power function (e.g., Shirk et al. 2010). These covariates included human footprint (4^{th} Power, 10 max), land cover (4th Power, 5 max), slope position (½ Power, 80 max) and topographical roughness (4th Power, 80 max). For the model developed for our study area, human footprint was derived from road density and

Table 2 Fully-averaged model results for the local habitat-selection model (Ash et al. 2021) including standardized regression coefficients (β), adjusted standard error (SE (Adj)), z-value (*z*), and significance (*p*).

Variable	ID	β	SE (Adj)	*z*	*p*
(Intercept)	-	-2.405	0.260	9.242	<0.001
% Open forest (16km)	TC2_PLAND_16000	-1.437	0.349	4.120	<0.001
% Bamboo (16km)	FT5_PLAND_16000	0.988	0.238	4.158	<0.001
Correlation length secondary forest (4km)	FT6_GYR_4000	-0.675	0.246	2.744	0.006
Standard deviation of compound topographic index (8km)	CTI_SD_8000	0.616	0.193	3.199	0.001
Camera effort (# trap nights)	Cam_eff	1.415	0.299	4.728	<0.001
% Shrubland/grassland (8km)	LC4_PLAND_8000	-0.486	0.202	2.404	0.016
Standard Deviation of terrain roughness index (1km)	TRI_SD_1000	0.384	0.158	2.423	0.015
Correlation length of open forest (8km)	TC2_GYR_16000	-0.704	0.344	2.045	0.041

Table 3 Reclassed landcover classes of 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018) to reflect resistance values for the Reddy et al. (2017) model for a max resistance (R_{max}) of 5. These classifications closely follow designations by Reddy et al. (2017): [1] closed-canopy forest, [2] scrub forest, [3] agricultural village mosaic, [4] urban areas, and [5] water bodies/ reservoirs.

Resistance Value (cost-distance unit / pixel)	Attributes / Land Cover Type
1	Dense Forest - Evergreen Forest + Forest + Mixed Forest + Flooded Forest + Mangroves
2	Scrub Forest - Shrubland + Grassland + Wetlands + Orchard/Plantation
3	Agriculture-Village Matrix - Rice + Cropland + Barren + Aquaculture
4	Urban/Built-Up Areas
5	Reservoirs + Surface Water

remote sensing analysis of night lights (WCS and CIESIN 2005). Land cover data were generated from the 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018) and reclassed into five resistance values (Table 3). As in the original study, topographical roughness and slope position were calculated using a digital elevation model (Jarvis et al. 2008) and the Geomorphometry & Gradient Metrics Toolbox (Evans et al. 2014) in ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011).

2.3 Krishnamurthy et al 2016 Indian resistance model

The third map was developed using a second resistance model for tigers in central India developed by Krishnamurthy et al. (2016). The model was developed using a scale-optimized path selection framework for comparison against single-scale models. The multi-scale model used in that study included three covariates:

agriculture-village matrix, open forest, and relative slope position (Table 4). Data for agriculture-village matrix and open forest in the original study were primarily local (Indian-derived). Thus, for our study area, we used global data for these covariates. Specifically, the agriculture–village matrix was generated by reclassifying 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018), combining aquaculture, rice, cropland, urban/built-up areas, and surface water classes. The dominant vegetation type represented in the model study area in central India was considered to be tropical dry-deciduous forest, notably more open than dense mixed evergreen forest in Thailand. Relatively open forest similar to Indian habitat was not well-represented in our study area, thus we opted to use tree cover data (Hansen et al. 2013) which was reclassed into a single forest cover class of 50% forest cover and above. As in the original study, slope position was calculated using a digital elevation model (Jarvis et al. 2008) and the Geomorphometry & Gradient Metrics Toolbox (Evans et al. 2014) in ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011) with a focal radius of 450m.

Table 4 Regression model for the multi-scale optimized model from Krishnamurthy et al. (2016), including unstandardized regression coefficients (β), standardized coefficient (STD(β)), standard error of the standardized coefficient (SE(β)), and variable significance in the final model (Pr(>|*z*|)).

Variable	**ID**	**β**	**STD(β)**	**SE(β)**	**Pr(>|*z*|)**
Agriculture-village matrix (0km shift)	Class0_0	-17.338	-3.77011	1.62389	0.0203
Open forest (18km shift)	Class5_18	17.215	2.18527	0.96996	0.0243
Relative slope position (3km shift)	SP_1	-0.693	-0.81603	0.65082	0.2099

2.4 Expert-based resistance model

We also evaluated an expert-derived resistance map based on reclassified 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018) data, incorporating major and minor roads (OpenStreetMap 2019). Land cover was reclassified into five resistance values (Table 5): Dense forest (1), Scrub forest (20), Agriculture-village matrix (50), Reservoirs/Surface water (80), and Urban areas (100). Minor and major roads (OpenStreetMap 2019) were assigned resistance values of 30 and 100 where overlapping land-cover values were lower. Decisions regarding resistance values were determined by discussion among study co-authors but were primarily informed by general patterns evident in the scientific literature on tigers. Specifically, tigers are broadly considered to be habitat generalists (Sunquist et al. 1999), though they require forest cover (Sunarto et al. 2012; Krishnamurthy et al. 2016; Reddy et al. 2017; Thatte et al. 2018), which was assigned the lowest resistance value in our study. In our study area, areas of the landscape with more open forest are typically more accessible and highly affected by human activities. Tigers typically avoid areas with high human disturbance (Karanth et al. 2011; Harihar and Pandav 2012; Ngoprasert et al. 2012; Barber-Meyer et al. 2013) and, in some cases, grasslands (Thatte et al. 2018). Thus, these areas and similar habitat were assigned a slightly higher resistance value. Following this evidence, areas with higher likely intensity of human activities, such as villages/agricultural areas and urban areas, were assigned proportionally higher resistance values. While tigers have been known to cross bodies of water (Naha et al. 2016), they are primarily terrestrial predators and, thus, water bodies were given higher resistance values compared to terrestrial resistance classes with the exception of urban/built-up areas. Research in our study area revealed use of minor roads within protected areas by tigers and strong aversion to major roads (Ash et al. 2020b). Authors in this study posited that tigers used certain minor roads without public access for efficient travel through the landscape, reflecting patterns observed in other studies (Kerley et al. 2002; Sunquist 2010; Carter et al. 2012). However, elevated vehicle traffic on roads may have strong negative effects on tigers (Kerley et al. 2002). Therefore, we assigned high resistance (100) to major roadways and moderate resistance to minor roadways (30) where overlapping base resistance values were lower.

2.5 Suitability of models to study area

Resistance maps had varying degrees of suitability for our study. The resistance map developed from the inversed Ash et al. (2021) model resulted in considerably high predicted resistance in areas outside DPKY even in large areas of intact forest cover. This contradicted existing evidence that tigers can at least traverse through forested areas and even heterogeneous landscapes at considerable distances (Smith 1993; Sunquist et al. 1999; Joshi et al. 2013; Krishnamurthy et al. 2016; Reddy et al. 2017). This was likely due to the third order sampling for the model, which derived tiger presence data exclusively within DPKY, resulting in a lack

Table 5 Reclassed landcover classes of 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018) to reflect approximate degrees of resistance for the expert-based resistance model.

Resistance Value (cost-distance unit / pixel)	Attributes / Land Cover Type
1	Dense Forest - Evergreen Forest + Forest + Mixed Forest + Flooded Forest + Mangroves
20	Scrub Forest - Shrubland + Grassland + Wetlands + Orchard/Plantation
50	Agriculture-Village Matrix - Rice + Cropland + Barren + Aquaculture
80	Reservoirs + Surface Water
100	Urban/Built-Up Areas

of representation of certain habitats outside this landscape. The Reddy model, when applied to our study area, overpredicted resistance through forest at lower elevations, particularly lowland forest. Topographical roughness and relative slope position exert a strong influence in this model, which led to over-prediction in mountainous terrain, despite little to no forest cover, and under-prediction in lowland forested areas. The Krishnamurthy model underpredicted along forested ridgelines in our study area, which were likely to be important areas for dispersing tigers based on existing knowledge and availability of habitat (Karanth 1995; Karanth and Nichols 1998). The model also underpredicted resistance in human-dominated areas and did not adequately predict patterns of tiger presence in DPKY. The expert model appeared to reflect patterns of likely tiger presence in DPKY, along forested ridgelines, and large blocks of forest while appropriately scaling up resistance in human-dominated areas. Comparing the expert-derived resistance map across our study area, and comparing it to other models of resistance, we determined the expert map more broadly captured likely resistance to movement in our study landscape. Based on this interpretation, we opted to utilize the expert-derived resistance map in our study, which was further transformed by power functions to account for varying functional forms of resistance (i.e., concave [r07], linear [r10], and convex [r15]).

2.6 Implications of divergent model predictions

The development and comparison of these models provides interesting insights. The high degree of divergence between these models, particularly the poor suitability of some models, highlights that the application of resistance models to other geographic areas can be problematic (Cushman et al. 2013). This further reinforces that care should be taken in developing resistance models and ensuring patterns in resistance reflect likely patterns of movement behavior in the landscapes to which they are applied. Generally, tigers are considered to be habitat generalists (Sunquist et al. 1999), though their presence, and thus, predictions in models, may reflect local conditions that are highly constrained by human-behavior. Habitat that tigers may otherwise utilize may not be present in an area being used for model development. Consequently, such models would underpredict tiger presence in such habitats when applied elsewhere. This can also be problematic if the same covariate sources from the original model are not available for other geographic areas, requiring approximation of covariates from other data (e.g., remote-sensed data). These approximations may not accurately reflect specific landscape configurations that have a disproportionate effect in original models and even minor differences could lead to considerable differences in predictions.

3. Modifying Resistance Surface to Reflect Highway Crossings

Using the expert-based resistance layer, we developed three highway mitigation scenarios to test the effect of highway crossing structures (SCEN). The first scenario (S1) used the base resistance layer described above. Importantly, no mitigation of highways was included in this layer.

The second highway mitigation scenario (S2) utilized the same base resistance map as S1; however, in this scenario, we modified resistance along a major highway (national highway route 304) which bisects DPKY between Khao Yai and Thap Lan national parks. The Thai government is currently in the process of completing several wildlife crossing structures along the highway with the objective of facilitating wildlife movement between the two parks (Stokes 2017). To account for the potential effect of these structures in facilitating movement of tigers in the complex, we assigned lower resistance values (20) at the locations of these structures, which include a highway overpass (~570m) and two tunnels in southern DPKY (~210m and ~150m) and two overpasses in northern DPKY (~260m and ~180m).

The third resistance scenario (S3) utilized the resistance map from S2, but also includes hypothetical wildlife crossing structures along another highway (national highway route 348) which bisects eastern DPKY's Ta Phraya National Park and Dong Yai Wildlife Sanctuary, acting as a potential impairment to movement beyond the complex. In this scenario, we follow the same process as S2, assigning lower resistance values (20) along the highway where it bisects otherwise contiguous forest in Ta Phraya National Park (NP). In this hypothetical scenario, we assign lower resistance simulating the presence of a wildlife crossing structure in this location (one overpass of ~570m).

4. Mortality Function Development

To investigate the potential effect of mortality on the simulated population (MORT), at each time step we filtered source points based on one of five mortality functions (M0, R1, R2, E1, and E2), representing spatially differential probability of survival (pixel values ranging 0 to 1).

4.1 M0 mortality

Function M0 represents the base scenario described in the main text in which source points were generated based on the maximum population growth rate, probabilistically distributed proportionally to resistant kernel densities, which represent the incidence function of the current generation, with no additional mortality applied.

4.2 R1 and R2 mortality

Functions R1 and R2 involved additional filtering steps of source points representing different mortality rates based on a tiger effective population size model from Reddy et al. (2017). The model predicts tiger effective population size as a function of the focal mean of protected area coverage within a 45km radius, mean forest cover within a 45km radius, and mean landscape resistance within a 42.5km radius (Table 6). In contrast to the resistance model derived from Reddy et al (2017) which defined resistance via specific habitat patterns not reflected in our study landscape, the effective population size model parsimoniously generated predictions broadly applicable to tigers throughout their range (i.e., broad extents of forest cover and protected area presence; Walston et al. 2010; Sunarto et al. 2012; Goodrich et al. 2015; Kafley et al. 2016). This model produced predictions reflecting reasonable and consistent patterns of high and low potential presence and, by extension, potential survivability across our landscape.

We applied Reddy's model to locally generated spatial layers to predict the potential effective population size of tigers in our study area. This was then used to predict mortality risk (R1), based on the idea that the risk of mortality would be high where the predicted potential effective population size is low (given this is essentially low-quality habitat that does not support tiger populations).

In order to investigate the sensitivity of simulations to variation in spatial mortality risk, we calculated the square root of the rescaled (0-1) potential effective population size layer. This function is further referred to as R2 and, in effect, it lowered the mortality risk in moderate to high suitability areas and increased the likelihood of source points being retained, except in the areas with the lowest potential to support a tiger population.

Table 6 Final averaged model from Reddy et al. (2017) describing tiger effective population size in central India including coefficient (β), standard error (SE), z-value (*z*) and variable significance (Pr(>|*z*|)).

Variable	β	SE	*z*	Pr(>|*z*|)
(Intercept)	61.45	11.48	15.18	5.13E-05
Proportion of landscape within 45km radius covered by protected areas	20.91	9.97	14.12	0.139
Mean landscape resistance within a 42.5km radius	-20.27	10.3	14.59	0.165
Mean forest cover within a 45km radius	20.06	10.4	14.73	0.173

4.3 E1 and E2 mortality

We also tested two additional expert-based mortality functions (E1 and E2) with spatially differential probability of survivability. Reliable information on survival rates of dispersing tigers is rare. However, where information is available, evidence suggests that survival probability of dispersing tigers, particularly outside protected areas, can be moderately to extremely low (Smith 1993; Goodrich et al. 2008). To account for this, we generated a simplified spatially differential mortality risk layer in which survival is a function of available tree cover, protection status, and presence of roads. Tigers generally have strong positive associations with forest cover and are often restricted to protected or undisturbed areas (Walston et al. 2010; Sunarto et al. 2012; Kafley et al. 2016; Reddy et al. 2017) and have negative associations with areas of high road density

(Kerley et al. 2002; Hebblewhite et al. 2014). Survival probability in this layer was defined by pixel values ranging from 0 to 1, starting with a base tree cover layer in which 0 represented no forest cover and 1 representing 100% forest cover (Hansen et al. 2013). Values were divided by 1.25 for forest within protected area boundaries to correspond roughly with mean annual survival of approximately 80% documented elsewhere in Thailand (82% in Duangchantrasiri et al. 2016) and divided by 10 for non-protected areas (approximately 10% survival). The layer was then divided by focal mean of road density within a 20km radius, rescaled between 0 and 1 to account for large-scale effects of roads on tiger persistence (Kerley et al. 2002; Hebblewhite et al. 2014). This resulted in a layer of spatial probability of survival capped at 0.8 in protected areas with 100% forest cover and no roads within a 20km radius, declining in probability as forest cover decreased and road density within 20km increased, lower by a factor of 10 outside protected areas. In summary, the formula for generating E1 was:

$$E1 = \frac{\begin{matrix}\text{Tree Cover Layer}\\ [0\text{ to }1]\end{matrix}}{\begin{matrix}\text{Protected Area Layer}\\ [\text{PA} = 1.25;\ \text{Non-PA} = 10]\end{matrix}} * \begin{matrix}(1 - \text{Focal Mean of Road Density at 20km})\\ [0\text{ to }1]\end{matrix}$$

To test the sensitivity of results to this mortality function, we also produced a modified expert-derived survivability scenario (E2) following the approach of E1 but modifying the maximum survivability outside protected areas from 10% to 50%. In effect, survivability outside protected areas with 100% tree cover and no roads within a 20km radius would, at most, be 0.5, declining in value as forest cover decreased and road density within 20km increased. In summary, the formula for generating E2 was:

$$E2 = \frac{\begin{matrix}\text{Tree Cover Layer}\\ [0\text{ to }1]\end{matrix}}{\begin{matrix}\text{Protected Area Layer}\\ [\text{PA} = 1.25;\ \text{Non-PA} = 5]\end{matrix}} * \begin{matrix}(1 - \text{Focal Mean of Road Density at 20km})\\ [0\text{ to }1]\end{matrix}$$

4.4 Applying mortality functions

Mortality functions were applied following the generation of source points for each timestep and parameter combination. At each timestep, mortality layers (values representing low [0] to high probability

[1] of survival) were subtracted by a random raster with values from 0 to 1. Source points overlapping with pixels in the difference raster < 0 were simulated mortalities and were removed. In effect, mortality-corrected source points were a function of kernel value (expected dispersers arriving at a location that time step), modeled likelihood of a disperser surviving at that location, and random chance. Resulting source points were then used for the next generation, up to nine total generations for all combinations of parameters.

References

Ash E, Kaszta Ż, Noochdumrong A, et al (2020a) Opportunity for Thailand's Forgotten Tigers: Assessment of Indochinese tiger Panthera tigris corbetti and prey from camera-trap surveys in Eastern Thailand. Oryx 55:204–211. https://doi.org/10.1017/S0030605319000589

Ash E, Kaszta Ż, Redford T, et al (2020b) Environmental factors, human presence, and prey interact to explain patterns of tiger presence in Eastern Thailand. Anim Conserv 24:268–279. https://doi.org/10.1111/acv.12631

Ash E, Macdonald DW, Cushman SA, et al (2021) Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: A case study of tigers (Panthera tigris) in Thailand. Landsc Ecol 36:455–474. https://doi.org/10.1007/s10980-020-01105-6

Barber-Meyer SM, Jnawali SR, Karki JB, et al (2013) Influence of prey depletion and human disturbance on tiger occupancy in Nepal. J Zool 289:10–18. https://doi.org/10.1111/j.1469-7998.2012.00956.x

Carter NH, Shrestha BK, Karki JB, et al (2012) Coexistence between wildlife and humans at fine spatial scales. Proc Natl Acad Sci 109:15360–15365. https://doi.org/10.1073/pnas.1210490109

Cushman SA, Mersmann TJ, Moisen GG, et al (2013) Using Habitat Models for Habitat Mapping and Monitoring. In: A technical guide for monitoring wildlife habitat. Gen. Tech. Rep. WO-89. US Department of Agriculture, Forest Service, Washington, D.C., pp 135–148

Duangchantrasiri S, Umponjan M, Simcharoen S, et al (2016) Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. Conserv Biol 30:639–648. https://doi.org/10.1111/cobi.12655

Evans JS, Cushman SA, Theobald D (2014) An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, version 2.0-0.

Goodrich JM, Kerley LL, Smirnov EN, et al (2008) Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. J Zool 276:323–329. https://doi.org/10.1111/j.1469-7998.2008.00458.x

Goodrich JM, Lynam A, Miquelle DG, et al (2015) Panthera tigris. IUCN Red List Threat. Species 2015 e.T15955A50659951

Hansen MC, Potapov P V., Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science (80-) 342:850–853. https://doi.org/10.1126/science.1244693

Harihar A, Pandav B (2012) Influence of connectivity, wild prey and disturbance on occupancy of tigers in the human-dominated western Terai Arc landscape. PLoS One 7:e40105. https://doi.org/10.1371/journal.pone.0040105

Hebblewhite M, Miquelle DG, Robinson H, et al (2014) Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. Biol Conserv 178:50–64. https://doi.org/10.1016/j.biocon.2014.07.013

Jarvis A, Reuter HI, Nelson A, Guevara E (2008) Hole-filled seamless SRTM data V4. In: Int. Cent. Trop. Agric. http://srtm.csi.cgiar.org

Joshi A, Vaidyanathan S, Mondol S, et al (2013) Connectivity of Tiger (Panthera tigris) Populations in the Human-Influenced Forest

Mosaic of Central India. PLoS One 8:e77980. https://doi.org/10.1371/journal.pone.0077980

Kafley H, Gompper ME, Sharma M, et al (2016) Tigers (Panthera tigris) respond to fine spatial-scale habitat factors: occupancy-based habitat association of tigers in Chitwan National Park, Nepal. Wildl Res 43:398–410. https://doi.org/10.1071/WR16012

Karanth KU (1995) Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture models. Biol Conserv 71:333–338. https://doi.org/10.1016/0006-3207(94)00057-W

Karanth KU, Gopalaswamy AM, Kumar NS, et al (2011) Monitoring carnivore populations at the landscape scale: Occupancy modelling of tigers from sign surveys. J Appl Ecol 48:1048–1056. https://doi.org/10.1111/j.1365-2664.2011.02002.x

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862. https://doi.org/10.2307/176521

Kerley LI, Goodrich JM, Miquelle DG, et al (2002) Effects of Roads and Human Disturbance on Amur Tigers. Conserv Biol 16:97–108. https://doi.org/10.1046/j.1523-1739.2002.99290.x

Krishnamurthy R, Cushman SA, Sarkar MS, et al (2016) Multi-scale prediction of landscape resistance for tiger dispersal in central India. Landsc Ecol 31:1355–1368. https://doi.org/10.1007/s10980-016-0363-0

Mateo-Sánchez MC, Balkenhol N, Cushman S, et al (2015) A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow? Landsc Ecol 30:1405–1420. https://doi.org/10.1007/s10980-015-0194-4

Naha D, Jhala Y V., Qureshi Q, et al (2016) Ranging, activity and habitat use by tigers in the mangrove forests of the Sundarban. PLoS One 11:1–16. https://doi.org/10.1371/journal.pone.0152119

Ngoprasert D, Lynam AJ, Sukmasuang R, et al (2012) Occurrence of Three Felids across a Network of Protected Areas in Thailand: Prey, Intraguild, and Habitat Associations. Biotropica 44:810–817. https://doi.org/10.1111/j.1744-7429.2012.00878.x

OpenStreetMap (2019) OpenStreetMap. www.openstreetmap.org. Accessed 10 Jun 2019

Reddy PA, Cushman SA, Srivastava A, et al (2017) Tiger abundance and gene flow in Central India are driven by disparate combinations of topography and land cover. Divers Distrib 23:863–874. https://doi.org/10.1111/ddi.12580

SERVIR-Mekong (2018) SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS). SERVIR-Mekong/USAID/NASA/ADPC/ICIMOD, Asian Disaster Preparedness Center (ADPC), Bangkok, Thailand

Shirk AJ, Wallin DO, Cushman SA, et al (2010) Inferring landscape effects on gene flow: a new model selection framework. Mol Ecol 19:3603–3619. https://doi.org/10.1111/j.1365-294X.2010.04745.x

Smith JLD (1993) The Role of Dispersal in Structuring the Chitwan Tiger Population. Behaviour 124:165–195. https://doi.org/10.1163/156853993X00560

Stokes D (2017) Thap Lan: Thailand's unsung forest gem under threat, but still abrim with life. In: Mongabay, 31 January 2017. https://news.mongabay.com/2017/01/thap-lan-thailands-unsung-forest-gem-under-threat-but-still-abrim-with-life/. Accessed 27 Mar 2021

Sunarto S, Kelly MJ, Parakkasi K, et al (2012) Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS One 7:e30859. https://doi.org/10.1371/journal.pone.0030859

Sunquist M (2010) What is a Tiger? Ecology and Behavior. In: Tilson R, Nyhus P (eds) Tigers of the World, Second Edition. Elsevier, New York, pp 19–34

Sunquist M, Karanth UK, Sunquist F (1999) Ecology, behaviour and resilience of the tiger and its conservation needs. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 5–18

Thatte P, Joshi A, Vaidyanathan S, et al (2018) Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations. Biol Conserv 218:181–191. https://doi.org/10.1016/j.biocon.2017.12.022

Walston J, Robinson JG, Bennett EL, et al (2010) Bringing the tiger back from the brink-the six percent solution. PLoS Biol 8:6–9. https://doi.org/10.1371/journal.pbio.1000485

Wan HY, Cushman SA, Ganey JL (2019) Improving habitat and connectivity model predictions with multi-scale resource selection functions from two geographic areas. Landsc Ecol 34:503–519. https://doi.org/10.1007/s10980-019-00788-w

WCS, CIESIN (2005) Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic). Wildlife Conservation Society, Center for International Earth Science Information Network - Columbia University, NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY

Supplementary Materials 2

Additional Results Tables

Note: Due to the volume of content in this section, tables are not included in this document. These tables can be accessed online at https://doi.org/10.3390/land9110415

Supplementary Materials 3

Supplementary Figures and Figure Animations

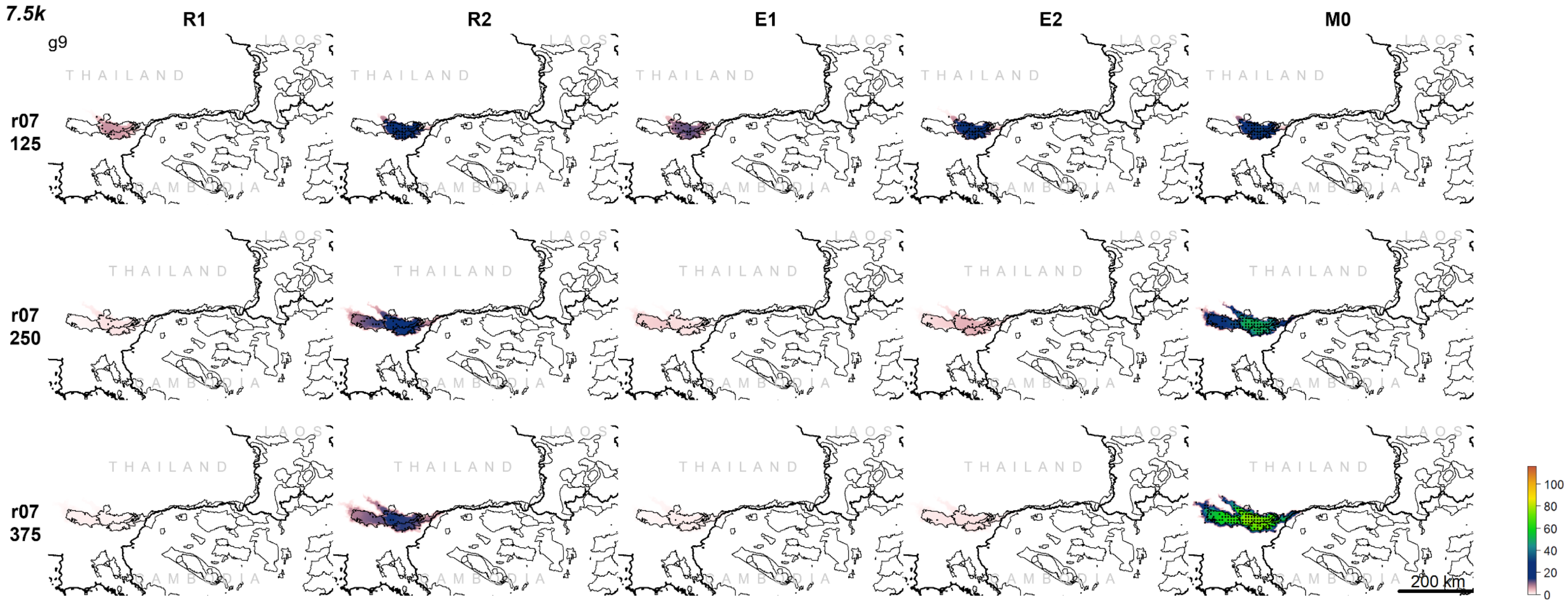

Fig. 1 Maps demonstrating divergence in cumulative resistance kernels and populations between combinations of mortality function (MORT – R1, R2, E1, E2, and M0) and dispersal ability (KERN – 125kcu, 250kcu, and 375kcu) at timestep 9, holding highway mitigation scenario (SCEN - S3), territory spacing (DENS - 7.5km), and resistance transformation (RES – r07) constant. An animation depicting changes in kernels over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig1 (https://www.wildcru.org/research/a-case-study-of-tigers/).

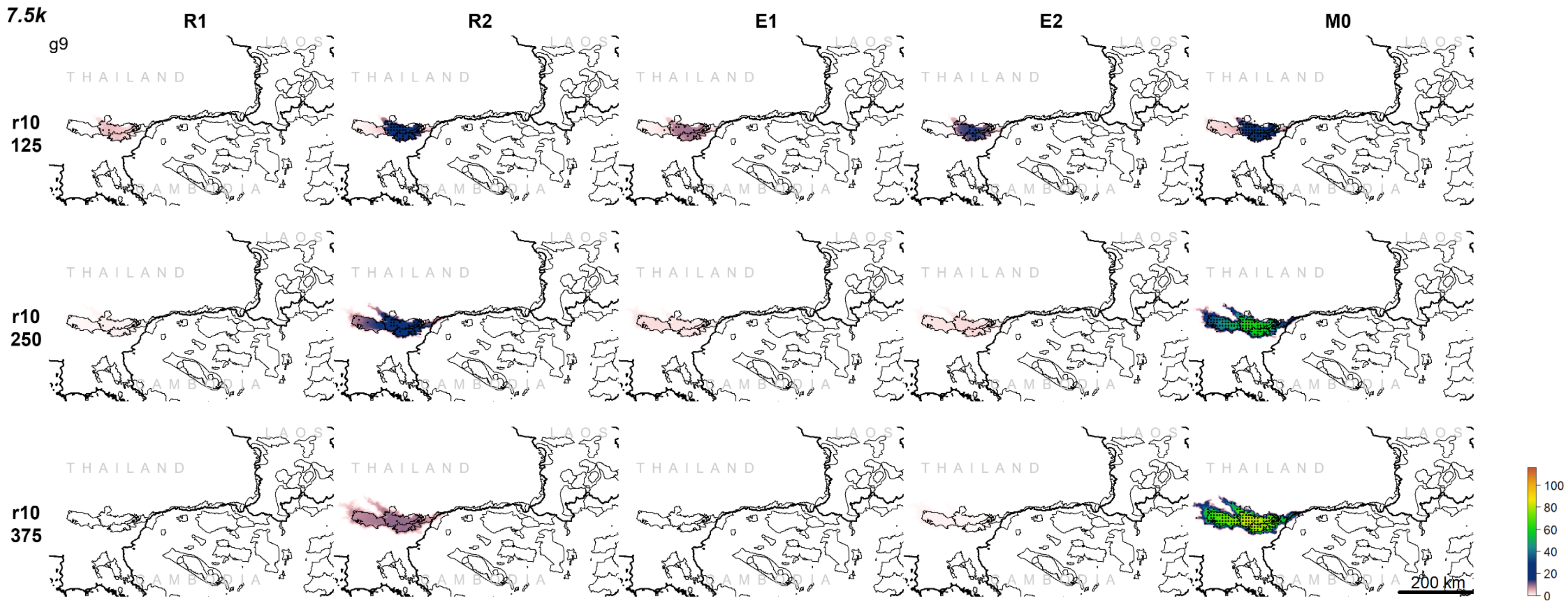

Fig. 2 Maps demonstrating divergence in cumulative resistance kernels and populations between combinations of mortality function (MORT – R1, R2, E1, E2, and M0) and dispersal ability (KERN – 125kcu, 250kcu, and 375kcu) at timestep 9, holding highway mitigation scenario (SCEN - S3), territory spacing (DENS - 7.5km), and resistance transformation (RES – r10) constant. An animation depicting changes in kernels over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig2 (https://www.wildcru.org/research/a-case-study-of-tigers/).

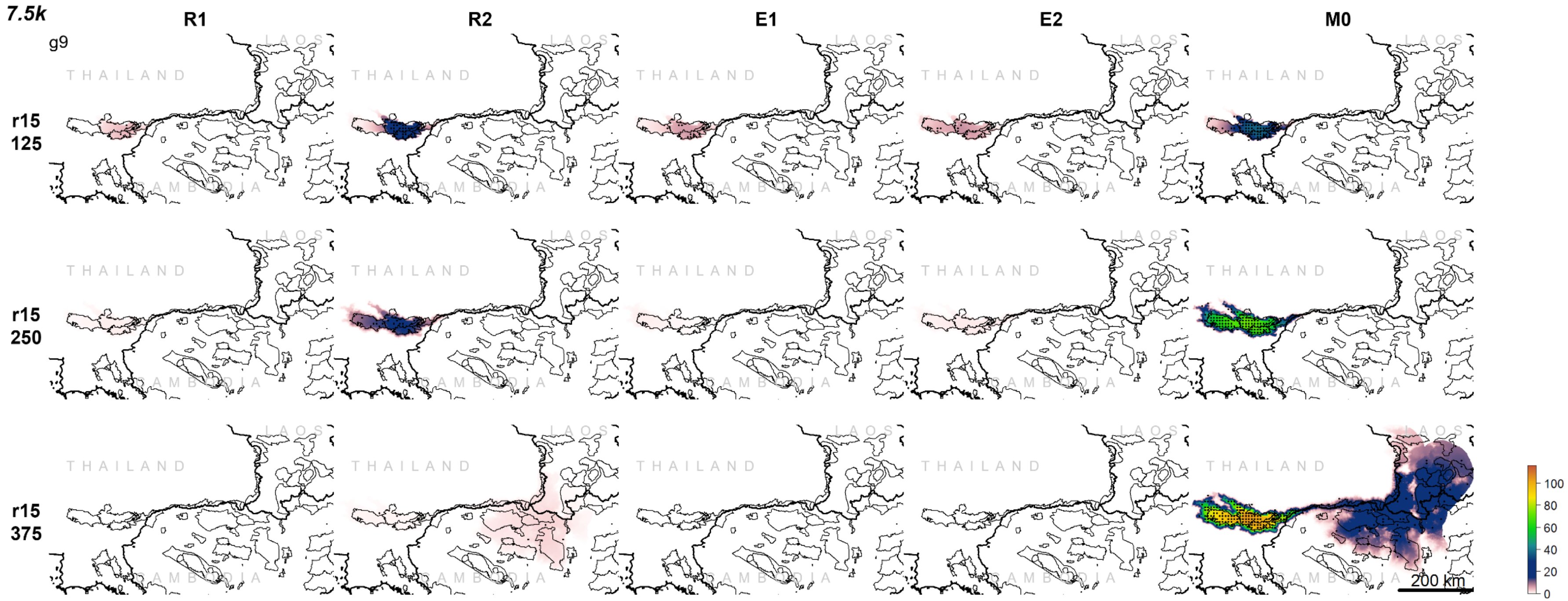

Fig. 3 Maps demonstrating divergence in cumulative resistance kernels and populations between combinations of mortality function (MORT – R1, R2, E1, E2, and M0) and dispersal ability (KERN – 125kcu, 250kcu, and 375kcu) at timestep 9, holding highway mitigation scenario (SCEN - S3), territory spacing (DENS - 7.5km), and resistance transformation (RES – r15) constant. An animation depicting changes in kernels over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig3 (https://www.wildcru.org/research/a-case-study-of-tigers/).

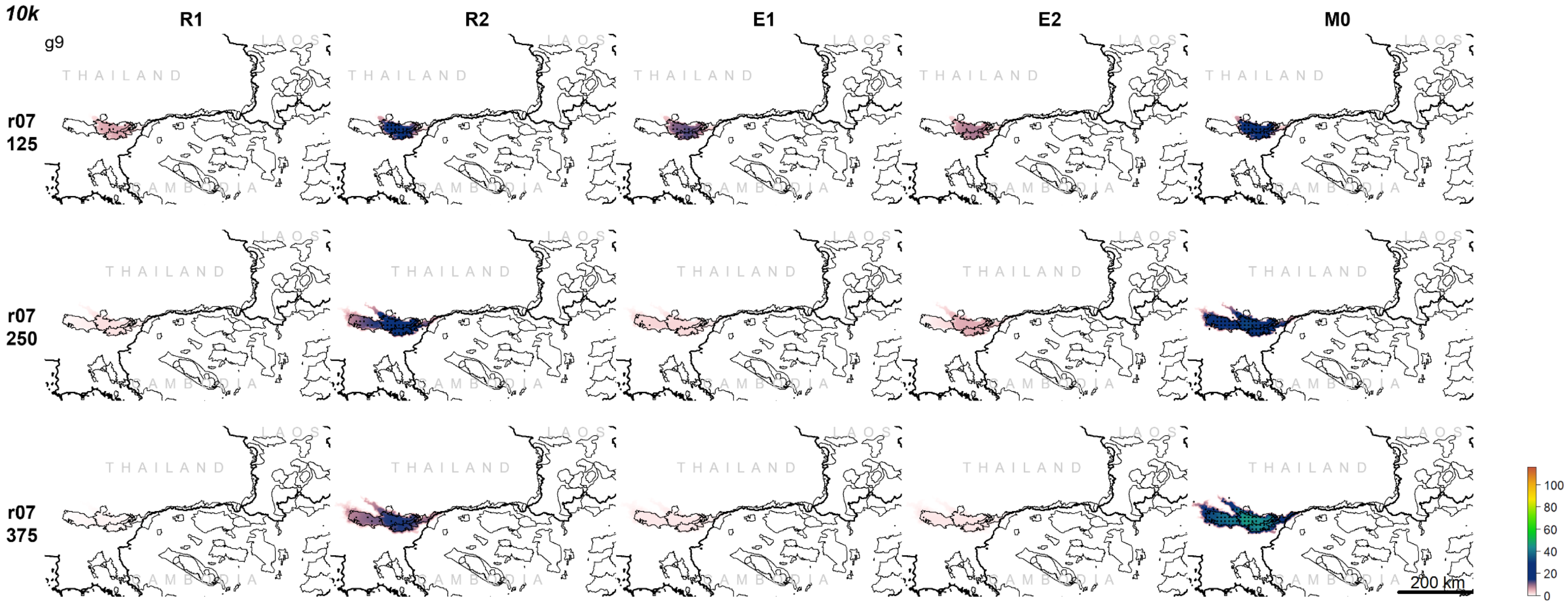

Fig. 4 Maps demonstrating divergence in cumulative resistance kernels and populations between combinations of mortality function (MORT – R1, R2, E1, E2, and M0) and dispersal ability (KERN – 125kcu, 250kcu, and 375kcu) at timestep 9, holding highway mitigation scenario (SCEN - S3), territory spacing (DENS - 10km), and resistance transformation (RES – r07) constant. An animation depicting changes in kernels over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig4 (https://www.wildcru.org/research/a-case-study-of-tigers/).

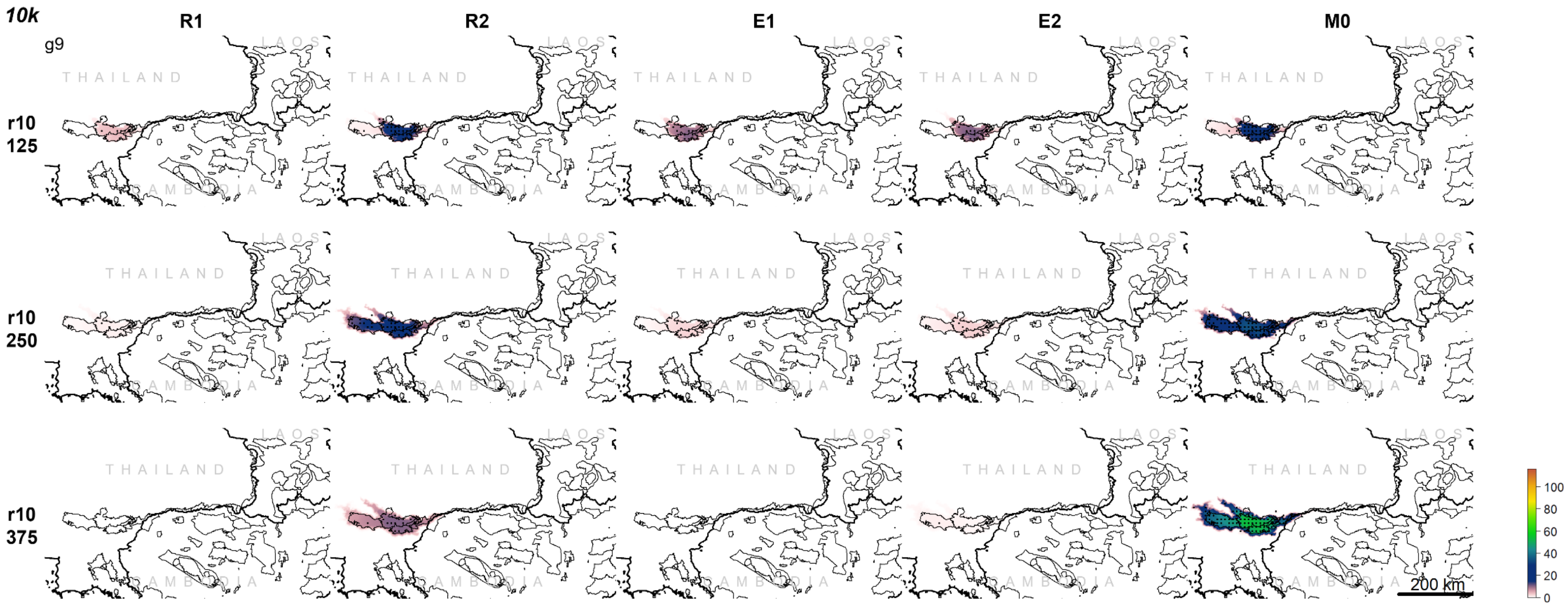

Fig. 5 Maps demonstrating divergence in cumulative resistance kernels and populations between combinations of mortality function (MORT – R1, R2, E1, E2, and M0) and dispersal ability (KERN – 125kcu, 250kcu, and 375kcu) at timestep 9, holding highway mitigation scenario (SCEN - S3), territory spacing (DENS - 10km), and resistance transformation (RES – r10) constant. An animation depicting changes in kernels over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig5 (https://www.wildcru.org/research/a-case-study-of-tigers/).

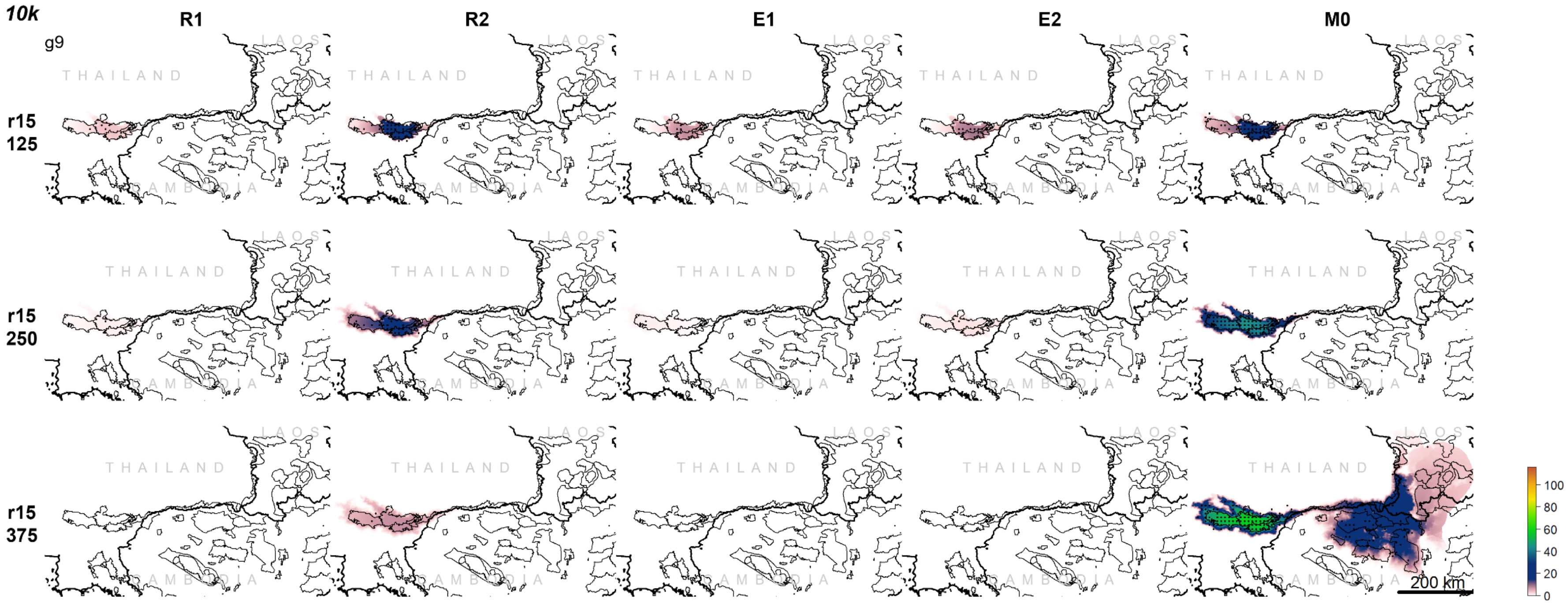

Fig. 6 Maps demonstrating divergence in cumulative resistance kernels and populations between combinations of mortality function (MORT – R1, R2, E1, E2, and M0) and dispersal ability (KERN – 125kcu, 250kcu, and 375kcu) at timestep 9, holding highway mitigation scenario (SCEN - S3), territory spacing (DENS - 10km), and resistance transformation (RES – r15) constant. An animation depicting changes in kernels over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig6 (https://www.wildcru.org/research/a-case-study-of-tigers/).

(a) (b) (c)

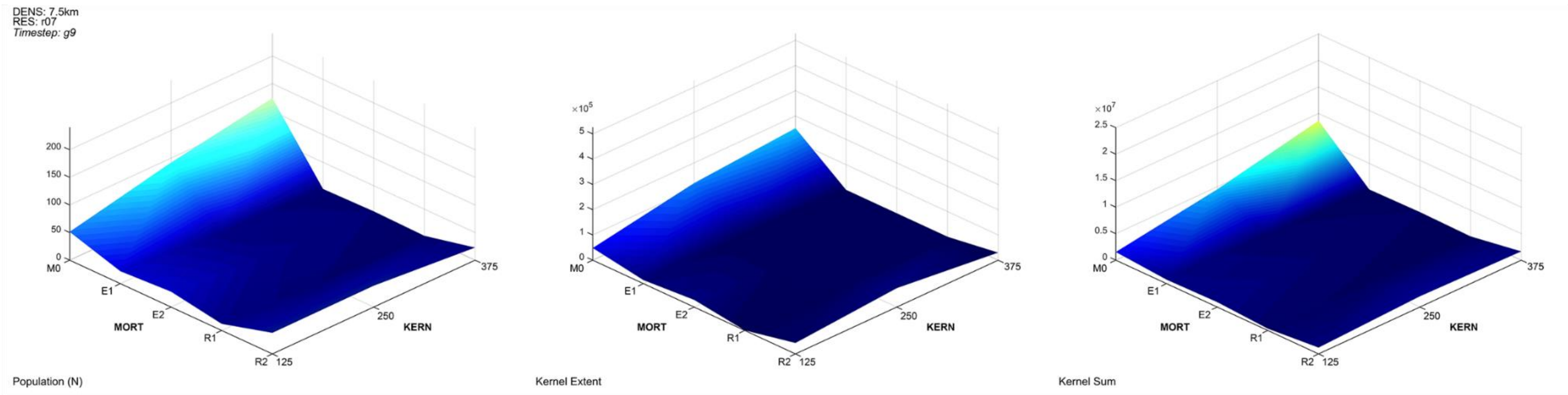

Fig. 7 Surface plots showing variation in predicted (a) population size, (b) kernel extent, (c) sum of kernel value for the 15 combinations of dispersal ability (KERN - 3 levels) and mortality risk (MORT - 5 levels) for resistance transformation 0.7 (RES – r07) and maximum population density 1/7.5km^2 (DENS – 7.5km) at timestep 9. An animation depicting changes in these metrics over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig7 (https://www.wildcru.org/research/a-case-study-of-tigers/).

(a) (b) (c)

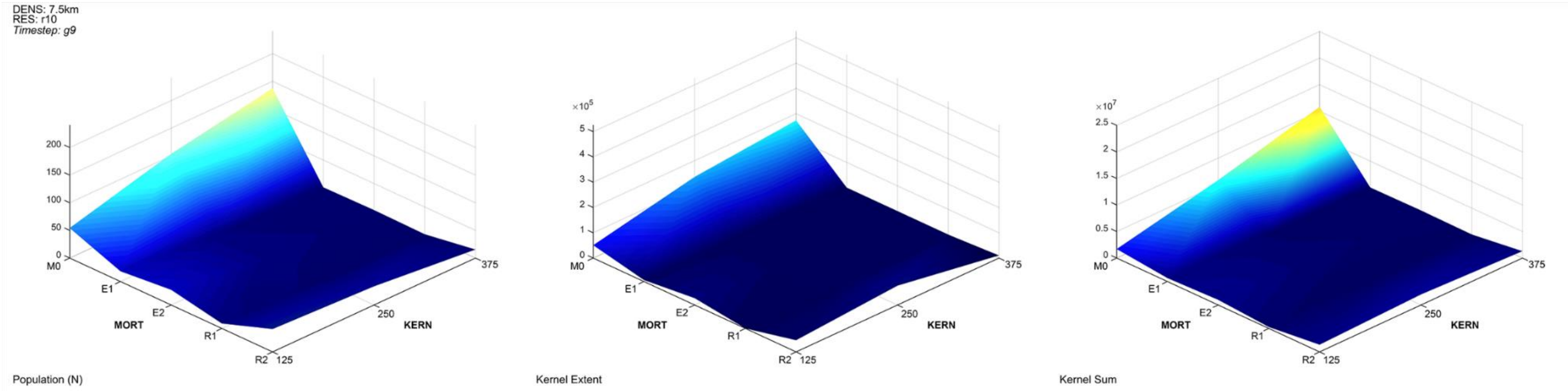

Fig. 8 Surface plots showing variation in predicted (a) population size, (b) kernel extent, (c) sum of kernel value for the 15 combinations of dispersal ability (KERN - 3 levels) and mortality risk (MORT - 5 levels) for resistance transformation 1.0 (RES – r10) and maximum population density 1/7.5km^2 (DENS – 7.5km) at timestep 9. An animation depicting changes in these metrics over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig8 (https://www.wildcru.org/research/a-case-study-of-tigers/).

(a) (b) (c)

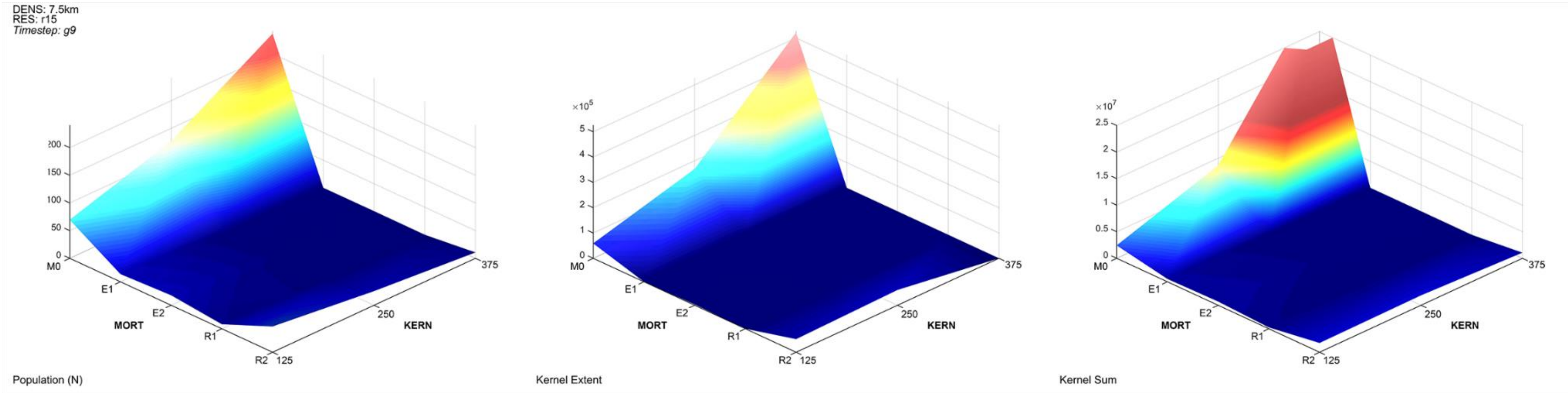

Fig. 9 Surface plots showing variation in predicted (a) population size, (b) kernel extent, (c) sum of kernel value for the 15 combinations of dispersal ability (KERN - 3 levels) and mortality risk (MORT - 5 levels) for resistance transformation 1.5 (RES – r15) and maximum population density 1/7.5km^2 (DENS – 7.5km) at timestep 9. An animation depicting changes in these metrics over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig9 (https://www.wildcru.org/research/a-case-study-of-tigers/).

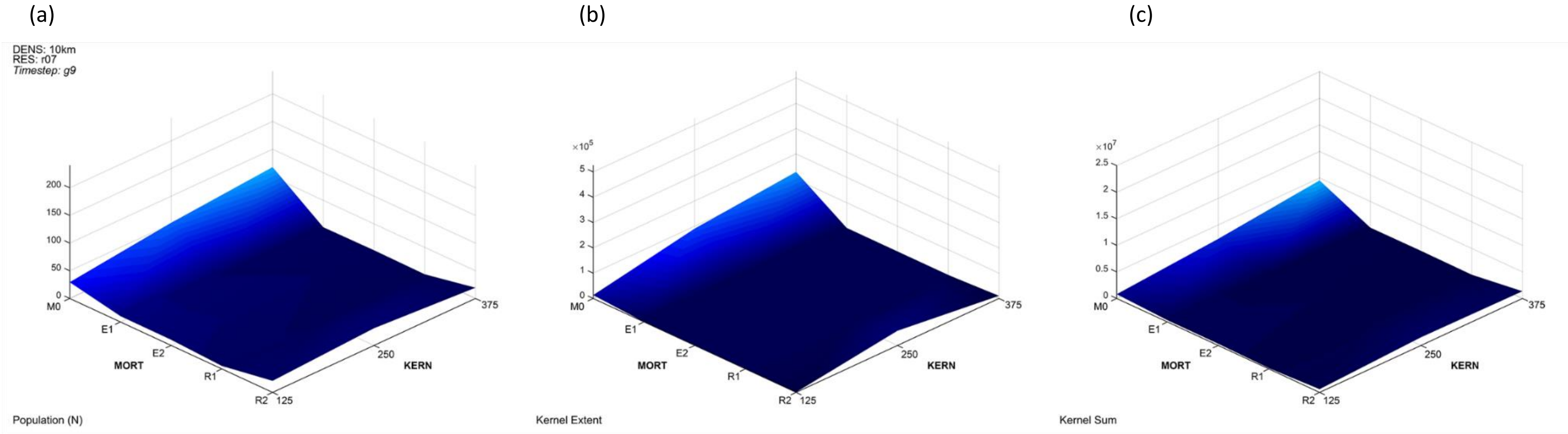

Fig. 10 Surface plots showing variation in predicted (a) population size, (b) kernel extent, (c) sum of kernel value for the 15 combinations of dispersal ability (KERN - 3 levels) and mortality risk (MORT - 5 levels) for resistance transformation 0.7 (RES – r07) and minimum population density 1/10km^2 (DENS – 10km) at timestep 9. An animation depicting changes in these metrics over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig10 (https://www.wildcru.org/research/a-case-study-of-tigers/).

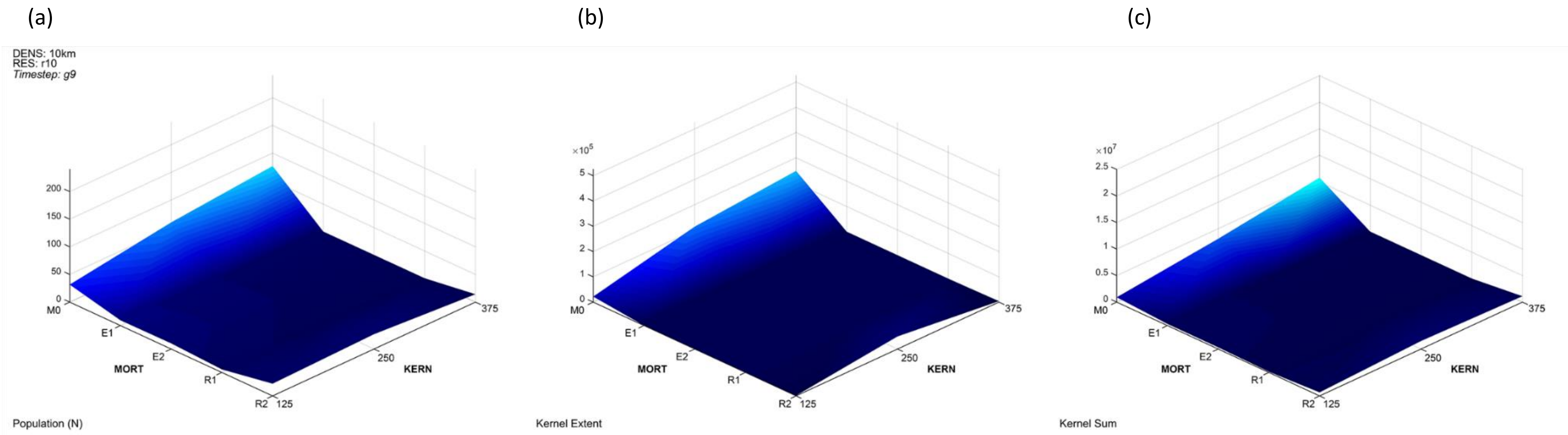

Fig. 11 Surface plots showing variation in predicted (a) population size, (b) kernel extent, (c) sum of kernel value for the 15 combinations of dispersal ability (KERN - 3 levels) and mortality risk (MORT - 5 levels) for resistance transformation 1.0 (RES – r10) and minimum population density 1/10km^2 (DENS – 10km) at timestep 9. An animation depicting changes in these metrics over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig11 (https://www.wildcru.org/research/a-case-study-of-tigers/).

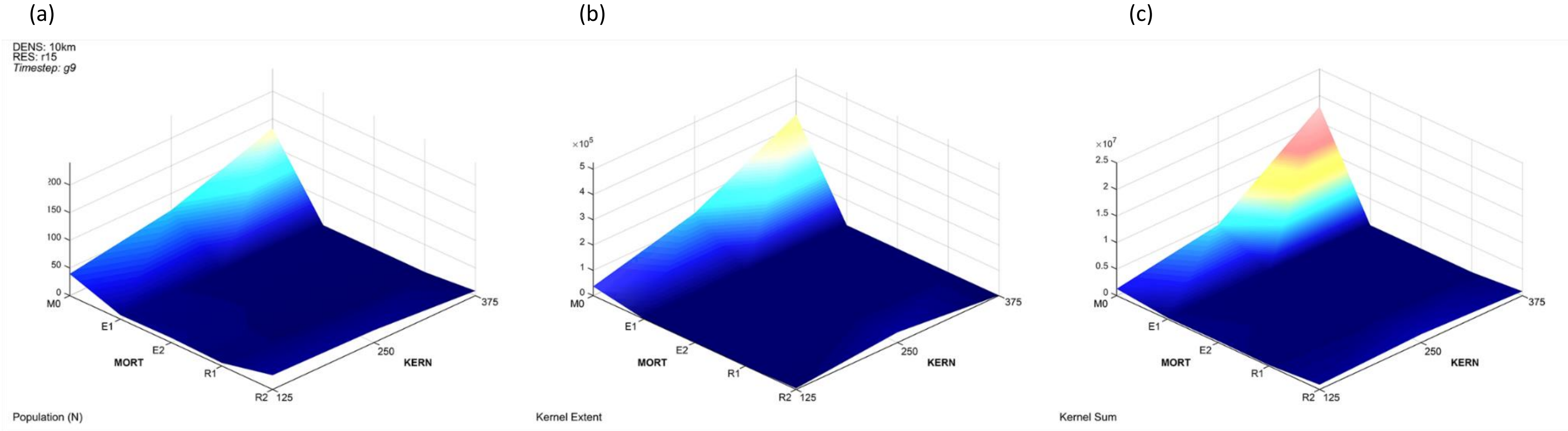

Fig. 12 Surface plots showing variation in predicted (a) population size, (b) kernel extent, (c) sum of kernel value for the 15 combinations of dispersal ability (KERN - 3 levels) and mortality risk (MORT - 5 levels) for resistance transformation 1.5 (RES – r15) and minimum population density 1/10km^2 (DENS – 10km) at timestep 9. An animation depicting changes in these metrics over all timesteps can be found at Ash_et_al_land-958248_SupplementaryMaterials3-Fig12 (https://www.wildcru.org/research/a-case-study-of-tigers/).

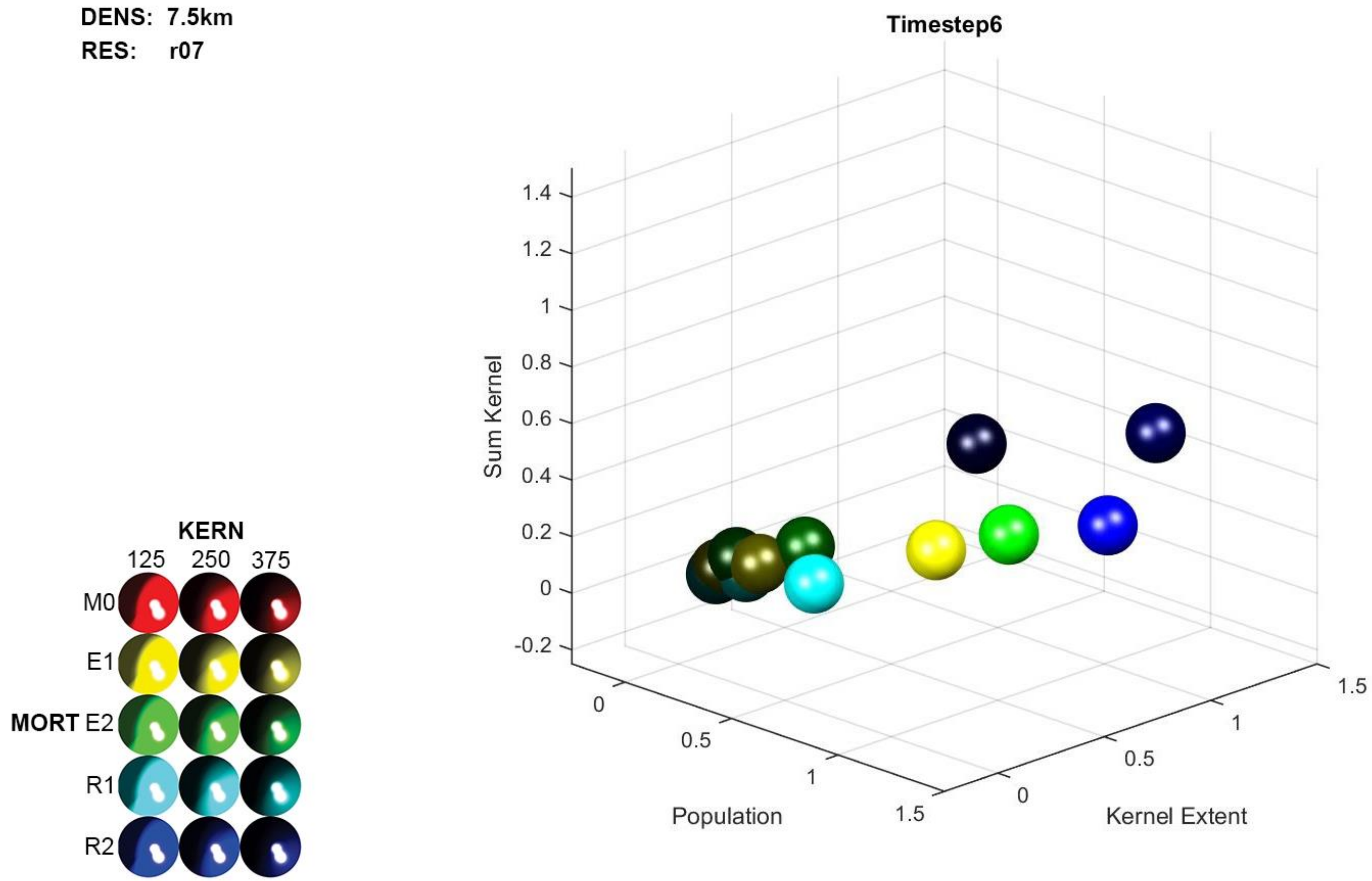

Fig. 13 Orthogonal views of the 3-dimensional trajectory of scenarios in a space defined by kernel extent, sum kernel value, and population size, for resistance transformation 0.7 (RES – r07) and maximum population density 1/7.5km^2 (DENS – 7.5km) at timestep 6. The colors of the spheres indicate different combinations of dispersal ability (KERN) and mortality risk (MORT). Extreme values of M0 extend outside axis limits. Animations of this plot can be viewed at Ash_et_al_land-958248_SupplementaryMaterials3-Fig13 (https://www.wildcru.org/research/a-case-study-of-tigers/).

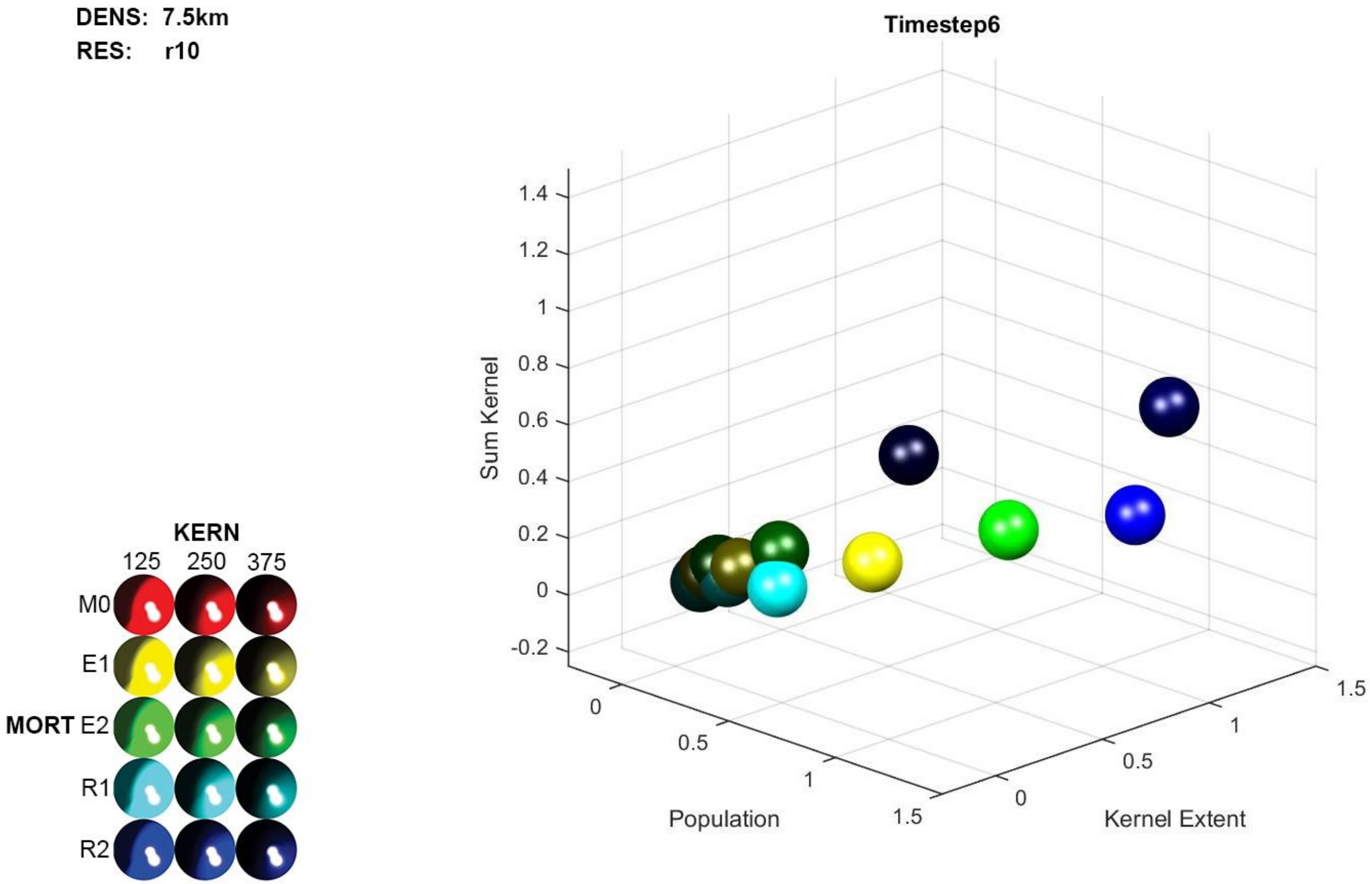

Fig. 14 Orthogonal views of the 3-dimensional trajectory of scenarios in a space defined by kernel extent, sum kernel value, and population size, for resistance transformation 1.0 (RES – r10) and maximum population density 1/7.5km^2 (DENS – 7.5km) at timestep 6. The colors of the spheres indicate different combinations of dispersal ability (KERN) and mortality risk (MORT). Extreme values of M0 extend outside axis limits. Animations of this plot can be viewed at Ash_et_al_land-958248_SupplementaryMaterials3-Fig14 (https://www.wildcru.org/research/a-case-study-of-tigers/).

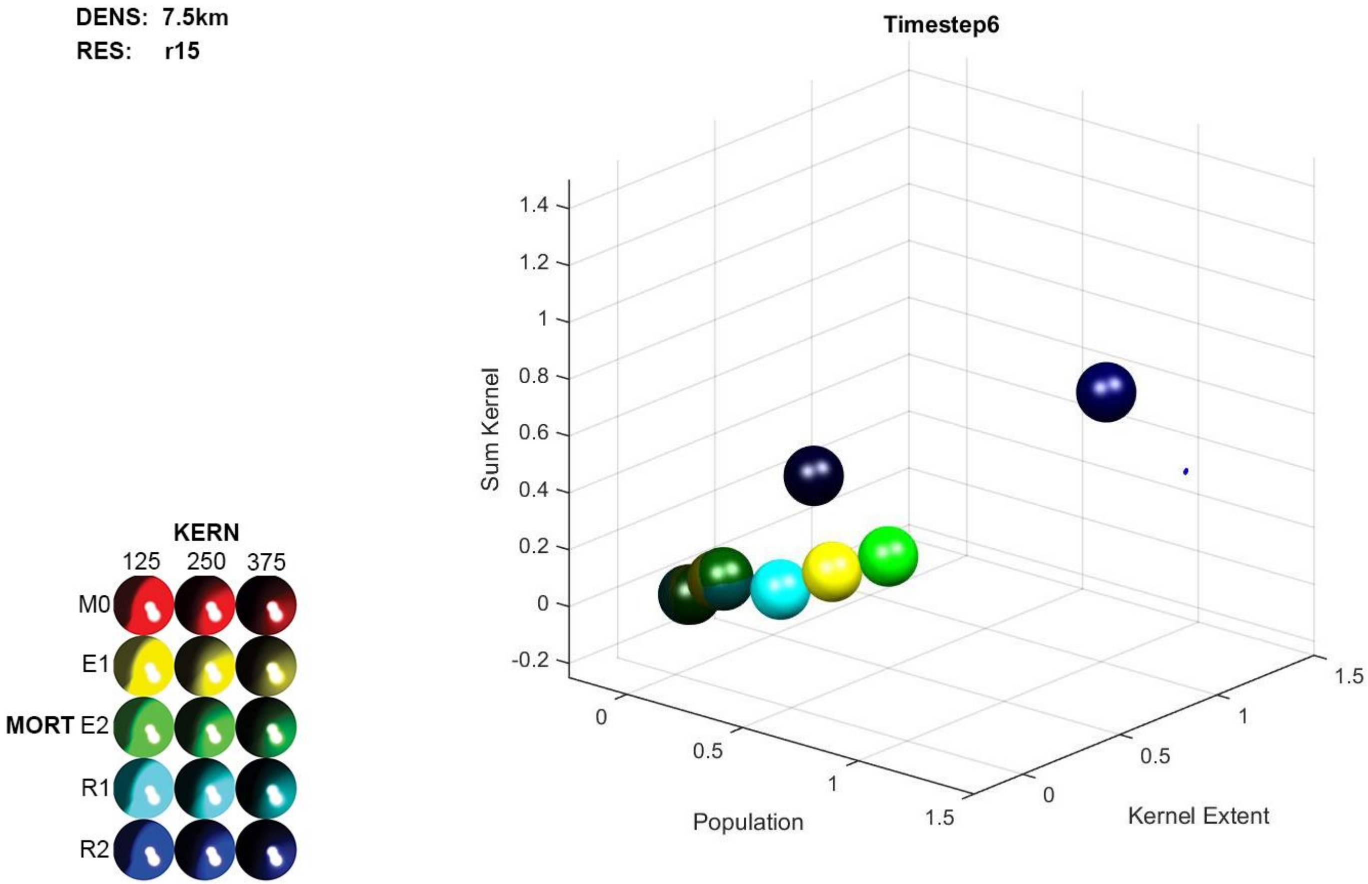

Fig. 15 Orthogonal views of the 3-dimensional trajectory of scenarios in a space defined by kernel extent, sum kernel value, and population size, for resistance transformation 1.5 (RES – r15) and maximum population density 1/7.5km^2 (DENS – 7.5km) at timestep 6. The colors of the spheres indicate different combinations of dispersal ability (KERN) and mortality risk (MORT). Extreme values of M0 extend outside axis limits. Animations of this plot can be viewed at Ash_et_al_land-958248_SupplementaryMaterials3-Fig15 (https://www.wildcru.org/research/a-case-study-of-tigers/).

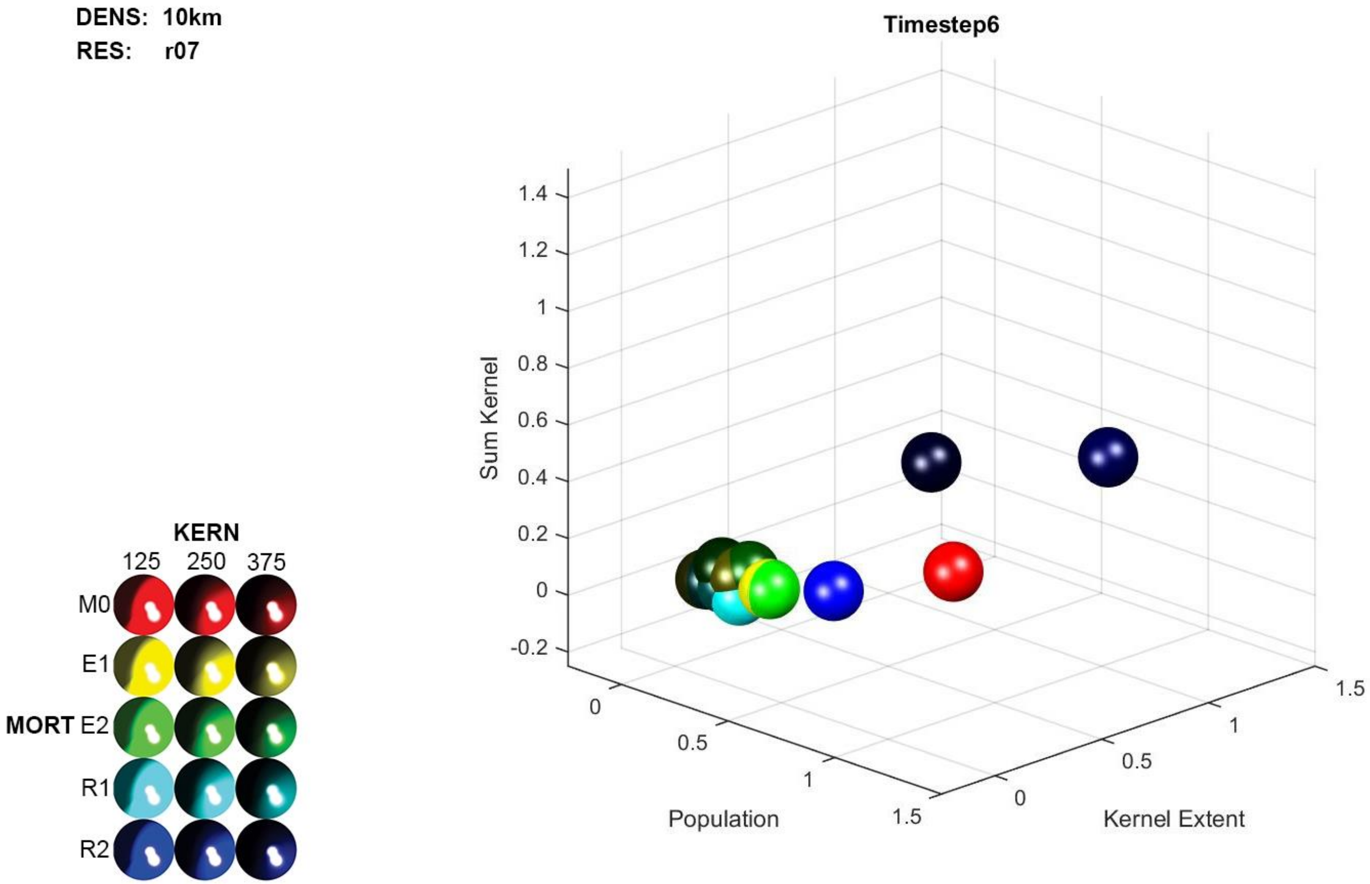

Fig. 16 Orthogonal views of the 3-dimensional trajectory of scenarios in a space defined by kernel extent, sum kernel value, and population size, for resistance transformation 0.7 (RES – r07) and minimum population density 1/10km^2 (DENS – 10km) at timestep 6. The colors of the spheres indicate different combinations of dispersal ability (KERN) and mortality risk (MORT). Extreme values of M0 extend outside axis limits. Animations of this plot can be viewed at Ash_et_al_land-958248_SupplementaryMaterials3-Fig16 (https://www.wildcru.org/research/a-case-study-of-tigers/).

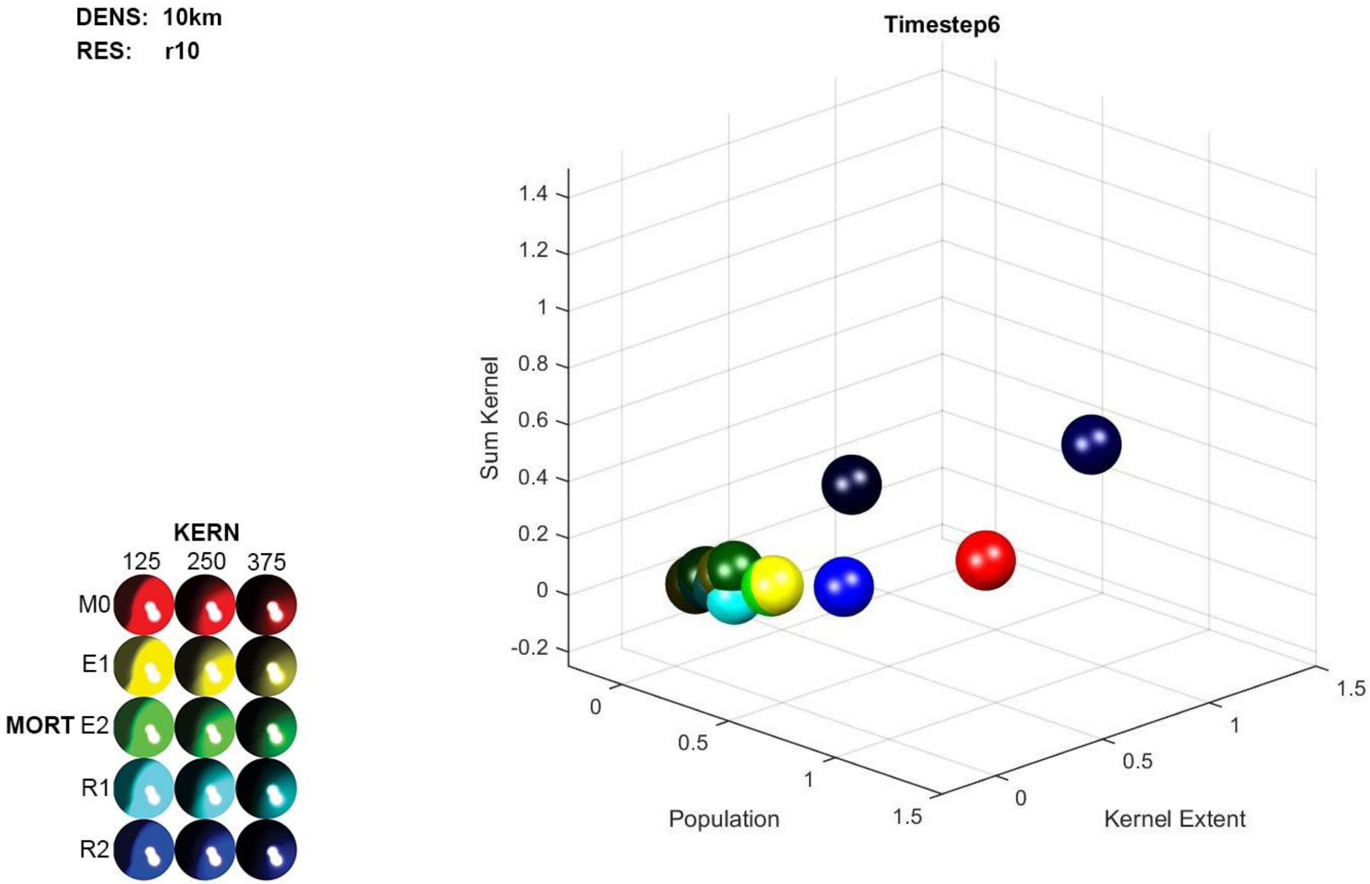

Fig. 17 Orthogonal views of the 3-dimensional trajectory of scenarios in a space defined by kernel extent, sum kernel value, and population size, for resistance transformation 1.0 (RES – r10) and minimum population density 1/10km^2 (DENS – 10km) at timestep 6. The colors of the spheres indicate different combinations of dispersal ability (KERN) and mortality risk (MORT). Extreme values of M0 extend outside axis limits. Animations of this plot can be viewed at Ash_et_al_land-958248_SupplementaryMaterials3-Fig17 (https://www.wildcru.org/research/a-case-study-of-tigers/).

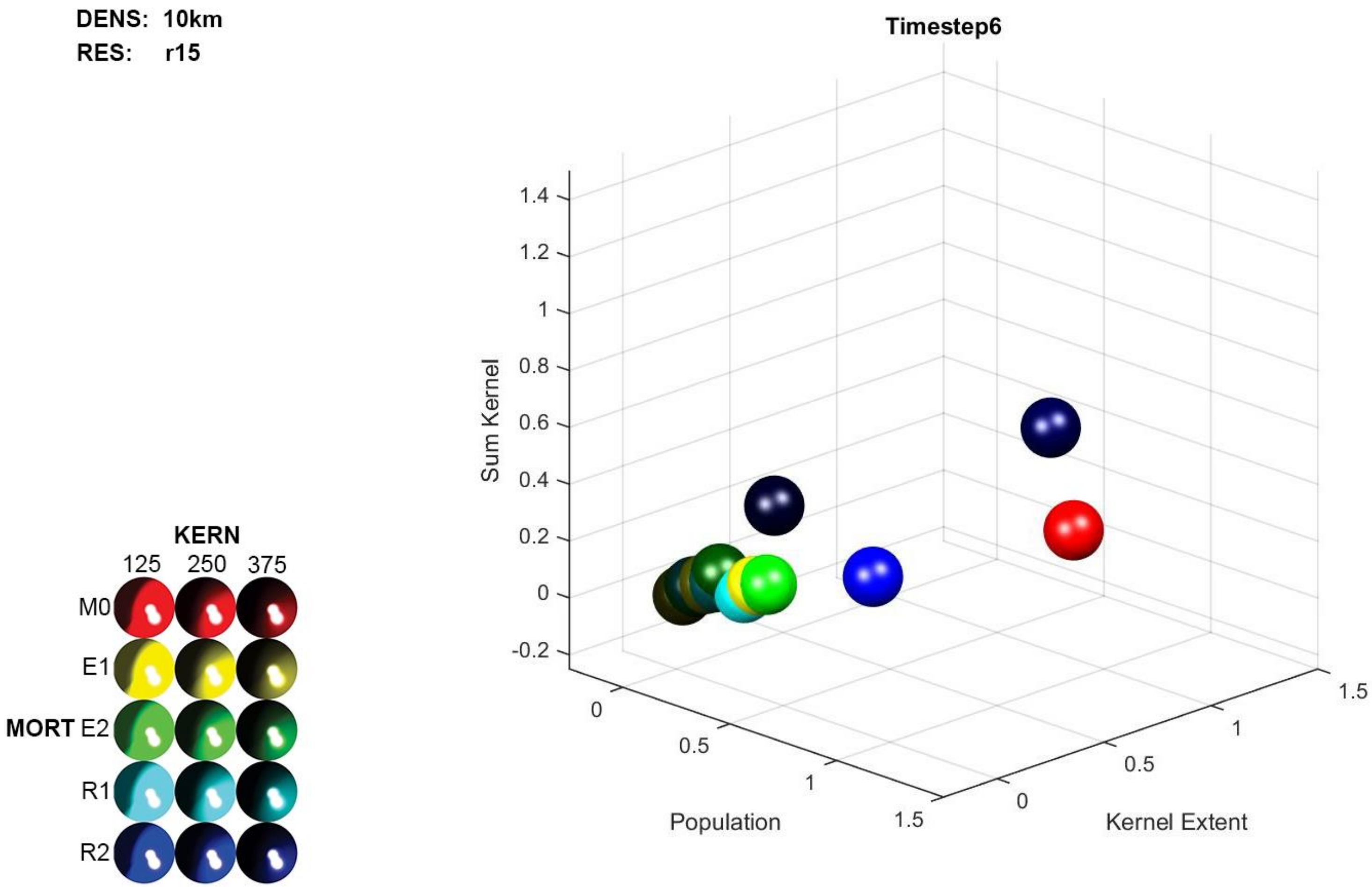

Fig. 18 Orthogonal views of the 3-dimensional trajectory of scenarios in a space defined by kernel extent, sum kernel value, and population size, for resistance transformation 1.5 (RES – r15) and minimum population density 1/10km^2 (DENS – 10km) at timestep 6. The colors of the spheres indicate different combinations of dispersal ability (KERN) and mortality risk (MORT). Extreme values of M0 extend outside axis limits. Animations of this plot can be viewed at Ash_et_al_land-958248_SupplementaryMaterials3-Fig18 (https://www.wildcru.org/research/a-case-study-of-tigers/).

Chapter 7

Tigers on the edge: Mortality and landscape change dominate individual-based spatially-explicit simulations of a small tiger population

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Title

Tigers on the edge: Mortality and landscape change dominate individual-based spatially-explicit simulations of a small tiger population

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Abstract

Context Reductions in the tiger's (*Panthera tigris*) range in Southeast Asia have been concurrent with large infrastructure expansion and landscape change. Thailand's Dong Phayayen-Khao Yai Forest Complex (DPKY), a landscape of tiger conservation priority, may be particularly vulnerable to such changes, necessitating investigations into effects on population dynamics.

Objectives To evaluate relative effects of landscape change scenarios on the probability of tiger persistence in DPKY and sensitivity of predictions to spatially-explicit mortality risk, landscape resistance, and tiger population density.

Methods We utilize individual-based, spatially-explicit population modelling to evaluate the trajectory and sensitivity of tiger population dynamics across 11 landscape change scenarios, 13 mortality functions, three nonlinear resistance transformations, and three maximum population densities across 20 generations.

Results Spatially-explicit mortality risk dominated predictions of population persistence, frequently resulting in population declines/extinction. Adjustment of moderate mortality risk to slightly convex and concave forms shifted extinction rates from 46% to 12% and 85%, respectively. Holding mortality constant at moderate levels, strong negative effects were predicted in landscape change scenarios incorporating road expansion (46%-74% extinction) and construction of dams (52%). Strong negative effects of combined development persisted even when habitat restoration measures were applied (96% extinction). Adjusting resistance and maximum population density had marginal effects.

Conclusions The high sensitivity and variability of predictions to spatial patterns of mortality risk suggest a population on a proverbial knife's edge. Our results underscore the importance of incorporating spatial patterns of mortality risk in population modelling, highlighting their potentially dominating influence on population dynamics and extinction risk in small populations.

Keywords *Panthera tigris;* Dong Phayayen-Khao Yai Forest Complex; sensitivity analysis; mortality risk; population viability analysis; population dynamics

1. Introduction

Tigers (*Panthera tigris*), which historically occurred across Asia, have suffered large contractions in range and population over the past century (Nowell and Jackson 1996; Goodrich et al. 2015). As human populations continue to expand, refugia for tigers are becoming increasingly scarce and fragmented. This is compounded by poaching and other threats, jeopardizing long-term population persistence (Wikramanayake et al. 2011; Goodrich et al. 2015; Wolf and Ripple 2016). This is particularly evident in Southeast Asia. Severe reductions in the tiger's range in the region (Sanderson et al. 2006; Lynam and Nowell 2011) have occurred at a time where national and transnational economic strategies have necessitated monumental investments in infrastructure and transformative land use change (Quintero et al. 2010; Wongwuttiwat and Lawanna 2018; Hughes 2019; Kaszta et al. 2020). With tigers in Southeast Asia seemingly at both figurative and, often literal, crossroads, understanding the effects of these changes on tiger population dynamics is crucial for developing effective conservation and management strategies.

Given anthropogenically-driven population and range declines over the past century, population dynamics and persistence of tigers currently is less a reflection of the species' biological or adaptive constraints than an indication of spatial patterns of human presence and activity (Sunquist et al. 1999; Walston et al. 2010; Goodrich et al. 2015). Observed demographic patterns governing species persistence are inexorably linked with spatially-dynamic processes such as large scale-changes to landscapes (Lande 1988; Kareiva and Wennergren 1995), which is of particular relevance for wide-ranging species such as the tiger. Understanding these links between species persistence and heterogeneous landscapes can be aided by models which incorporate spatially-explicit frameworks (Kareiva 1990; Dunning et al. 1992). Spatially-explicit models can enable evaluation of the effect of changes in the landscape on population dynamics (Dunning Jr et al. 1995), elucidate interactions between landscape structure, physiognomy, and species traits (Cantrell and Cosner 1993), and identify potential extinction thresholds (Kareiva and Wennergren 1995).

Several recent studies have conducted spatially-explicit simulations of a range of realistic development scenarios and conservation interventions, assessing their effect on vulnerable species (Cushman et al. 2016; Thatte et al. 2018; Macdonald et al. 2018; Kaszta et al. 2019, 2020). Importantly, when spatially-heterogenous mortality risk is included in these simulations, it can exert a disproportionate influence on population persistence (Kramer-Schadt et al. 2004; Cushman 2006; Kaszta et al. 2019, 2020). Despite its potential effect, studies may not explicitly incorporate mortality in modelling relationships between species populations and changes to landscapes (Thatte et al. 2018; Kaszta et al. 2019). It is crucial to investigate not only the effect of changes in landscape configuration on population connectivity and habitat, but also how associated changes in the spatial pattern of mortality risk affect the population and its probability of extinction. Predictions of population dynamics across landscapes may also be sensitive to population size or density (Cushman et al. 2013; Ash et al. 2020a), though the degree to which higher relative population densities may mitigate effects of mortality in large carnivores is subject to speculation (Karanth and Stith 1999; Chapron et al. 2008). Rapid land use change and economic development across the tiger's range also have implications for landscape resistance to movement, which may have drastic and complex effects for highly vagile species (Carr and Fahrig 2001; Carr et al. 2002; Cushman 2006). Importantly, predictions may be sensitive to both the means by which factors in population models are parameterized and the strength of their interactions (Dunning Jr et al. 1995; McCarthy et al. 1995).

Thailand's Dong Phayayen-Khao Yai Forest Complex (DPKY) is both an illustrative proxy for Southeast Asia's tigers and is a dynamic landscape for which spatially-explicit simulations may be valuable. The UNESCO World Heritage Site supports one of the region's remaining tiger breeding populations (Ash et al. 2020c), though the effects of human pressure on the landscape has been the subject of concern (IUCN World Heritage Outlook 2020). The landscape contains large extents of forest cover of varying contiguity and protection status, with potential opportunities to expand tiger habitat, though the complex remains entrenched within an increasingly human-dominated landscape at the nexus of important economic corridors (Wongwuttiwat and Lawanna 2018). Roads in and around the complex have and may undergo further expansion and increased use, while the placement of wildlife crossing structures along highways could potentially mitigate road effects on population fragmentation (IUCN World Heritage Outlook 2020; Paansri et al. 2021). Lastly, growing water insecurity could increase pressure to construct new dams/reservoirs, potentially inundating parts of the complex (Marks 2011; IUCN World Heritage Outlook 2020; Manorom 2020).

Given the importance of DPKY within regional tiger conservation strategies (Ash et al. 2020c), investigating the potential effect of future development and conservation initiatives is of critical importance. In this study, we utilize an individual-based, spatially-explicit population modelling approach to evaluate the relative effects of potential landscape change scenarios on the probability of tiger persistence in DPKY. Concurrently, we evaluate the relative effect of, and sensitivity of predictions to, spatially-differential mortality risk, landscape resistance transformation, and maximum potential population density. Through this study, we aim to generate insight for the development of conservation and management strategies in DPKY while highlighting key considerations for spatially-explicit population modelling for other threatened species.

2. Methods

2.1 Study site

Eastern Thailand's Dong Phayayen-Khao Yai Forest Complex (DPKY) consists of five protected areas across 6,155km^2 - Khao Yai National Park, Thap Lan National Park, Pang Sida National Park, Ta Phraya National Park and Dong Yai Wildlife Sanctuary – and supports a small, isolated breeding population of Indochinese tigers (*P. t. corbetti*; Ash et al. 2020c). The complex is primarily surrounded by a human-dominated landscape of urban areas, villages, agriculture, roads, and other infrastructure. While most of the landscape outside DPKY has been converted by human activities, limited patches of forest occur outside the complex adjacent to existing protected areas. The complex is divided by major highways, including Routes 304 and 348, though the former has been the site of a recently completed series of wildlife crossing structures, potentially mitigating fragmentary effects. Restricted or managed roads include a private road (Route 3446) running through Ta Phraya National Park, and an unpaved former public road (Route 3462) which runs through Pang Sida and Thap Lan national parks, managed by park authorities. Outside the complex, minor roads connecting villages and urban areas are abundant. The reserve complex is the source of major watersheds and a number of man-made dams and reservoirs; these largely occur at the boundaries of, but, in some cases within, protected areas, and are largely maintained for the purposes of local water security and use, such as for agricultural irrigation. The complex is also relatively close to developed urban areas of varying size (including Saraburi [~28km] and Nakhon Ratchasima [~40km]) and, due to its proximity to the Cambodian border, is close to both formal and informal border crossings.

2.2 Population modelling approach

We evaluate tiger population trajectories using CDPOP (*Cost Distance POPulations*; Landguth and Cushman 2010) across combinations of four key factors: (1) landscape change scenario (SCN), (2) maximum population density (DEN), (3) resistance surface transformation (RST), and (4) mortality function (MRT; see sections below). We vary each factor by several levels, described below, to evaluate the relative effect of these factors on resulting simulated population (*N*).

CDPOP uses an individual-based, spatially-explicit framework to model mating, dispersal and mortality through space and time. Simulated movement across the landscape in this approach requires two

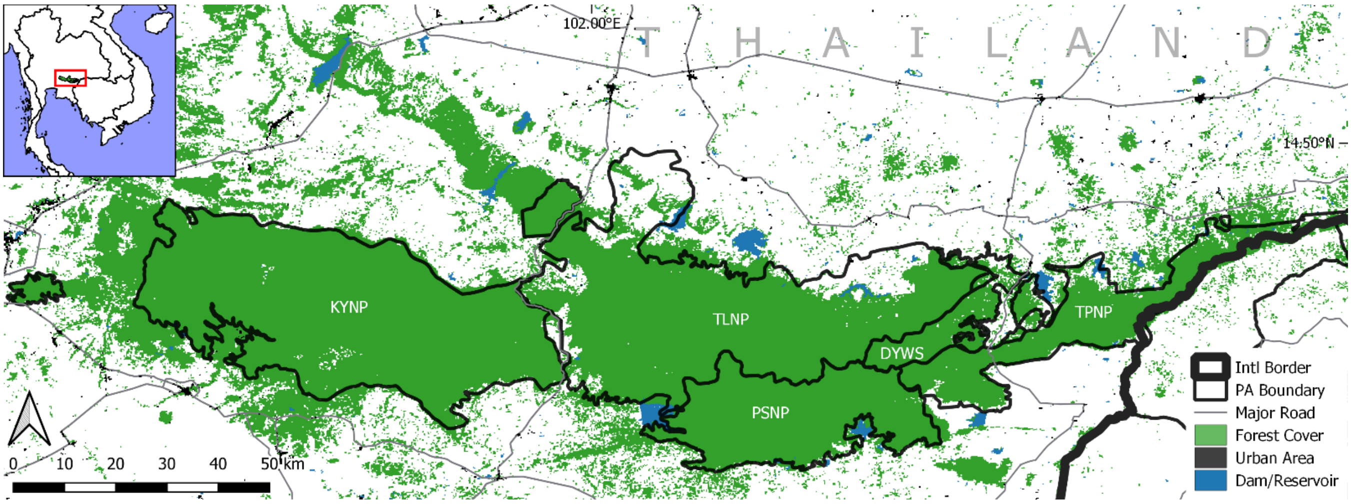

Fig. 1 Thailand's Dong Phayayen-Khao Yai Forest Complex (DPKY), spanning 6,155km^2 across five protected areas, including Khao Yai National Park (KYNP), Thap Lan National Park (TLNP), Pang Sida National Park (PSNP), Dong Yai Wildlife Sanctuary (DYWS), and Ta Phraya National Park (TPNP). Landscape attributes, including forest cover, roads, dams/reservoirs, urban extent, border crossings, and protected area coverage were modified and transformed across various landscape change scenarios, which can be viewed in Supplementary Materials 1 (SERVIR-Mekong 2018; OpenStreetMap 2019; UNEP-WCMC and IUCN 2019).

input layers: (1) a set of initial population source locations, reflecting the current state and potentially occupiable locations, and (2) a cost-distance matrix defining cumulative cost to movement between all occupiable locations, governed by a resistance surface. Individual movement in the simulation is defined by sex-dependent movement parameters, differentiated for mating and dispersal behaviour. In lieu of local empirically-derived parameters, these and other simulation parameters in our models were based on other studies on tigers and other wide-ranging felids (Thatte et al. 2018; Kaszta et al. 2019, 2020). A full summary of parameters can be found in Supplementary Materials 1.

2.2.1 Base resistance definition

We developed resistance surfaces to define spatial patterns of the study landscape, with which individuals in simulations would interact. Resistance surfaces are commonly used in modelling species movement across dynamic landscapes (Spear et al. 2010; Zeller et al. 2012; Graves et al. 2014) and reflect step-wise cost to individual movement, with high pixel values representing high resistance to movement and low values imparting little resistance. In our study, resistance surfaces were developed at a 250m resolution, using ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011) as well as the *raster* package in R (R Development Core Team 2019; Hijmans 2020).

We derived current landscape resistance from an expert-based resistance surface developed for DPKY by Ash et al. (2020a) who identified the resistance model used in their paper as the most representative of likely patterns of resistance among four candidate models. This expert-based surface was based on 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018) land cover data, classified into dense forest (resistance value of 1), scrub forest (resistance of 20), agriculture/village matrix (resistance of 50), reservoirs/surface water (resistance of 80), and urban areas (resistance of 100). Minor (resistance of 30) and major roads (resistance of 100; OpenStreetMap 2019) were also included. We utilized this base resistance surface as a foundation for the development of further landscape change scenarios.

2.2.2 Generating study extent, occupiable locations, and cost-distance matrices

We generated a cost-distance surface in ArcGIS to define the extent of the simulation landscape and determine all areas to which tigers can potentially disperse and establish home ranges. This was determined via a cost-distance function applied to the resistance surface, originating from DPKY's contiguous forest boundary, generating a kernel of 45,000 cost distance units. This represented a max dispersal distance of 45km at a resistance of 1, corresponding to the maximum scale in Reddy et al. (2017) used to evaluate associations of tiger effective population and landscape features. The resistance surface was then cropped to the resulting cost-distance kernel. To determine occupiable locations within the lattice of our study extent, we resampled the cost-distance kernel to 10km resolution, which was then converted to points. This effectively distributed points as centroids of theoretical, potentially occupiable tiger home ranges at a population density of 1/100km^2, occurring in the upper range of population density estimates for the DPKY complex (Ash et al. 2020b). Next, using the resistance surface (at 250m resolution) and all occupiable points at 1/100km^2 density as inputs, we generated cost-distance matrices in UNICOR (Landguth et al. 2012), defining the cost-weighted distance between every pair of potentially occupiable locations.

2.2.3 Generating population source points

To produce initial source points for simulations, we selected a sample of 30 points, representing the upper range of the current tiger population estimates within DPKY boundaries (Ash et al. 2020b), generated probabilistically and proportional to predicted tiger habitat suitability. We determined the locations for these points by subtracting a random raster, with values from 0-1, from a rescaled multiple spatial scale- and functional form (shape)-optimized tiger habitat suitability model developed by Ash et al. (2021) for DPKY, with values reflecting predicted presence on a scale from 0 to 1. We then selected a random sample of 30 source points from resulting pixels with values greater than 0 (e.g., Macdonald et al. 2018; Kaszta et al. 2019).

2.3 Sensitivity analysis

To account for uncertainty in model parameters and evaluate the sensitivity of population models to parameter settings, we varied two factors described in previous steps: (1) resistance surface and (2) potential population density (DEN). This follows the approach of a DPKY landscape connectivity study by Ash et al. (2020a), which found that predicted tiger population size and connectivity were sensitive to these factors.

2.3.1 Resistance transformation (RST)

Parameterization of resistance surfaces in population connectivity and related studies is ideally informed by movement, genetics, and other empirical data (Zeller et al. 2012). Given the lack of availability of these data, inherent uncertainty in developing resistance surfaces, and accounting for potential non-linear relationships with resistance, we modified resistance via three power function resistance transformations (RST; *sensu* Reddy et al. 2017). We transformed base resistance (RST10) to the 0.5 (RST05) and 2.0 power (RST20). We then rescaled the result to original minimum and maximum values and resampled them to 250m resolution. These power functions adjust the intensity and form of resistance from linear (RST10) to concave (RST05) or convex (RST20) functional forms.

2.3.2 Population density (DEN)

In order to evaluate the effect of tiger population density on predicted population trajectory, in addition to generating occupiable home range points at 10km resolution (1/100km^2), we tested two additional maximum tiger densities (DEN). These included points generated at a 7.5km resolution, corresponding to a tiger population density of approximately 1.78/100km^2, within a range of estimates reported in western Thailand (Duangchantrasiri et al. 2016). We also generated points at a 6km resolution, corresponding to a relatively high theoretical density of 2.78/100km^2. A total of 104 points were generated at 10km, 187 points at 7.5km, and 291 points at 6km, defining area-specific habitat carrying capacity (*K*). We then generated cost-distance matrices for each combination of transformed resistance surface (RST) and population density (DEN).

2.4 Mortality functions

The explicit incorporation of spatially-differential mortality risk in landscape-scale population modelling studies has been shown to dramatically affect conclusions pertaining to landscape connectivity and population persistence (Kramer-Schadt et al. 2004; Cushman 2006; Kaszta et al. 2019, 2020). In this study, we aimed to evaluate the effect of spatially-differential mortality risk (MRT) and sensitivity of simulations to different mortality function development approaches based on landscape resistance, predicted poacher presence, expert-based surfaces, and an effective population size model. We developed a total of 13 functions using these approaches, representing the probability of a tiger that has dispersed to a given pixel dying before reproducing. We present these in Table 1 and describe them in additional detail in Supplementary Materials 1.

For comparative purposes, we tested a null mortality function in our simulations (M0) in which no additional mortality was applied. In effect, this function represents the maximum theoretical population growth rate, dictated by resistance surface, movement, available habitat, and demographic parameters.

We developed a habitat-based mortality approach in which mortality is a function of local, empirically-based predicted tiger habitat suitability (MSSO model from Ash et al. 2021), landscape change

Table 1 Summary of mortality functions (MRT), development approach, and data sources. Each function was adapted accordingly to reflect changes under each landscape change scenario (SCN) and resampled at each density (DEN). Resulting functions were rescaled between 1-100, reflecting low to high probability of mortality, for incorporation into CDPOP.

Mortality Type	Mortality Function (MRT)	Method	Data Source
No additional mortality	M0	-	-
Habitat-based	MH10	Mortality as a function of resistance, habitat-suitability prediction, and protected area status. Buffers applied to infrastructure with effect declining logarithmically over 17,400m for roads/dams, and 5,000m for urban areas.	SERVIR-Mekong 2018; OpenStreetMap 2019; UNEP-WCMC and IUCN 2019; Ash et al. 2020a; IUCN World Heritage Outlook 2020
	MH05	Adjusted MH10 by 0.5 power function/rescaled	
	MH075	Adjusted MH10 by 0.75 power function/rescaled	
	MH15	Adjusted MH10 by 1.5 power function/rescaled	
	MH20	Adjusted MH10 by 2.0 power function/rescaled	
Poacher-based	MP1	Predicted poacher presence from random forest model from environmental/human covariates, averaged over 10 bootstrap samples	Royal Forestry Department 2000; WCS and CIESIN 2005; Jarvis et al. 2008; Hansen et al. 2013; Evans et al. 2014; European Space Agency 2015; Ash et al. 2020e.
Expert-based	ME1	Mortality as a function of tree cover, PA coverage, and road density within 20km window	Hansen et al. 2013; OpenStreetMap 2019; UNEP-WCMC and IUCN 2019; Ash et al. 2020a
	ME2	ME1, with reduced effect of PA coverage	
	ME3	Mortality as a function of tree cover, PA coverage, and distance to road	
	ME4	ME3, with road mortality effect doubled	
Inverse Effective Population	MR1	Inverted/rescaled prediction of effective population size from Reddy et al 2017	WCS and CIESIN 2005; Jarvis et al. 2008; Hansen et al. 2013; Evans et al. 2014; Reddy et al. 2017; SERVIR-Mekong 2018; Ash et al. 2020a
	MR2	Reduced mortality effect of MR1 (square root of MR1 rescaled from 0-1).	

scenario, resistance surface, and protected area coverage. This approach assumes mortality risk is higher where habitat-suitability is low and resistance is high, with greater risk outside protected areas. To test sensitivity, we transformed resulting mortality surfaces by a range of power functions (0.5, 0.75, 1.0, 1.5, and 2.0), rescaling each between 1-100 to reflect varying intensity and non-linear probabilities of mortality. A total of five functions were developed using this approach (MH05, MH075, MH10, MH15, and MH20).

We tested an additional mortality function (MP1) derived from a local empirical model of predicted poaching presence. This was generated using a random forest model in which environmental and anthropogenic factors served as explanatory variables, with poacher presence generated from camera-trap surveys (Ash et al. 2020d) as the response, averaged across 10 bootstrapped iterations. In this function, predicted poaching presence (including both timber and wildlife poachers) is assumed to be correlated with overall probability of mortality (1-100) due to the risk of direct mortality, such as from targeted hunting/snaring, and indirect effects, such as from prey depletion.

We also incorporated four expert-derived functions (ME1, ME2, ME3, and ME4) based on functions tested in Ash et al. (2020a). This approach defined spatially-differential mortality risk based on available tree cover, protected area coverage, and road presence. In ME1 and ME2, the effect of roads was included via rescaled road density within a 20km radius. In ME3 and ME4, the effect of roads was included as a function of distance.

Lastly, we tested two additional mortality functions used in Ash et al. (2020a; MR1 and MR2), derived from an India-based effective tiger population model (Reddy et al. 2017). In this approach, probability of mortality is a function of broad-scale protected area coverage, mean forest cover, and mean landscape resistance with the assumption that mortality risk is inversely proportional to predicted effective population size.

2.5 Landscape change scenarios (SCN)

In order to account for a broad range of potential changes to the landscape, in addition to the base resistance surface described above (herein described as B0), we developed additional resistance surfaces based on a range of landscape change scenarios (SCN; Table 2). In lieu of specific development and landscape change plans, we explored a range of potential and hypothetical changes to this landscape. These included five development scenarios (D1-D5) and two restoration scenarios (R1 and R2). Further, in addition to developing landscape change scenarios independently, we developed three additional resistance surfaces to test the collective effects of landscape changes (D0, R0, and DR0). These landscape changes were also included in sensitivity analysis of resistance surfaces described in section 2.3 above. While the extent to which such changes will be realized is uncertain, proactive assessments of potential impacts can be valuable in understanding likely effects prior to changes taking place (Cushman et al. 2016). This is particularly important given such changes, particularly development, can occur rapidly and without warning.

2.5.1 Development scenarios

We tested potential effects of increased infrastructure development and human activity (e.g., agricultural or urban expansion) via a range of development scenarios. In order to investigate the potential importance of forest cover in and around DPKY for tiger movement and persistence, we developed a resistance surface (D1) in which all existing forest cover outside protected areas is converted to comparatively high-resistance agriculture/village matrix (resistance of 50; *sensu* Cushman et al. (2016).

In scenario D2, we evaluated potentially increased effects of roads in and around DPKY by doubling the original resistance of both minor (new resistance of 60) and major (new resistance of 200) roads. Further, in scenario D3, we tested the impact of a potential re-opening of decommissioned Route 3462 (IUCN World Heritage Outlook 2020) by digitizing the former public road and with a resistance value of 100.

Scenario D4 included 7 proposed dams built at major rivers throughout the complex which could potentially inundate parts of protected areas (IUCN World Heritage Outlook 2020). Dams and subsequent inundation zones were simulated via ArcGIS 10.3.1, with dam heights corresponding to the recently completed Huay Samong Dam (Naruebodindrachinta reservoir; ~33m). At each approximate dam location, we extracted a section of digital elevation surface from a minimum elevation at the proposed location up to an additional 29m, simulating a potential inundation area from a dam height of 33m with a supply level 4m below capacity. The resulting surface was treated as a potential inundation zone and assigned a resistance of 80, matching existing reservoirs in the base resistance surface.

In scenario D5, we aimed to simulate hypothetical expansion of urban centres and border areas as a result of economic development and increased trade with neighbouring Cambodia (Kobayashi et al. 2017; Wongwuttiwat and Lawanna 2018). We simulated growth in urban and border areas by applying the 'Expand' function in ArcGIS. Each urban pixel was expanded by 1 into neighbouring cells, roughly doubling total urban extent through expansion of existing urban areas. We also simulated the development of hypothetical border

Table 2 Summary of landscape change scenarios, corresponding resistance surface development method, and data sources. Base resistance was developed using spatial data from 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018), OpenStreetMap (2019), and Ash et al. (2020a), with information on potential development and restoration projects from IUCN World Heritage Outlook (2020). Additional information can be found in Supplementary Materials 1.

Landscape Change Scenario (SCN)	Description	Method
Base		
B0	Base scenario (Current)	Base resistance as in Ash et al. (2020a) with no modifications
Development		
D1	Tree cover outside PAs removed	All pixels outside PAs with value corresponding to tree cover assigned resistance of 50 (agriculture)
D2	Increased road traffic	Resistance value of roads doubled (major roads = 200; minor roads = 60)
D3	Route 3462 re-opened	Route digitized and assigned resistance value of major road (100)
D4	Dam/reservoir development	8 proposed/potential dams created at major rivers; reservoir inundation area simulated with ArcGIS for ~30m dam height and assigned resistance value of 80.
D5	Urban/border areas expanded	Urban pixel area (100 resistance) doubled using ArcGIS Expand function with 5000m point density buffer as in Elliot et al. (2014). Two new border crossings generated at Ta Phraya NP - urban pixels (100 resistance) generated along 5,000m road length at border to match comparable TH-KH border infrastructure.
Restoration		
R1	Reforestation/Expanded PAs	Human-impacted forest within and adjacent to PAs assigned resistance value of 1; PAs expanded to reforested and forest reserve areas.
R2	Wildlife Crossing Structures	Mitigation of Route 304 (KYNP-TLNP) and 348 (DYWS-TPNP) as in Ash et al. (2020a); current and hypothetical crossing structure pixel areas assigned resistance value of 20 (scrub forest)
Combined		
D0	Combined development	All development scenarios, as described above
R0	Combined restoration	All restoration scenarios, as described above
DR0	All scenarios combined	All development and restoration scenarios, as described above

crossings at Ta Phraya NP in which urban pixels were generated randomly at two candidate border locations. Urban pixels were generated as a function of distance from border road with the number of pixels generated capped at the number present at the nearest major border crossing (Aranyaprathet-Poipet). We simulated associated increases in road traffic at these border crossings by increasing resistance values of private road Route 3446 and other connecting minor roads from 30 (B0) to 100. Further, to simulate the potential diffusive effect of increased urbanization, we applied a 5,000m point density buffer from all urban pixels (*sensu* Elliot et al. 2014), declining linearly from a max resistance of 50.

2.5.2 Restoration scenarios

In addition to development scenarios, we also developed two restoration scenarios to evaluate the potential effects of forest reforestation, expansion of protected areas (scenario R1), and construction of wildlife crossing structures on key roads (scenario R2).

In scenario R1, we identified several areas for potential reforestation, primarily adjacent to existing protected areas, using satellite imagery (Google, US Dept of State Geographer, Image Landsat/Copernicus) and forest quality records generated during camera-trap field surveys (Ash et al. 2020c). Resistance values in these areas were reclassified with a resistance value of 1. In addition, to examine the potential effect of increased protected area coverage, where existing or reforested areas occurred outside and adjacent to PAs, we converted forest coverage to polygons and merged them with protected area shapefiles (UNEP-WCMC and IUCN 2019) as hypothetical protected areas extensions. This resulted in an approximate increase of protected area coverage by ~14% (+887km^2) and forest cover by ~212km^2.

In scenario R2, we tested the addition of wildlife crossing structures along two major roads in the complex, Route 304 and Route 348 (Ash et al. 2020a). This included a highway overpass (~570m) and two tunnels in southern DPKY (~210m and ~150m) and two overpasses in northern DPKY (~260m and ~180m). Though not currently planned, we also included a hypothetical crossing structure located along Route 348 where the highway crosses a forested section of Ta Phraya National Park (one overpass of ~570m). At these locations, we reclassified the resistance of the area occupied by crossing structures as 20 (corresponding to the resistance value of scrub forest).

2.5.3 Combined scenarios

In addition to developing landscape change scenarios independently, we developed three additional resistance surfaces to test the potential additive and interactive effects of these changes. These included: (1) Scenario D0, which reflected full development by incorporating all landscape changes of development scenarios (D1-D5); (2) Scenario R0, which included all restoration scenarios (R1 and R2); and (3) Scenario DR0, incorporating all development and restoration changes.

2.6 Running simulations

We ran simulations in CDPOP for 1,287 factor combinations of 11 landscape change scenarios (SCN), three max population densities (DEN), three resistance transformations (RST), and 13 mortality functions (MRT). For each combination, we simulated 20 non-overlapping generations which were repeated over 10 Monte Carlo replicates (257,400 total simulations). We evaluated model sensitivity and relative importance of factors by comparing simulated population values (N) at the final timestep (generation 20) with factorial analysis of variance (ANOVA) and post-hoc Tukey honest significant difference tests (Tukey 1949) across main effects (SCN, DEN, RST, MRT) and their interactions.

3. Results

Simulations resulted in stark and significant differences in simulated tiger population by generation 20 (N_{20}) with varying degrees of sensitivity to changes in factors. Differences in N_{20} between factors in this study were highly significant for all main effects and interactions, with the exception of SCN:DEN:RST and SCN:DEN:RST:MRT (Supplementary Materials 2, Table 1). Here, we discuss overall model sensitivity results with a detailed assessment of the effect of landscape change scenario and other factors under the same mortality function approach.

3.1 Model sensitivity

Simulated N_{20} were most sensitive to mortality function (MRT), with dramatic differences in population trajectory based on mortality approach (Fig. 2, Fig. 3; Supplementary Materials 2, Fig. 1-6). Simulations with no additional mortality (M0) resulted in populations expanding to carrying capacity, dictated by density (DEN; 100% [$n=990$] of simulations resulted in population growth; Table 3). In contrast, all simulations with expert-derived mortality functions and one effective population size-based function (ME1, ME2, ME3, ME4, and MR1; $n=4,950$) resulted in extinction by timestep 20 ($N_{20}=0$). The adjusted effective population size mortality function (MR2) was less severe. In MR2, 63.7% ($n=631$) of simulations resulted in extinction, 26.8% ($n=265$) resulted in population declines ($30>N_{20}>0$), and 9.5% ($n=94$) produced stable or increasing populations (N_{20}≥*30*). In simulations where mortality was based on predicted poaching presence (MP1), simulations resulted in extinction in 65.5% (*n=648*) of cases, 27.2% (*n=269*) produced declining populations, and 7.4% resulted in (*n=73*) stable or increasing populations. Resistance-based mortality (MH) produced divergent results. Functions with concave, higher relative mortality risk (MH05 and MH075) resulted in extinction rates of 99.1% (*n=981*) and 85.4% (*n=845*), respectively. Under moderate relative mortality risk (MH10), 45.9% (*n=454*) of simulations resulted in extinction, 23.5% (*n=233*) resulted in population declines, and (*n=303*) 30.6% resulted in stable or increasing populations. Lastly, where relative mortality risk was low and convex (MH15 and MH20), extinction rates were 12.4% (*n=123*) and 4.2% (*n=42*), respectively, while respective rates of population growth were 79.4% (*n=786*) and 92% (*n=911*).

Patterns of simulated N_{20} when adjusting landscape change scenario (SCN) were not as strong as those when adjusting mortality, but were nonetheless clear (Table 3). The percentage of simulations which resulted in extinction ranged from 61.5% (*n=720*) for scenario R1 (habitat restoration) to 77% (*n=901*) for scenario D0 (combined development). Conversely, the percentage of simulations which resulted in stable or increasing populations ranged from 14.7% (*n=172*) for D0 to 30.4% (*n=356*) for R0 (combined restoration). Predicted N_{20} was less sensitive to non-linear transformation of landscape resistance (RST). Extinction rates were generally lower in simulations with higher, concave landscape resistance. Specifically, simulations resulted in extinction in 64.5% (*n=2,765*) of cases for RST05 and 70.9% (*n=3,040*) of cases for the convex RST20. In comparison, the percentage of simulations which resulted in stable or increasing populations ranged from 22.4% (*n=960*) under RST20 to 26.8% (*n=1,148*) under RST05.

Simulations were least sensitive to adjustment of population density (DEN). Density did not change the profile of response, but affected means linearly, primarily influencing carrying capacity (*K*). At the highest density included (6KM), a higher percentage of simulations resulted in population growth (25.6%; *n=1,098*) with slightly lower extinction rates (67.2%; *n=2,882*) relative to lower densities (10KM [N_{20}≥*30: 24.5%;* N_{20}=0: 67.5%], 7.5KM [N_{20}≥*30: 23.9%;* N_{20}=0: 67.5%). However, overall differences were marginal.

3.2 Results under moderate mortality

(a) *(b)*

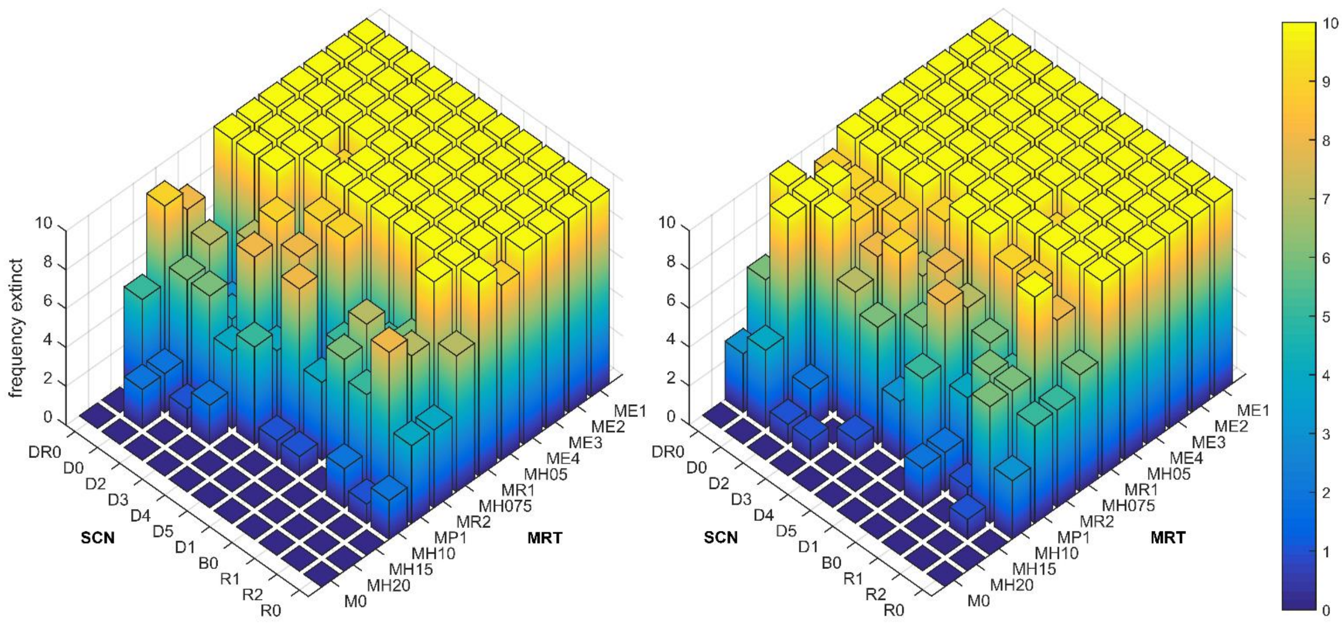

Fig. 2 Summary of number of simulations resulting in population extinction by landscape change scenario (SCN) and mortality function (MRT) under (a) 6km density (DEN) and resistance transformed by 0.5 power function (RST05), and (b) 10km density (DEN) and resistance transformed by 2.0 power function (RST20).

(a) *(b)*

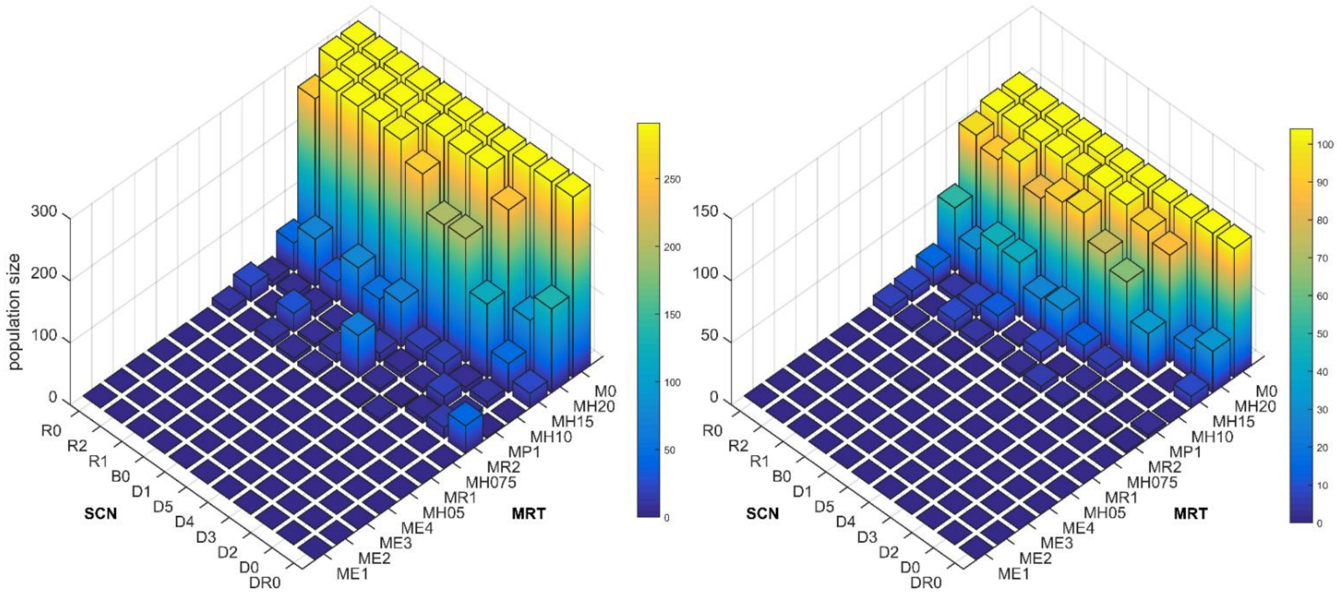

Fig. 3 Summary of simulated population at generation 20 by landscape change scenario (SCN) and mortality function (MRT) under (a) 6km density (DEN) with resistance transformed by 0.5 power function (RST05), and (b) 10km density (DEN) with resistance transformed by 2.0 power function (RST20).

Mortality had a disproportionately large effect in our study as the majority of mortality functions produced extreme values ($N_{20}=0$ or $N_{20}=K$), precluding an assessment of nuanced differences between factors such as landscape change scenario. Here, we review results holding mortality constant at moderate levels (MH10), under which N_{20} exhibited particular sensitivity to parametric variation.

3.2.1 Landscape change scenario

Holding mortality function constant (MH10), N_{20} was most sensitive to differences in landscape change scenario (Table 4; Supplementary Materials 2, Table 2). Under the base scenario (B0), median population at generation 20 ($\widetilde{N}_{20}$) was 27.5, differing only slightly from starting N_1 (30). Population trajectories were varied - approximately 48.9% of simulations resulted in stable or increasing populations, 27.8% resulted in population declines, and 23.3% ended in extinction.

Development had an almost universally negative influence on population trajectory. A substantial majority of simulations with development-based landscape change scenarios resulted in population declines or extinctions. When comparing results between landscape change scenario and B0, half of scenarios resulted in very highly significant differences in mean population ($\overline{N}_{20}$; $p<0.0001$) while half resulted in no significant difference (Table 4).

The combined development and restoration scenario (DR0), produced the greatest difference in observed mean of N_{20} compared to the base scenario ($\overline{N}_{20}$ =-39.9***) and had an $\widetilde{N}_{20}$ of *0.* Approximately 95.6% of simulations under this scenario resulted in extinction, 4.4% resulted in population declines, and 0% produced population increases. Results under the combined development scenario (D0) were similarly severe. Under D0, simulations had a mean difference in $\overline{N}_{20}$ of -38.3 (***) compared to B0, $\widetilde{N}_{20}$=0, and extinctions or declines in 83.3% and 15.6% of cases, respectively. The landscape change scenario where overall road use/resistance increased (D2) was also notably severe. Scenario D2 had a mean difference of $\overline{N}_{20}$=-35.8(***) compared to B0, $\widetilde{N}_{20}$ = 0, and extinction and population declines in 74.4% and 20.0% of cases, respectively. The landscape change scenario incorporating the construction of additional dams/reservoirs (D4) also had a comparatively negative effect ($\overline{N}_{20}$ =-27.0***, $\widetilde{N}_{20}$ = 0); in D4, 52.2% of simulations resulted in

Table 3 Summary of simulated population at generation 20 within landscape change scenario (SCN), population density (DEN), resistance transformation (RST), and mortality function (MRT) for all simulations. Values include mean ($\overline{N}_{20}$), median ($\widetilde{N}_{20}$), percentage of simulations resulting in extinctions (*%N₂₀=0*), population declines (not including extinctions; *%N₂₀ ↓*), and stable/increasing populations (*%N₂₀ →↑*).

		$\overline{N}_{20}$	$\widetilde{N}_{20}$	$\%N_{20}=0$	$\%N_{20}\downarrow$	$\%N_{20}\rightarrow\uparrow$
SCN	B0	47.1	0	64.2%	8.2%	27.6%
	D1	46.4	0	63.3%	9.4%	27.3%
	D2	33.2	0	71.9%	6.4%	21.7%
	D3	41.0	0	67.4%	8.4%	24.3%
	D4	40.9	0	68.2%	6.9%	24.9%
	D5	46.3	0	65.2%	6.9%	27.9%
	R1	49.4	0	61.5%	9.1%	29.3%
	R2	47.4	0	65.6%	6.8%	27.6%
	D0	21.2	0	77.0%	8.3%	14.7%
	R0	49.7	0	61.5%	8.1%	30.4%
	DR0	22.0	0	75.6%	8.6%	15.8%
DEN	10KM	23.8	0	67.5%	8.0%	24.5%
	7.5KM	38.0	0	67.5%	8.6%	23.9%
	6KM	59.5	0	67.2%	7.2%	25.6%
RST	RST05	42.5	0	64.5%	8.8%	26.8%
	RST10	40.7	0	66.9%	8.2%	24.9%
	RST20	38.0	0	70.9%	6.8%	22.4%
MRT	M0	194.0	187.0	0.0%	0.0%	100.0%
	ME1	0.0	0.0	100.0%	0.0%	0.0%
	ME2	0.0	0.0	100.0%	0.0%	0.0%
	ME3	0.0	0.0	100.0%	0.0%	0.0%
	ME4	0.0	0.0	100.0%	0.0%	0.0%
	MH05	0.0	0.0	99.1%	0.9%	0.0%
	MH075	2.4	0.0	85.4%	12.7%	1.9%
	MH10	24.6	8.0	45.9%	23.5%	30.6%
	MH15	125.9	104.0	12.4%	8.2%	79.4%
	MH20	162.9	174.0	4.2%	3.7%	92.0%
	MP1	7.0	0.0	65.5%	27.2%	7.4%
	MR1	0.0	0.0	100.0%	0.0%	0.0%
	MR2	8.6	0.0	63.7%	26.8%	9.5%

extinction, 30.0% resulted in population declines, and 17.8% resulted in stable/increasing populations. Development of Route 3462 through DPKY (D3) also produced significantly lower mean population ($\overline{N}_{20}$ = -22.9***) compared to B0, and low relative $\widetilde{N}_{20}$ (9.5). Under this scenario, approximately 45.6% of simulations resulted in extinction, 32.2% resulted in population declines, and 22.2% resulted in stable or increasing populations. These development scenarios were similarly strong in their effect, with differences in $\overline{N}_{20}$ only significant between D3 and DR0/D0(*).

Significant differences in $\overline{N}_{20}$ were not observed for two development scenarios: D1, in which tree cover outside PAs was converted to village/agriculture matrix; and D5, representing doubling of urban area coverage and development of border crossings. Notably, in all restoration scenarios tested (R1 – reforestation/increased PA coverage; R2 – wildlife crossing structures; R0 – all restoration measures), $\overline{N}_{20}$ did not differ significantly from the base scenario (B0).

3.2.2 Resistance transformation

Varying resistance surface transformation (RST), holding mortality constant at MH10, had similar, clear patterns of difference in $\overline{N}_{20}$ as observed in overall results (Tables 3 and 4). Concave/higher resistance (RST05) produced an $\overline{N}_{20}$=28.8, and simulations resulted in extinctions in 37.6% of cases, declines in 26.4% of cases, and stable/increasing populations in 36.1% of cases. In contrast, convex/lower resistance (RST20) had an $\overline{N}_{20}$=21.2 and simulations resulted in extinction in 53.0% of cases, percentage of population declines in 22.4% of cases, and stable/increasing populations in 24.5% of cases. Differences in observed $\overline{N}_{20}$ were only significant between RST20-RST05 (-7.6*; Supplementary Materials 2, Table 4).

3.2.3 Population density

Holding mortality constant at moderate levels (MH10) and varying population density (DEN) did not produce strong, clear patterns in N_{20} (Supplementary Materials 2, Table 4) compared with other factors. Differences in $\overline{N}_{20}$ were marginal (10KM $\overline{N}_{20}$=23.6; 7.5KM $\overline{N}_{20}$=21.4; 6KM $\overline{N}_{20}$=29.0), as were differences in rates of extinction (10KM = 47.0%; 7.5KM = 46.4%; 6KM = 44.2%). The percentage of simulations which resulted in population declines was highest for 7.5KM (25.8%) and lowest for 10KM (21.8%), while the percentage of simulations which produced stable/increasing populations was highest for 6KM (32.7%) and lowest for 7.5KM (27.9%). The only significant difference between $\overline{N}_{20}$ across population density was observed between 7.5KM-6KM (-7.60*).

3.2.4 Interactions between factors

Results from ANOVA under constant, moderate mortality (MH10) were significant for all main effects (Supplementary Materials 2, Table 2) while two-way and three-way interactions between factors were not.

Table 4 Summary of simulated population at generation 20 under different landscape change scenarios (SCN), holding mortality constant at moderate levels (MH10). Values include mean ($\bar{N}_{20}$), median ($\tilde{N}_{20}$), percentage of simulations resulting in extinctions (*%N₂₀=0*), population declines (not including extinctions; $\%N_{20}\downarrow$), stable/increasing populations ($\%N_{20}\rightarrow\uparrow$), difference in observed $\bar{N}_{20}$ (Diff) compared to the base scenario (B0), and significance (*p*).

SCN	$\bar{N}_{20}$	$\tilde{N}_{20}$	$\%N_{20}=0$	$\%N_{20}\downarrow$	$\%N_{20}\rightarrow\uparrow$	Diff	*p*
B0	40.4	27.5	23.3%	27.8%	48.9%	-	-
D1	35.0	26.0	24.4%	30.0%	45.6%	-5.5	0.981
D2	4.6	0.0	74.4%	20.0%	5.6%	**-35.8**	**<0.0001*****
D3	17.5	9.5	45.6%	32.2%	22.2%	**-22.9**	**<0.0001*****
D4	13.4	0.0	52.2%	30.0%	17.8%	**-27.0**	**<0.0001*****
D5	29.2	14.0	36.7%	30.0%	33.3%	-11.2	0.319
R1	41.8	31.5	22.2%	23.3%	54.4%	1.3	1.000
R2	39.2	28.0	23.3%	28.9%	47.8%	-1.2	1.000
D0	2.1	0.0	83.3%	15.6%	1.1%	**-38.3**	**<0.0001*****
R0	47.3	34.0	23.3%	16.7%	60.0%	6.9	0.910
DR0	0.5	0.0	95.6%	4.4%	0.0%	**-39.9**	**<0.0001*****

When examining specific interactions within and between factor groups with Tukey HSD testing, the majority of significant differences were observed when landscape change scenario (SCN) varied. Only one significant interaction was observed when holding SCN constant (B0:6KM:RST20-B0:6KM:RST05; $\bar{N}_{20}$=-61.2*; Supplementary Materials 2, Table 5). There were only five instances where interactions with other factors produced significant differences in $\bar{N}_{20}$ between B0 and landscape change scenarios not considered significant without interactions (D1-B0, D5-B0, R1-B0, R2-B0, and R0-B0). These were observed with D1-B0 and D5-B0 when varying DEN and RST (D1:75KM:RST20-B0:6KM:RST05, $\bar{N}_{20}$=-64.1*; D5:75KM:RST05-B0:6KM:RST05, $\bar{N}_{20}$=-61.5*; D5:75KM:RST20-B0:6KM:RST05, $\bar{N}_{20}$=-61.2*; D5:RST20-B0:RST05, $\bar{N}_{20}$=-30.9*; and D1:RST20-B0:RST05, $\bar{N}_{20}$=-29.8*). Differences in $\bar{N}_{20}$ between restoration scenarios (R1, R2, and R0) and the base scenario (B0) were not significant under any interaction.

4. Discussion

Population dynamics are driven by demographic processes interacting with the influences of heterogeneous landscapes. In this study, we simulated population dynamics of an isolated tiger population of conservation priority using an individual-based, spatially-explicit approach. Our goal was to quantify the relative effects of landscape change scenario, mortality, resistance to dispersal, and population density. Our most important finding is that spatially-differential mortality risk, and the approach used to define this risk, dominated predictions of population persistence. Second, we documented significant differences in population trajectories depending on landscape change scenario. Notably, we documented strong negative effects of development on population size and persistence, even when habitat restoration measures were applied. Resistance transformation and its interaction with mortality had a marginal effect, while adjusting maximum population density did not substantially influence population trajectory. The high sensitivity of predictions to spatially-explicit patterns of mortality risk, and the high variability in simulated population trajectories among simulations, starkly highlight the vulnerability of this small and isolated, but regionally important tiger population. Our results provide clear predictions to aid in the development of management and conservation strategies for this population. In addition, our study also provides valuable insight to inform the development of spatially-explicit population models for other threatened species.

4.1 Mortality

Predictions of population trajectory and persistence were overwhelmingly driven by spatially-differential mortality risk. Among the 13 mortality functions applied across our simulations, nine produced extinction rates greater than 50% with five resulting in extinction rates of 100% by generation 20. Concurrently, we documented significant differences in predicted population depending on the mortality approach applied, with predictions notably sensitive to minor adjustments in probability of mortality. Moderate, curvilinear adjustments in resistance-based mortality, for example, produced opposing predictions of population trajectory. Overall, this strong sensitivity to mortality risk and the observation of frequent or universal extinction among realistic mortality functions highlights, (1) the high risk faced by this small and isolated tiger population, and (2) the dominant effect of mortality risk in driving population dynamics and extinction risk of small populations.

The clear and strong effect of mortality in our simulations has important implications. Our results are consistent with a related population simulation study conducted on tigers in this landscape, in which the incorporation of spatially-differential mortality risk dramatically shifted predictions of population dynamics, extinction risk, and broad-scale landscape connectivity (Ash et al. 2020a). Specifically, Ash et al. (2020a) used a different modelling approach, employing spatially-dynamic resistance kernel modelling (Cushman 2015; Barros et al. 2019) to evaluate population size, extinction risk, and spread. Their study found that, under all realistic scenarios of mortality risk, population range expansion was highly constrained and population declines or extinctions were frequent. Other tiger population modelling studies have reported that marginal increases in poaching rates produced large increases in predicted extinction risk (Kenney et al. 1995; Linkie et al. 2006; Chapron et al. 2008) and reductions in population connectivity (Carroll and Miquelle 2006), particularly for small, isolated populations. These trends have also been observed in simulations of other large felids (Kramer-Schadt et al. 2004; Newby et al. 2013; Kaszta et al. 2019; Naude et al. 2020). It is evident from our simulations that the degree of mortality risk within DPKY is likely the most critical determining factor for the future of this population. Thus, detecting and mitigating sources of mortality will likely be critical to achieving short- and long-term tiger population persistence in this landscape. Importantly, efforts to increase population density (such as by improving habitat or prey density) or improve movement across the landscape could be destined to fail if mortality risk is not effectively addressed.

The disproportionate effect of mortality in our study also has implications for conservation of other small populations and the development of similar spatially-explicit population models for other species. Broadly, our results appear to reflect the inherent vulnerability of small populations to stochastic processes, allee effects, and related dynamics of extinction risk (Caughley 1994; Dennis 2002; Fagan and Holmes 2006). In such small populations, even marginal increases in mortality risk may act in concert with demographic stochasticity to drive populations to extinction. More specifically, our findings are similar to other modelling studies in which the inclusion of spatially-differential mortality risk dramatically changed predictions of population dynamics, connectivity, and the effect of large-scale development (e.g., Kramer-Schadt et al. 2004; Cushman 2006; Kaszta et al. 2019; Kaszta et al. 2020). Kaszta et al. (2019) and Kramer-Schadt et al. (2004) highlight that the deleterious impacts of development/infrastructure are evident not only in their effect on habitat, but also in reducing population viability through reduced connectivity and road deaths. Further, as evidenced in our study and others (Kaszta et al. 2019; Ash et al. 2020a), differences in the approach used to parameterize mortality across space and its degree of severity, even to a marginal degree, can have considerable influence on model predictions. This underscores the importance not only of incorporating spatial variation in mortality risk in population simulations, but conducting sensitivity analysis to evaluate its degree of influence on predictions. It also reinforces that, for the conservation of small and endangered populations, measuring and mitigating mortality risk is a critical part of any conservation strategy.

4.2 Landscape change scenarios

A central goal of our study was to discern the relative effects of various landscape change scenarios on predicted long-term population dynamics. Notably, we documented strong and significant differences in predicted populations between current conditions and scenarios of landscape change, when holding mortality risk constant at moderate levels.

We documented strong negative effects in scenarios in which the primary change to the landscape involved intensification or development of major roadways in the complex (D2/D3), which resulted in significantly lower predicted population size and relatively high predicted rates of extinction. Roads are commonly associated with negative effects on biodiversity (Coffin 2007). These effects have been known to exert a particularly strong influence on the viability and connectivity of populations of tigers (Kerley et al. 2002; Thatte et al. 2018) and other large carnivores (Kramer-Schadt et al. 2004; Kaszta et al. 2019). In recent studies on clouded leopards (*Neofelis nebulosa* and *N. diardi*), which applied a similar spatially-explicit approach to evaluate relative effects of development scenarios, linear structures such as roads and railways were associated with significant declines in predicted population size (Kaszta et al. 2019, 2020). Notably, our results are consistent with other evidence from the DPKY complex which documented broad-scale, negative associations between tigers and roads (Ash et al. 2020d).

Development of dams/reservoirs along the periphery of protected areas had a similarly strong and significant negative effect. While a number of studies have been dedicated to quantifying the varied ecological impacts of dams (Jones et al. 2016; Wu et al. 2019), investigations into the potential implications for terrestrial mammals upstream from such projects are comparatively lacking. The impact of dams for wide-ranging carnivores may be greater than localized habitat loss (Kaszta et al. 2020). It is possible that reservoirs created by dams may improve access into remote areas for illicit activities such as poaching in a similar way to roads (Bennett and Robinson 2000) and could catalyse further infrastructure development or land use change in their vicinity (Lillesund et al. 2017). For small populations such as DPKY, even marginal associated increases in mortality risk and disturbance along park peripheries could be enough to shift population trajectories. The predicted negative effects of dams in our study merits targeted research on their potential effects on tigers and other large carnivores.

We did not find significant differences between predicted population in the base scenario and scenarios simulating habitat loss outside protected areas (D1) or expansion of urban/border areas (D5). It is possible that this is due to the primary area of change occurring within an already human-dominated matrix of high resistance and mortality risk. Importantly, the structure of the DPKY system is represented by a single block of mid- to high-quality tiger habitat (Ash et al. 2021) that is not substantially subdivided by a developed matrix. Thus, the fact that tigers do not reside in, nor are required to move through the surrounding matrix, may explain the lack of strong effects of additional development outside this block. For areas in which tigers occur in a metapopulation, conditions in the matrix between populations could have considerable implications for movement and persistence (Thatte et al. 2018).

Restoration scenarios such as reforestation with expanded protected area coverage (R1) and installation of highway crossing structures did not significantly differ in associated predictions compared to the base scenario. This may be attributed to the small-scale nature of these simulated changes relative to the size of the landscape. In the case of highway crossing structures, their potential effect on simulated population from connectivity may be marginal relative to mortality risk, which was not measurably reduced by these structures and was the dominant driver of population dynamics in our study. Our results are consistent with a related study in DPKY which did not document significant effects of such structures on simulated population and connectivity, particularly compared with other factors such as mortality (Ash et al. 2020a).

Importantly, the impacts of landscape change scenarios in our simulation extend beyond physical changes to the landscape, but also include the effect of these changes on the spatial pattern of mortality risk. Predicted population dynamics in our study are strongly influenced by synergistic effects between landscape patterns and mortality risk. Studies of threatened populations which do not account for the associated variation in mortality risk with landscape change may underestimate the effect of these changes on population persistence (Thatte et al. 2018; Kaszta et al. 2019). Further, the strong effect of landscape change in our study and inseparable link between demography and landscape dynamics (Lande 1988; Kareiva and Wennergren 1995) reinforces the importance of considering future potential landscape configurations when modelling long-term population dynamics, particularly in terms of how landscape change affects spatial patterns of mortality risk.

4.3 Combined landscape change scenarios

In addition to the independent evaluation of specific landscape changes, we also explored differences in predicted population when these changes were combined. Scenarios which incorporated all development measures (D0 and DR0) had a profoundly negative effect on predicted population size and produced very high extinction rates. Importantly, incorporation of restoration measures failed to even marginally mitigate the simulated negative effects of extensive development and its associated increases in mortality risk.

Where infrastructure is likely to negatively impact tiger populations, measures such as road crossing structures for wildlife, rehabilitation and restoration of habitat, or financial compensation have been recommended as a means to offset their impacts (Quintero et al. 2010). However, a degree of caution is merited when considering such measures. Results from our study and others suggest that these measures may be insufficient in ameliorating the long-term implications of habitat loss, fragmentation, and increased mortality risk resulting from development scenarios and may fail to justify new infrastructure development in the habitat of vulnerable species (Ash et al. 2020a). Rehabilitation and restoration of habitat must result from strategic planning and evaluation, and designed for specific purposes such as enhancing or enabling population connectivity. For example, simulations by Kaszta et al. (2019) suggested that targeted restoration of forest corridors could mitigate the effects of road development on clouded leopard population size and connectivity to a limited degree. However, the same study documented an interactive effect between the re-alignment of certain linear structures and increased mortality, depressing population size relative to original plans. Both our study and Kaszta et al. (2019) underscore the potentially catastrophic synergy between development and spatial patterns of mortality risk in driving patterns of extinction.

4.4 Resistance transformation

While sensitivity analysis suggested that landscape resistance to dispersal had lower comparative influence on model predictions, we documented a significant difference between predicted population size based on the form and intensity of landscape resistance. Higher, concave resistance (RST05) resulted in higher predicted mean population size relative to lower, convex resistance (RST20) and had an interactive effect with mortality. High resistance may preclude movement critical to persistence in a metapopulation (Cushman 2006; Rudnick et al. 2012). However, movement by tigers into human-dominated matrices is often highly risky due to the risk of direct mortality, conflict with humans, and lack of natural prey (Smith 1993; Goodrich et al. 2008). In our isolated population, high resistance may have had the effect of discouraging and reducing movement to areas of high-risk that would otherwise increase mortality probability. Specifically, when landscape resistance was high outside of optimal, low-risk habitat, populations were predicted to remain higher because dispersing individuals avoided high risk areas due to high resistance to movement. The ability of a vagile species to navigate an unfriendly landscape may increase the effect of landscape barriers and dispersal-related mortality on population viability relative to those with limited movement ability (Carr and Fahrig 2001; Carr et al. 2002; Kramer-Schadt et al. 2004; Ash et al. 2020a). It is possible, albeit perhaps non-intuitive, that a highly disturbed matrix could yield benefits to certain species compared to one that is partially disrupted, if it discourages movement through or settlement in areas with low fitness and high risk (Cantrell and Cosner 1993). Further, if negative effects of movement in such areas exceed potential benefits, this may ultimately undermine population persistence (Burkey 1989). Such patterns have been observed in studies of other species which have reported high dispersal associated with declining populations where mortality risk is high (Cushman 2006; Cushman et al. 2010). However, studies on the real-world effects of these patterns on large carnivore movement and persistence are lacking (Cushman et al. 2016).

4.5 Population density

Adjustment of maximum population density in our study had a minimal effect, primarily dictating the ceiling of population in simulations incorporating little to no additional mortality risk. A study by Karanth and Stith (1999) suggests that tiger populations with a higher carrying capacity, supported by high prey abundance, may be able to persist despite elevated mortality, such as from poaching. We did not detect a clear pattern in which high population carrying capacity measurably reduced negative impacts on simulated population from mortality or landscape change scenario. This reinforces our findings of mortality acting as the primary driver of population dynamics. Further, these results are consistent with other studies highlighting the potentially severe, long-term effect of increases in mortality on population persistence, even in relatively large populations or those with high potential density (Kenney et al. 1995; Chapron et al. 2008; Tian et al. 2011).

4.7 Limitations/caveats

The strength of our assessment lies in the comparison of the relative effects and interactions of factors across a realistic range of landscape change scenarios and parameters in order to inform potential management interventions and areas of future research (Dunning Jr et al. 1995; Reed et al. 2002; Linkie et al. 2006; Kaszta et al. 2019). Our approach of incorporating sensitivity analysis is particularly useful given the inherent uncertainty in defining parameters for such simulations (Boyce 1992; Dunning Jr et al. 1995). Where available, our individual-based, spatially-explicit simulations are guided by empirical data (Ash et al. 2020b, c, 2021) and credible parameters governing tiger behaviour utilized in similar simulations elsewhere in the tiger's range (Thatte et al. 2018). This robust approach grounds our assessment within the realm of plausible reality. However, we wish to underscore that the focus of this study was not to make predictions of specific population sizes in relation to landscape change scenarios or mortality rates. Our findings are beneficial in identifying the types of landscape change likely to be most impactful among those tested, and degree of sensitivity of this population to key factors (notably mortality). These insights may aid in official planning where they can be compared with specific development and management plans in concert with up-to-date information on this tiger population and factors that could affect population persistence.

We note that exploration of restorative landscape changes or assessment of alternative development scenarios (such as re-alignment of infrastructure; *sensu* Kaszta et al. 2019) are relatively limited. Given the high degree of long-established human presence outside protected area boundaries, opportunities to evaluate broader-scale habitat restoration and other measures were inherently constrained in this landscape. We did not investigate long-term genetic trajectories in this population, though this too will likely be a factor in population persistence, which can be severely undermined by inbreeding depression (van Noordwijk 1994; Vasudev et al. 2017). Notably, while mortality probability varied across space, it was held constant over our simulations. In reality, there is certain to be stochastic variation in this and other factors over time. We also did not consider potential catastrophic environmental stochasticity, such as disease, whose effects may be further exacerbated in small populations (Harihar et al. 2018). The potentially strong and pervasive effects of climate change may also threaten population persistence across landscapes (Marks 2011; Rudnick et al. 2012; Wasserman et al. 2012; Dar et al. 2021). We recommend additional, targeted studies to evaluate the impacts of potential associated habitat changes. However, it remains clear from our study that such long-term factors for tigers in this landscape may be moot if the calamitous effects of mortality are ignored.

4.8 Conservation implications/recommendations

The tiger population in DPKY has been described as a population of national, regional, and global priority (Ash et al. 2020c), particularly given the catastrophic range and population declines elsewhere in Southeast Asia (Sanderson et al. 2006; Lynam and Nowell 2011). Our results suggest that this population may be situated on a proverbial knife's edge. Predictions of population trajectory and persistence in our study were highly sensitive, particularly to mortality risk. Importantly, we found that marginal shifts in mortality, particularly combined with landscape change, drastically shifted predictions. When holding mortality risk constant at moderate levels (MH10), roughly half of simulations produced extinctions. When transforming this function to slightly convex (MH15) and concave (MH075) forms, extinction rates diverged to 12% to 85%, respectively. These results reflect the high degree of sensitivity and vulnerability of small, isolated populations to stochastic processes (Kenney et al. 1995; Vasudev et al. 2017; Thatte et al. 2018).

The tiger population in DPKY is not unique in respect to being smaller than recommended for long-term viability (Wikramanayake et al. 2011; Kenney et al. 2014). Such populations may be supported by rescue effects through immigration (Linkie et al. 2006; Banerjee et al. 2010; Thatte et al. 2018). However, many populations, including DPKY, are likely too isolated for this to be the case without active intervention. Small populations may benefit from the tiger's naturally high fecundity (Karanth and Stith 1999), though high mortality, combined with isolation, can quickly drive populations to extinction (Chapron et al. 2008). Empty forests throughout Southeast Asia (Lynam and Nowell 2011; Rasphone et al. 2019; Ash et al. 2020c) highlight that requisite factors such as presence of forest cover, potential habitat, and prey mean little for species like tigers if unsustainable mortality is not prevented.

Evidence from our study, consistent with others on tigers (Kenney et al. 1995; Linkie et al. 2006; Chapron et al. 2008), reinforces the point that preventing mortality, whether from poaching or development in tiger habitat, is likely the most critical measure to be considered in developing management and conservation strategies. Our results strongly reinforce recommendations in Thailand's national tiger action plan against the development of infrastructure in tiger habitat (Pisdamkam et al. 2010). In addition, designing comprehensive and timely population monitoring is critical in order to detect and respond to emerging threats such as poaching (Duangchantrasiri et al. 2016) or disease (e.g., canine distemper virus, Seimon et al. 2013; Terio and Craft 2013), which could quickly overwhelm small, vulnerable populations. For isolated populations such as DPKY, active population management measures, such as translocations, may be an option to prevent the effects from inbreeding depression from being realized over longer time periods

(Kenney et al. 2014). Additional simulations investigating the potential effect of translocations on heterozygosity and allelic richness may be particularly helpful in informing the development of such measures. Lastly, we believe our approach can be helpful for investigating the effects of dynamic and changing landscapes on other populations of tigers and other species at similar conservation crossroads.

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References

Ash E, Cushman SA, Macdonald DW, et al (2020a) How Important Are Resistance, Dispersal Ability, Population Density and Mortality in Temporally Dynamic Simulations of Population Connectivity? A Case Study of Tigers in Southeast Asia. Land 9:415. https://doi.org/10.3390/land9110415

Ash E, Hallam C, Chanteap P, et al (2020b) Estimating the density of a globally important tiger (Panthera tigris) population: Using simulations to evaluate survey design in Eastern Thailand. Biol Conserv 241:108349. https://doi.org/10.1016/j.biocon.2019.108349

Ash E, Kaszta Ż, Noochdumrong A, et al (2020c) Opportunity for Thailand's Forgotten Tigers: Assessment of Indochinese tiger Panthera tigris corbetti and prey from camera-trap surveys in Eastern Thailand. Oryx 55:204–211. https://doi.org/10.1017/S0030605319000589

Ash E, Kaszta Ż, Redford T, et al (2020d) Environmental factors, human presence, and prey interact to explain patterns of tiger presence in Eastern Thailand. Anim Conserv 24:268–279. https://doi.org/10.1111/acv.12631

Ash E, Macdonald DW, Cushman SA, et al (2021) Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: A case study of tigers (Panthera tigris) in Thailand. Landsc Ecol 36:455–474. https://doi.org/10.1007/s10980-020-01105-6

Banerjee K, Jhala Y V, Pathak B (2010) Demographic structure and abundance of Asiatic lions Panthera leo persica in Girnar Wildlife Sanctuary, Gujarat, India. Oryx 44:248–251. https://doi.org/10.1017/S0030605309990949

Barros T, Carvalho J, Fonseca C, Cushman SA (2019) Assessing the complex relationship between landscape, gene flow, and range expansion of a Mediterranean carnivore. Eur J Wildl Res 65:44. https://doi.org/10.1007/s10344-019-1274-6

Bennett EL, Robinson JG (2000) Hunting of Wildlife in Tropical Forests : Implications for Biodiversity and Forest Peoples. World Bank, Washington, DC

Boyce MS (1992) Population viability analysis. Annu Rev Ecol Syst 23:481–497

Burkey TV (1989) Extinction in Nature Reserves: The Effect of Fragmentation and the Importance of Migration between Reserve

Fragments. Oikos 55:75–81. https://doi.org/10.2307/3565875

Cantrell RS, Cosner C (1993) Should a Park Be an Island? SIAM J Appl Math 53:219–252

Carr LW, Fahrig L (2001) Effect of Road Traffic on Two Amphibian Species of Differing Vagility. Conserv Biol 15:1071–1078. https://doi.org/10.1046/j.1523-1739.2001.0150041071.x

Carr LW, Fahrig L, Pope SE (2002) Impacts of Landscape Transformation by Roads. In: Gutzwiller KJ (ed) Applying Landscape Ecology in Biological Conservation. Springer New York, New York, NY, pp 225–243

Carroll C, Miquelle DG (2006) Spatial viability analysis of Amur tiger Panthera tigris altaica in the Russian Far East: The role of protected areas and landscape matrix in population persistence. J Appl Ecol 43:1056–1068. https://doi.org/10.1111/j.1365-2664.2006.01237.x

Caughley G (1994) Directions in Conservation Biology. J Anim Ecol 63:215–244. https://doi.org/10.2307/5542

Chapron G, Miquelle DG, Lambert A, et al (2008) The impact on tigers of poaching versus prey depletion. J Appl Ecol 45:1667–1674. https://doi.org/10.1111/j.1365-2664.2008.01538.x

Coffin AW (2007) From roadkill to road ecology: a review of the ecological effects of roads. J Transp Geogr 15:396–406. https://doi.org/10.1016/j.jtrangeo.2006.11.006

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biol Conserv 128:231–240. https://doi.org/10.1016/j.biocon.2005.09.031

Cushman SA (2015) Pushing the envelope in genetic analysis of species invasion. Mol Ecol 24:259–262

Cushman SA, Compton BW, McGarigal K (2010) Habitat Fragmentation Effects Depend on Complex Interactions Between Population Size and Dispersal Ability: Modeling Influences of Roads, Agriculture and Residential Development Across a Range of Life-History Characteristics. In: Cushman SA, Huettmann F (eds) Spatial Complexity, Informatics, and Wildlife Conservation. Springer Japan, Tokyo, pp 369–385

Cushman SA, Elliot NB, Macdonald DW, Loveridge AJ (2016) A multi-scale assessment of population connectivity in African lions (Panthera leo) in response to landscape change. Landsc Ecol 31:1337–1353. https://doi.org/10.1007/s10980-015-0292-3

Cushman SA, Landguth EL, Flather CH (2013) Evaluating population connectivity for species of conservation concern in the American Great Plains. Biodivers Conserv 22:2583–2605. https://doi.org/10.1007/s10531-013-0541-1

Dar SA, Singh SK, Wan HY, et al (2021) Projected climate change threatens Himalayan brown bear habitat more than human land use. Anim Conserv. https://doi.org/10.1111/acv.12671

Dennis B (2002) Allee effects in stochastic populations. Oikos 96:389–401. https://doi.org/10.1034/j.1600-0706.2002.960301.x

Duangchantrasiri S, Umponjan M, Simcharoen S, et al (2016) Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. Conserv Biol 30:639–648. https://doi.org/10.1111/cobi.12655

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological Processes That Affect Populations in Complex Landscapes. Oikos 65:169–175. https://doi.org/10.2307/3544901

Dunning Jr JB, Stewart DJ, Danielson BJ, et al (1995) Spatially explicit population models: current forms and future uses. Ecol Appl 5:3–11. https://doi.org/10.2307/1942045

Elliot NB, Cushman SA, Macdonald DW, Loveridge AJ (2014) The devil is in the dispersers: predictions of landscape connectivity change with demography. J Appl Ecol 51:1169–1178. https://doi.org/10.1111/1365-2664.12282

European Space Agency (2015) 300 m annual global land cover time series from 1992 to 2015. Climate Change Initiative (CCI), European Space Agency (ESA)

Evans JS, Cushman SA, Theobald D (2014) An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, version 2.0-0.

Fagan WF, Holmes EE (2006) Quantifying the extinction vortex. Ecol Lett 9:51–60. https://doi.org/10.1111/j.1461-

0248.2005.00845.x

Goodrich JM, Kerley LL, Smirnov EN, et al (2008) Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. J Zool 276:323–329. https://doi.org/10.1111/j.1469-7998.2008.00458.x

Goodrich JM, Lynam A, Miquelle DG, et al (2015) Panthera tigris. IUCN Red List Threat. Species 2015 e.T15955A50659951

Graves T, Chandler RB, Royle JA, et al (2014) Estimating landscape resistance to dispersal. Landsc Ecol 29:1201–1211. https://doi.org/10.1007/s10980-014-0056-5

Hansen MC, Potapov P V., Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science (80-) 342:850–853. https://doi.org/10.1126/science.1244693

Harihar A, Chanchani P, Borah J, et al (2018) Recovery planning towards doubling wild tiger Panthera tigris numbers: Detailing 18 recovery sites from across the range. PLoS One 13:e0207114. https://doi.org/10.1371/journal.pone.0207114

Hijmans RJ (2020) raster: Geographic Data Analysis and Modeling, Comprehensive R Archive Network (CRAN), version 3.0-12

Hughes AC (2019) Understanding and minimizing environmental impacts of the Belt and Road Initiative. Conserv Biol 33:883–894. https://doi.org/10.1111/cobi.13317

IUCN World Heritage Outlook (2020) Dong Phayayen-Khao Yai Forest Complex: 2020 Conservation Outlook Assessment. IUCN World Heritage Programme & IUCN World Commission on Protected Areas (WCPA), Gland

Jarvis A, Reuter HI, Nelson A, Guevara E (2008) Hole-filled seamless SRTM data V4. In: Int. Cent. Trop. Agric. http://srtm.csi.cgiar.org

Jones IL, Bunnefeld N, Jump AS, et al (2016) Extinction debt on reservoir land-bridge islands. Biol Conserv 199:75–83. https://doi.org/10.1016/j.biocon.2016.04.036

Karanth KU, Stith BM (1999) Prey depletion as a critical determinant of tiger population viability. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 100–113

Kareiva P (1990) Population dynamics in spatially complex environments: theory and data. Philos Trans - R Soc London, B 330:175–190. https://doi.org/10.1098/rstb.1990.0191

Kareiva P, Wennergren U (1995) Connecting landscape patterns to ecosystem and population processes. Nature 373:299–302. https://doi.org/10.1038/373299a0

Kaszta Ż, Cushman SA, Hearn AJ, et al (2019) Integrating Sunda clouded leopard (Neofelis diardi) conservation into development and restoration planning in Sabah (Borneo). Biol Conserv 235:63–76. https://doi.org/10.1016/j.biocon.2019.04.001

Kaszta Ż, Cushman SA, Htun S, et al (2020) Simulating the impact of Belt and Road initiative and other major developments in Myanmar on an ambassador felid, the clouded leopard, Neofelis nebulosa. Landsc Ecol 35:727–746. https://doi.org/10.1007/s10980-020-00976-z

Kenney J, Allendorf FW, McDougal C, Smith JLD (2014) How much gene flow is needed to avoid inbreeding depression in wild tiger populations? Proc R Soc B Biol Sci 281:20133337–20133337. https://doi.org/10.1098/rspb.2013.3337

Kenney JS, Smith JLD, Starfield AM, McDougal CW (1995) The Long-Term Effects of Tiger Poaching on Population Viability. Conserv Biol 9:1127–1133. https://doi.org/10.1046/j.1523-1739.1995.9051116.x-i1

Kerley LI, Goodrich JM, Miquelle DG, et al (2002) Effects of Roads and Human Disturbance on Amur Tigers. Conserv Biol 16:97–108. https://doi.org/10.1046/j.1523-1739.2002.99290.x

Kobayashi K, Rashid KA, Furuichi M, Anderson WP (2017) Economic integration and regional development: the ASEAN economic community. Routledge, Abingdon, United Kingdom

Kramer-Schadt S, Revilla E, Wiegand T, Breitenmoser U (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. J Appl Ecol 41:711–723. https://doi.org/10.1111/j.0021-8901.2004.00933.x

Lande R (1988) Demographic models of the northern spotted owl (Strix occidentalis caurina). Oecologia 75:601–607. https://doi.org/10.1007/BF00776426

Landguth EL, Hand BK, Glassy J, et al (2012) UNICOR: a species connectivity and corridor network simulator. Ecography (Cop) 35:9–14. https://doi.org/10.1111/j.1600-0587.2011.07149.x

Landguth LE, Cushman SA (2010) cdpop: A spatially explicit cost distance population genetics program. Mol Ecol Resour 10:156–161. https://doi.org/10.1111/j.1755-0998.2009.02719.x

Lillesund VF, Hagen D, Michelsen O, et al (2017) Comparing land use impacts using ecosystem quality, biogenic carbon emissions, and restoration costs in a case study of hydropower plants in Norway. Int J Life Cycle Assess 22:1384–1396. https://doi.org/10.1007/s11367-017-1263-5

Linkie M, Chapron G, Martyr DJ, et al (2006) Assessing the viability of tiger subpopulations in a fragmented landscape. J Appl Ecol 43:576–586. https://doi.org/10.1111/j.1365-2664.2006.01153.x

Lynam A, Nowell K (2011) Panthera tigris ssp. corbetti. IUCN Red List Threat. Species 2011 e.T136853A4346984

Macdonald EA, Cushman SA, Landguth EL, et al (2018) Simulating impacts of rapid forest loss on population size, connectivity and genetic diversity of Sunda clouded leopards (Neofelis diardi) in Borneo. PLoS One 13:e0196974. https://doi.org/10.1371/journal.pone.0196974

Manorom K (2020) Thailand’s Big Water Challenge. In: Dipl. 23 March 2020. https://thediplomat.com/2020/03/thailands-big-water-challenge/. Accessed 8 Mar 2021

Marks D (2011) Climate Change and Thailand: Impact and Response. Contemp Southeast Asia 33:229–258. https://doi.org/10.1355/cs33-2d

McCarthy MA, Burgman MA, Ferson S (1995) Sensitivity analysis for models of population viability. Biol Conserv 73:93–100. https://doi.org/10.1016/0006-3207(95)90029-2

Naude VN, Balme GA, O’Riain J, et al (2020) Unsustainable anthropogenic mortality disrupts natal dispersal and promotes inbreeding in leopards. Ecol Evol 10:3605–3619. https://doi.org/10.1002/ece3.6089

Newby JR, Scott Mills L, Ruth TK, et al (2013) Human-caused mortality influences spatial population dynamics: Pumas in landscapes with varying mortality risks. Biol Conserv 159:230–239. https://doi.org/10.1016/j.biocon.2012.10.018

Nowell K, Jackson P (1996) Wild Cats : Status Survey and Conservation Action Plan. IUCN/SSC Cat Specialist Group, International Union for the Conservation of Nature, Gland, Switzerland

OpenStreetMap (2019) OpenStreetMap. www.openstreetmap.org. Accessed 10 Jun 2019

Paansri P, Sangprom N, Suksavate W, et al (2021) Spatial Modeling of Forage Crops for Tiger Prey Species in the Area Surrounding Highway 304 in the Dong Phayayen-Khao Yai Forest Complex. Environ Nat Resour J 19:220–229. https://doi.org/10.32526/ennrj/19/2020234

Pisdamkam C, Prayurasiddhi T, Kanchanasaka B, et al (2010) Thailand Tiger Action Plan - 2010-2012. Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

Quintero JD, Roca R, Morgan A, et al (2010) Smart Green Infrastructure in Tiger Range Countries: A multi-Level Approach. Sustainable Development - East Asia and Pacific Region, Discussion Papers, The World Bank & Global Tiger Initiative, Washington D.C.

R Development Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing. v.3.6.1. Vienna

Rasphone A, Kéry M, Kamler JF, Macdonald DW (2019) Documenting the demise of tiger and leopard, and the status of other carnivores and prey, in Lao PDR’s most prized protected area: Nam Et - Phou Louey. Glob Ecol Conserv 20:e00766. https://doi.org/10.1016/j.gecco.2019.e00766

Reddy PA, Cushman SA, Srivastava A, et al (2017) Tiger abundance and gene flow in Central India are driven by disparate combinations of topography and land cover. Divers Distrib 23:863–874. https://doi.org/10.1111/ddi.12580

Reed JM, Mills LS, Dunning Jr. JB, et al (2002) Emerging Issues in Population Viability Analysis. Conserv Biol 16:7–19. https://doi.org/10.1046/j.1523-1739.2002.99419.x

Royal Forestry Department (2000) Study of the Status and Database Design of Natural Resources in Khao Yai, Thap Lan, Pang Sida, and Ta Phraya National Parks [Thai]. Royal Forestry Department, Government of Thailand and Geo Asia Co. Ltd., Bangkok, Thailand

Rudnick DA, Ryan SJ, Beier P, et al (2012) The role of landscape connectivity in planning and implementing conservation and restoration priorities. Ecological Society of America, Washington DC

Sanderson E, Forrest J, Loucks C, et al (2006) Setting Priorities for the Conservation and Recovery of Wild Tigers: 2005-2015 - The Technical Assessment. WCS, WWF, Smithsonian, and NFWF-STF, New York - Washington, DC

Seimon TA, Miquelle DG, Chang TY, et al (2013) Canine distemper virus: an emerging disease in wild endangered Amur tigers (Panthera tigris altaica). MBio 4:e00410-13. https://doi.org/10.1128/mBio.00410-13

SERVIR-Mekong (2018) SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS). SERVIR-Mekong/USAID/NASA/ADPC/ICIMOD, Asian Disaster Preparedness Center (ADPC), Bangkok, Thailand

Smith JLD (1993) The Role of Dispersal in Structuring the Chitwan Tiger Population. Behaviour 124:165–195. https://doi.org/10.1163/156853993X00560

Spear SF, Balkenhol N, Fortin MJ, et al (2010) Use of resistance surfaces for landscape genetic studies: Considerations for parameterization and analysis. Mol Ecol 19:3576–3591. https://doi.org/10.1111/j.1365-294X.2010.04657.x

Sunquist M, Karanth UK, Sunquist F (1999) Ecology, behaviour and resilience of the tiger and its conservation needs. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 5–18

Terio KA, Craft ME (2013) Canine distemper virus (CDV) in another big cat: Should CDV be renamed carnivore distemper virus? MBio 4:e00702-13. https://doi.org/10.1128/mBio.00702-13

Thatte P, Joshi A, Vaidyanathan S, et al (2018) Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations. Biol Conserv 218:181–191. https://doi.org/10.1016/j.biocon.2017.12.022

Tian Y, Wu J, Smith AT, et al (2011) Population viability of the Siberian Tiger in a changing landscape: Going, going and gone? Ecol Modell 222:3166–3180. https://doi.org/10.1016/j.ecolmodel.2011.06.003

Tukey JW (1949) One degree of freedom for non-additivity. Biometrics 5:232–242

UNEP-WCMC, IUCN (2019) Protected Planet. The World Database on Protected Areas (WDPA), UNEP-WCMC, Cambridge, U.K., www.protectedplanet.net

van Noordwijk AJ (1994) The interaction of inbreeding depression and environmental stochasticity in the risk of extinction of small populations. In: Loeschcke V, Jain SK, Tomiuk J (eds) Conservation Genetics. Birkhäuser Basel, Basel, pp 131–146

Vasudev D, Nichols JD, Ramakrishnan U, et al (2017) Assessing Landscape Connectivity for Tigers and Prey Species: Concepts and Practice. In: Karanth KU, Nichols JD (eds) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore, pp 255–288

Walston J, Robinson JG, Bennett EL, et al (2010) Bringing the tiger back from the brink-the six percent solution. PLoS Biol 8:6–9. https://doi.org/10.1371/journal.pbio.1000485

Wasserman TN, Cushman SA, Shirk AS, et al (2012) Simulating the effects of climate change on population connectivity of American marten (Martes americana) in the northern Rocky Mountains, USA. Landsc Ecol 27:211–225. https://doi.org/10.1007/s10980-011-9653-8

WCS, CIESIN (2005) Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic).

Wildlife Conservation Society, Center for International Earth Science Information Network - Columbia University, NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY

Wikramanayake E, Dinerstein E, Seidensticker J, et al (2011) A landscape-based conservation strategy to double the wild tiger population. Conserv Lett 4:219–227. https://doi.org/10.1111/j.1755-263X.2010.00162.x

Wolf C, Ripple WJ (2016) Prey depletion as a threat to the world's large carnivores. R Soc Open Sci 3:160252. https://doi.org/10.1098/rsos.160252

Wongwuttiwat J, Lawanna A (2018) The digital Thailand strategy and the ASEAN community. Electron J Inf Syst Dev Ctries 84:e12024. https://doi.org/10.1002/isd2.12024

Wu H, Chen J, Xu J, et al (2019) Effects of dam construction on biodiversity: a review. J Clean Prod 221:480–489. https://doi.org/10.1016/j.jclepro.2019.03.001

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landsc Ecol 27:777–797. https://doi.org/10.1007/s10980-012-9737-0

Supplementary Materials 1

1. Landscape Change Scenarios

The process for developing the base resistance surface was originally described by Ash et al. (2020a), which evaluated four approaches for predicting resistance: (1) A locally-developed, scale-optimized habitat suitability model from Ash et al. (2021); (2) A multivariate optimized resistance model developed by Reddy et al. (2017), describing the relationship between tiger genetic distance and land cover variables in central India; (3) A resistance model for tigers in central India developed by Krishnamurthy et al. (2016) using a scale-optimized path selection framework; and (4) An expert-derived resistance map based on reclassified 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018) data, incorporating major and minor roads (OpenStreetMap 2019). Authors of the study determined that the expert map more broadly captured likely resistance to movement in the study landscape and utilized the expert-based resistance surface in their evaluation of landscape connectivity for tigers. This expert-based resistance layer was used in our study to represent current estimates of landscape resistance to tiger movement.

1.1 B0 – Base scenario

The base landscape change scenario, defines resistance based on 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018) land cover data, classified into dense forest (resistance value of 1), scrub forest (20), agriculture/village matrix (50), reservoirs/surface water (80), and urban areas (100). Minor (30) and major roads (100; OpenStreetMap 2019) were also included in the base resistance surface (Table 1). This base resistance surface was used as a foundation for producing development and restoration scenarios.

Table 1 Resistance values derived from reclassified landcover from 2018 SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS; SERVIR-Mekong 2018) and road network data (OpenStreetMap 2019), as described in Ash et al. (2020a).

Resistance Value (cost-distance unit / pixel)	Attributes / Land Cover Type
1	Dense Forest (*Evergreen Forest, Forest, Mixed Forest, Flooded Forest, Mangroves*)
20	Scrub Forest (*Shrubland, Grassland, Wetlands, Orchard/Plantation*)
30	Minor Roads
50	Agriculture-Village Matrix (*Rice, Cropland, Barren, Aquaculture*)
80	Reservoirs + Surface Water
100	Urban/Built-Up Areas, Major Roads

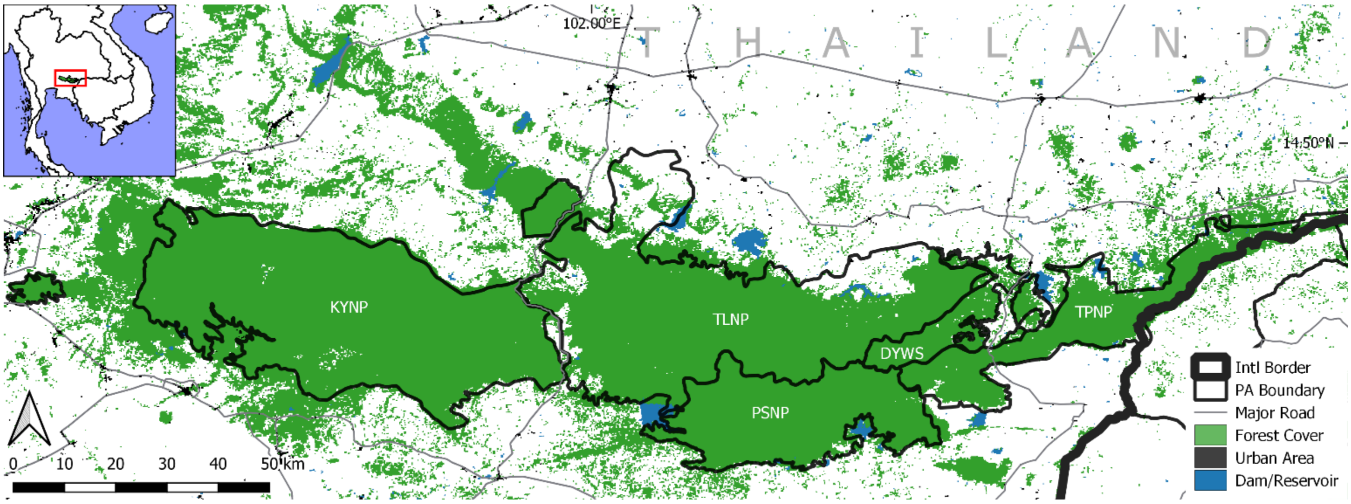

Fig. 1 Base map of the study area representing current forest cover, reservoirs, urban areas, and major roads. Minor roads are not shown.

1.2 D1 – Tree cover loss outside PAs

Forest cover outside protected areas can represent important potential tiger habitat and aid in the dispersal of tigers through human-dominated landscapes (Kanagaraj et al. 2011; Joshi et al. 2013; Krishnamurthy et al. 2016; Reddy et al. 2017). To investigate the potential importance of such forest cover in and around DPKY for tiger movement and persistence, we developed a resistance surface (D1) in which all existing forest cover was converted to comparatively high-resistance agriculture/village matrix (resistance of 50), comparable to a hypothetical scenario conducted by Cushman et al. (2016).

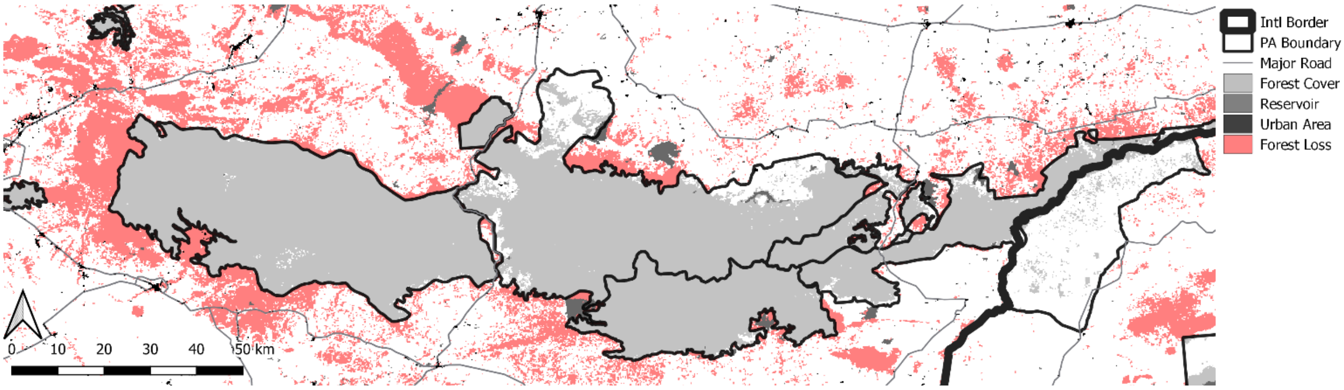

Fig. 2 Scenario D1, depicting areas of simulated forest loss outside current protected areas.

1.3 D2 – Increased road resistance

Evidence suggests that the presence of roads may strongly influence persistence of large mammals (Kerley et al. 2002; Kramer-Schadt et al. 2004; Coffin 2007; Jackson and Fahrig 2011; Thatte et al. 2018) and its effects on tigers may be particularly strong or occur over broad scales (Kerley et al. 2002; Hebblewhite et al. 2014; Ash et al. 2020c). As Thailand continues to develop and serve as a crucial economic link for the region, road use is expected to increase (Limanond et al. 2011; Yu 2017; Wongwuttiwat and Lawanna 2018). This is of particular relevance to DPKY which is situated at the confluence of economic corridors linking Thailand's Laem Chabang deep sea port with Lao PDR and Cambodia (Dang and Yeo 2017; Kobayashi et al. 2017). In scenario D2, we tested for the potential effects of increased road use and potential intensification of roads in and around DPKY by doubling the resistance of both minor (60) and major (200) roads.

Fig. 3 Scenario D2, in which existing major roads were assigned a resistance value double of that of the base scenario (200).

1.4 D3 – Development of route 3462

Currently, an unpaved, former public road (Route 3462) runs along a north-south orientation through Pang Sida and Thap Lan national parks. This road is closed to public access and is managed by park authorities. In a review of possible threats to the Outstanding Universal Value (OUV) to the UNESCO World Heritage Site, IUCN World Heritage Outlook (2020) reports concerns over potential plans to re-open or further develop this road. Thailand's Department of National Parks, Wildlife and Plant Conservation (DNP) has stated that such plans would not be approved. Whether this may change in the future under increasing pressure from economic development remains an uncertainty. In scenario D3, we tested the potential effect of re-opening and developing Route 3462 by digitizing the former public road, assigning a resistance value of 100 to match the value of major roads, and incorporating this feature into the base resistance surface.

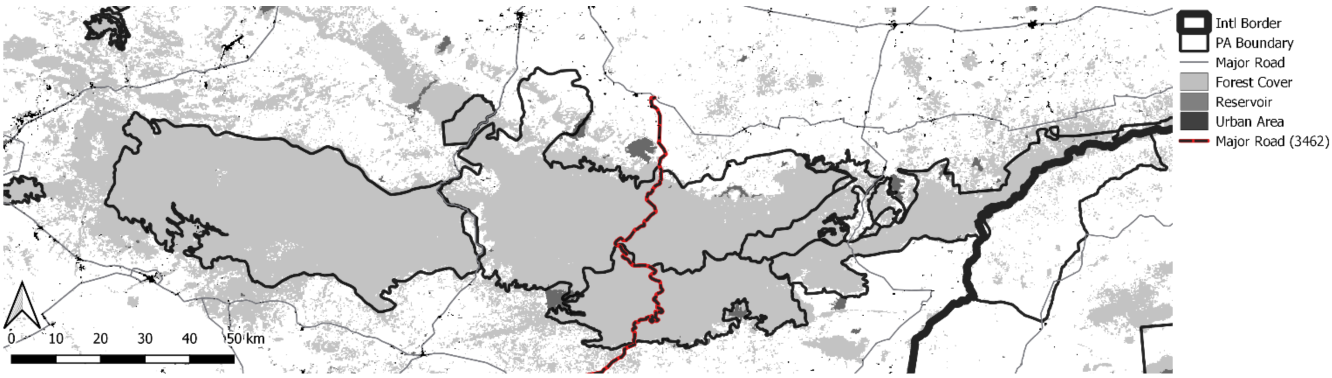

Fig. 4 Scenario D3, depicting the location of a theoretical developed route 3462 through Thap Lan NP and Pang Sida NP. This road was assigned a resistance value of 100.

1.5 D4 – Dam construction

Water security is emerging as a considerable socio-economic challenge in more arid parts of Thailand (Manorom 2020). This may be further exacerbated by the potential for increasing frequency of droughts caused by climate change (Marks 2011; Seeboonruang 2016). Further, this may prompt increasing pressure for additional dams and reservoirs in the complex to serve local communities, including potential projects that could inundate parts of DPKY (IUCN World Heritage Outlook 2020). We developed a scenario (D4) in which 7 potential dams are built at major rivers throughout the complex, partially inundating existing forest within protected areas. Dams and subsequent inundation zones were simulated via a digital elevation model (Jarvis et al. 2008) in ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011). Given the exact locations and heights of proposed dams have not yet been confirmed, we simulated the extent of potential inundation zones based on approximate locations and dam heights corresponding to the recently completed Huay Samong Dam (Naruebodindrachinta reservoir; ~33m) located to the southwest of Pang Sida and Thap Lan national parks. At each approximate dam location, a section of digital elevation surface was extracted, corresponding to the minimum elevation at the proposed location plus an additional 29m. This was calculated to simulate a dam height of 33m at a supply level 4m below capacity. The resulting surface was treated as a potential inundation zone and assigned a resistance of 80, matching existing reservoirs, and was burned into the base resistance surface (B0). To validate this approach, these steps were carried out at the existing location of the Huay Samong Dam. The resulting simulated inundation zone (Naruebodindrachinta reservoir) was reproduced to a high degree of accuracy relative to the maximum extent of the existing reservoir. In addition, to account for forest clearing to accommodate related infrastructure around the dam, pixels corresponding to forest values (1 or 20) in the vicinity of the dam (<1,000m) were reclassified to a resistance value of 50 (agriculture-village matrix).

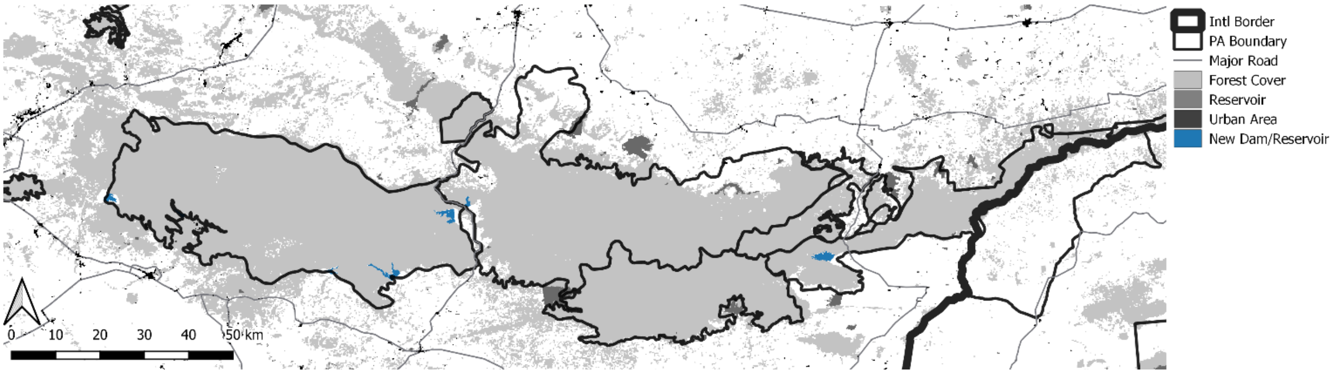

Fig. 5 Scenario D4, depicting simulated inundation zones for prospective dams.

1.6 D5 – Urban and border crossing growth

In addition to increased road use, growing economic development of Thailand may facilitate additional growth of urban centres surrounding DPKY. Further, increasing trade with neighbouring Cambodia under regional economic agreements (Kobayashi et al. 2017; Wongwuttiwat and Lawanna 2018) could intensify human activity at border crossings located in and around the complex. Growth in urban and border areas was simulated by applying the 'Expand' function in ArcGIS. Each urban pixel was expanded by 1 into neighbouring cells, roughly doubling total urban extent through expansion of existing urban areas. Further, to simulate a potential effect of urbanization on neighbouring areas, we applied a 5,000m point density buffer (*sensu* Elliot et al. 2014), declining linearly from a max resistance of 50.

We also generated urban pixels (resistance of 100) representing two hypothetical border crossings at Ta Phraya NP. At two candidate locations we extracted a 5,000m road length section at each crossing (2,500m in each direction from the border) and generated a Euclidean distance buffer of 5,000m at 90m resolution, which was rescaled logarithmically between 0-1. From this, we subtracted a random raster with pixels ranging from 0-1 and extracted any pixels >0. Next, we selected a random sample of pixels corresponding to the number of urban pixels located at the nearest major Thai-Cambodian border crossing (Aranyaprathet-Poipet) within a similar 5,000mx5,000m border section (815 pixels). In effect, generation of urban extent at these simulated border crossings was a function of distance from border road, proportional extent to a current border crossing, and random chance. As with other urban areas under this scenario, we applied a 5,000m point density buffer declining linearly from a max resistance of 50 to simulate the diffusive anthropogenic effect of these crossings. Further, to simulate increased road traffic associated with these border crossings, resistance values of private road Route 3446 and other connecting minor roads were increased from 30 (B0) to 100.

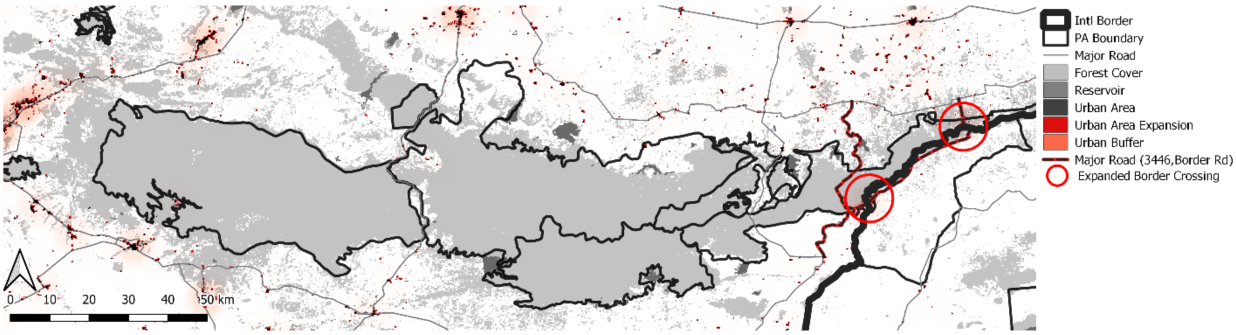

Fig. 6 Scenario D5, depicting areas of urban expansion, simulated hypothetical border crossings, and upgraded border roads (resistance increased from 30 to 100).

1.7 R1 – Reforestation and PA expansion

Evidence suggests the availability of broad forest cover with minimal human footprint is critical for the presence and persistence of tiger populations (Sunarto et al. 2012; Reddy et al. 2017). Human activities have introduced varying degrees of pressure on forest cover in and around DPKY, clearing or denuding forested areas that may otherwise serve as potential tiger habitat. DPKY has been the site of reforestation and reclamation activities over the course of its history (Ash 2015; IUCN World Heritage Outlook 2020), which may serve as an opportunity to improve or expand tiger habitat. Areas of forest reserve land adjacent to protected areas have previously been gazetted as protected area extensions, which may serve as a means to expand the area under formal protection in the complex. In scenario R1, several areas for potential reforestation, primarily adjacent to existing protected areas, were identified using satellite imagery Google, US Dept of State Geographer, Image Landsat/Copernicus) and forest quality records from field surveys in marginal forest habitat (Ash et al. 2020b). Resistance values in these areas were reclassified with a resistance value of 1. In addition, to examine the potential effect of increased protected area coverage, existing or reforested areas occurring outside and adjacent to PAs were converted to polygons and merged with protected area shapefiles (UNEP-WCMC and IUCN 2019) as hypothetical protected areas extensions. This resulted in an approximate theoretical increase of protected area coverage by ~14% (+887km^2) and forest cover by ~212km^2.

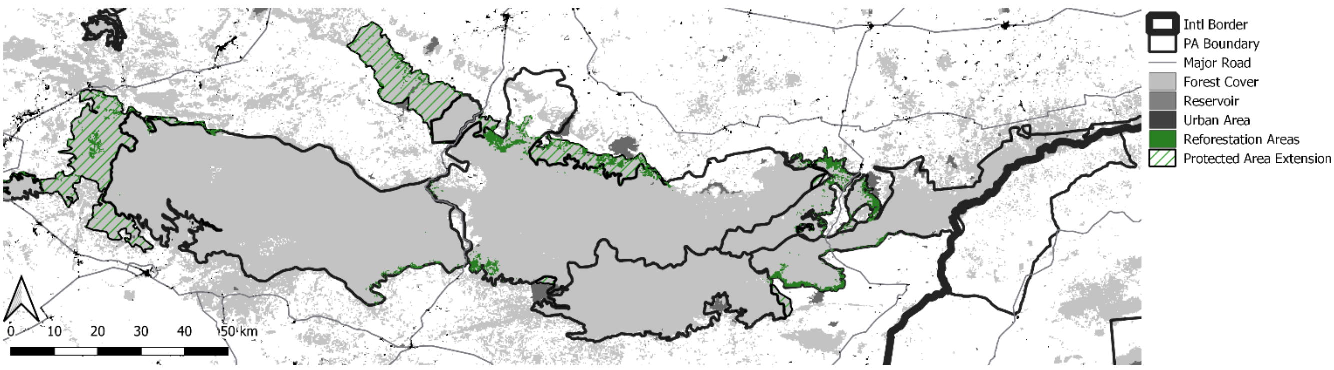

Fig. 7 Scenario R1, depicting areas of simulated forest cover gain from reforestation and hypothetical protected area extensions.

1.8 R2 – Wildlife crossing structures

Completion of wildlife crossing structures along highway Route 304 (Fig. 8) may facilitate movement of tigers and other wildlife throughout the complex. Addition of similar structures along Route 348 in eastern DPKY could serve to mitigate the effects of this highway and promote expansion of the tigers' range in the complex. In scenario R2, we test the addition of wildlife crossing structures along these roads, as in Ash et al. (2020a). This includes a highway overpass (~570m) and two tunnels in southern DPKY (~210m and ~150m) and two overpasses in northern DPKY (~260m and ~180m). We also included a hypothetical crossing structure located along Route 348 where the highway crosses a forested section of Ta Phraya National Park (one overpass of ~570m). At these locations, we reclassified the resistance of the area occupied by crossing structures as 20 (corresponding to the resistance value of scrub forest).

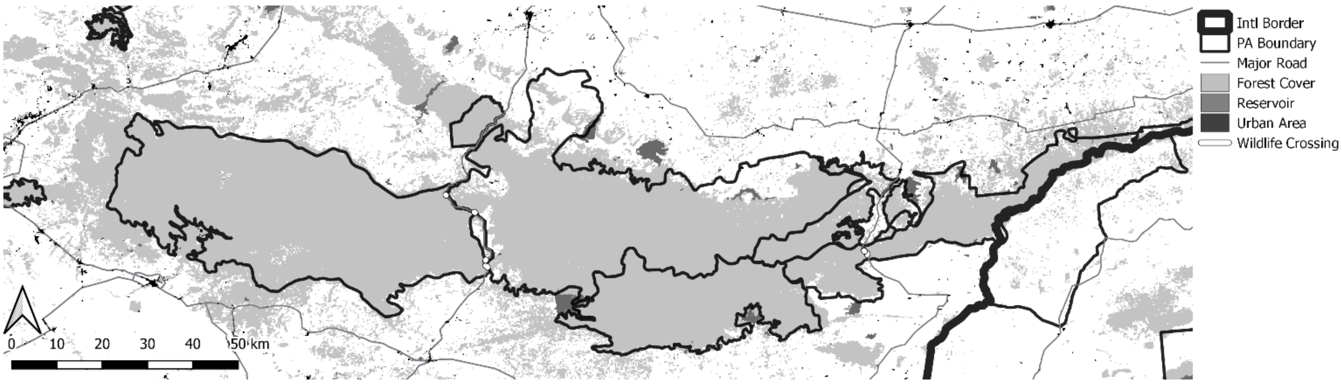

Fig. 8 Scenario R2, depicting locations of wildlife crossing structures along highways 304 and 348. Road pixels at these locations were re-assigned a resistance value of 20 (corresponding to scrub forest).

1.9 D0/DR0/R0 – Combined scenarios

Lastly, in addition to developing landscape change scenarios independently, we developed three additional resistance surfaces to test the collective effects of changes. This includes scenario D0, which incorporated all changes described in the development scenarios (D1-D5), scenario R0, which incorporated all restoration scenarios, and scenario DR0, which combined all the development and restoration scenarios.

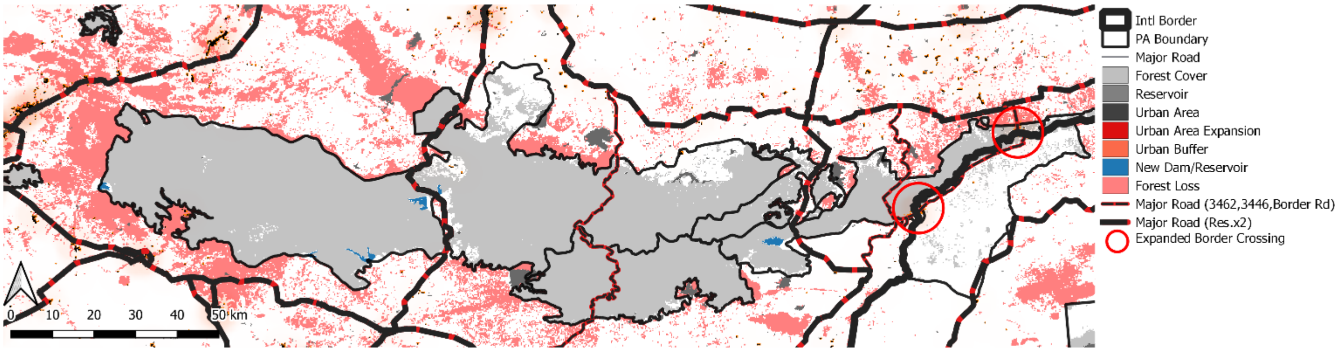

Fig. 9 Scenario D0, combining all development scenarios.

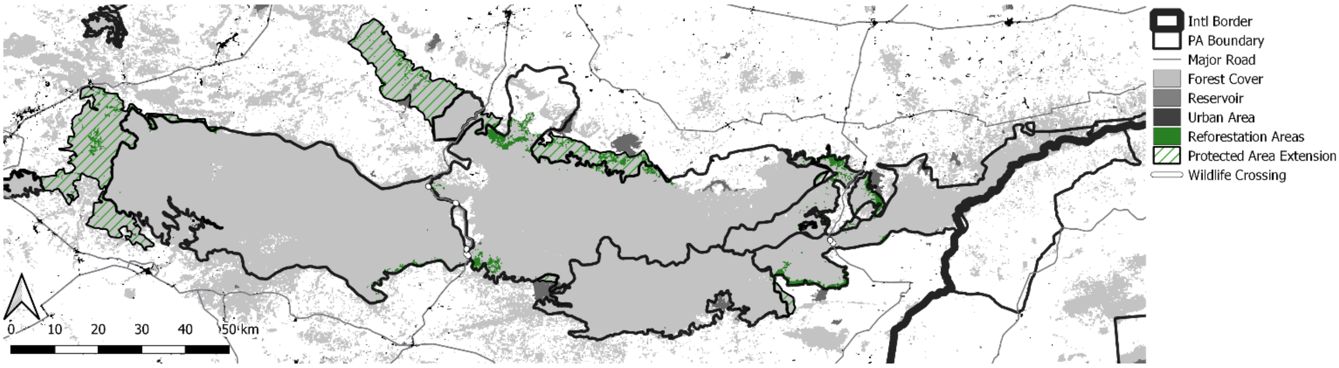

Fig. 10 Scenario R0, combining all restoration scenarios.

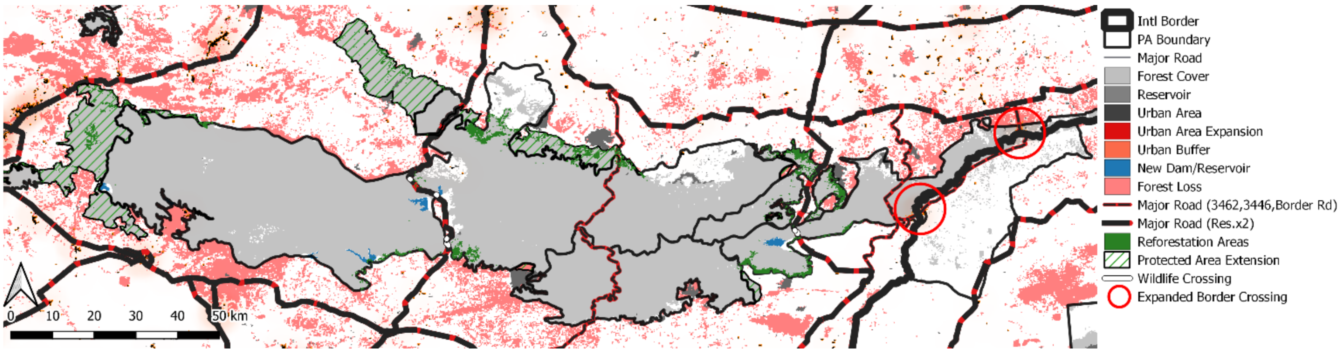

Fig. 11 Scenario DR0, combining all development and restoration scenarios.

2. Mortality Functions

In population connectivity studies, mortality may be implicitly incorporated through resistance surfaces (Diniz et al. 2020), though the relationship between resistance surface and mortality may be unclear. The explicit incorporation of spatially-differential mortality risk in landscape-scale population modelling studies has been shown to dramatically affect conclusions pertaining to landscape connectivity and population persistence (Kramer-Schadt et al. 2004; Cushman 2006; Kaszta et al. 2019, 2020; Ash et al. 2020a). In addition to testing no additional spatial mortality risk (M0), we developed a range of probabilistic mortality surfaces (13 in total) developed through several approaches, based on (1) landscape resistance (MH05, MH075, MH10, MH15, and MH20), (2) predicted poacher presence (MP1), (3) expert-based surfaces defined by protected area coverage, tree cover, and presence of roads (ME1, ME2, ME3, and ME4), and (4) an effective population size model (MR1 and MR2). These mortality surfaces represent the probability of a tiger that has dispersed to a given pixel dying before reproducing.

2.1 Mortality based on habitat suitability and landscape resistance

We developed a range of five mortality functions (MH05, MH075, MH10, MH15, and MH20) derived explicitly as a function of predicted tiger habitat suitability and landscape resistance. Forested areas of low resistance (1-20) were adjusted by a habitat suitability prediction surface from layer from Ash et al. (2021), inverted and rescaled between 0-20 percent mortality probability. In effect, the highest quality habitat would have a low probability of mortality (~2%-8%) with a max mortality probability of 20% (corresponding with a mean ~80% annual survival documented in well-protected forest in Western Thailand; Duangchantrasiri et al. 2016). Outside PAs, the mortality risk in forest areas was doubled, with most unprotected forest corresponding to roughly 40% mortality probability before further adjustments. Similar to Kaszta et al. (2020), long-distance effects of anthropogenic structures, such as roads, dams/reservoirs, and urban areas were included as buffers, with mortality probability declining logarithmically up to the distance of 17,400m for roads and dams, and over 5,000m for urban areas. To evaluate the sensitivity of population simulations to these mortality risk patterns we transformed the base risk layer by power functions of 0.5 (function MH05), 0.75 (MH075), 1.0 (MH10), 1.5 (MH15), and 2.0 (MH20), rescaled between their original minimum and 100 (maximum mortality probability). These transformations either increased the mortality risk of poor-quality habitat (0.5 and 0.75) or reduced the relative risk of poor-quality habitat (1.5 and 2.0).

2.2 Mortality based on poaching probability

Poaching is considered one of the greatest threats to the persistence of tiger populations throughout their range (Goodrich et al. 2015). We developed an additional mortality function based on predicted poaching presence under each landscape change scenario. This function assumes the probability of mortality in an area, and population persistence over 20 generations, is correlated with broad-scale patterns of poaching pressure. Explanatory variables were selected from a suite of environmental data produced across 7 spatial scales and anthropogenic data, with binary poacher presence documented from camera-trap data as the response (Ash et al. 2020c; Ash et al. 2021; Table 2). This function was derived using a random forest model in R (Liaw and Wiener 2002; R Development Core Team 2019), averaged from 10 bootstrapped iterations where, in each iteration, 80% of data were used for training and 20% for validation. We scale-optimized each variable by running random forest model selection on all variables using the 'rf.modelSel' function in the *rfUtilities* package (Evans and Murphy 2018). For each variable, we selected the scale with the highest MIR (Model Improvement Ratio), which resulted in a total of 34 variables. To produce a final random forest model consisting of the best and most parsimonious combination of variables, the model selection process was repeated with only scale-optimized variables. Model performance was evaluated based on OOB (Out-of-Bag error), PCC (Percent Correctly Classified), AUC (Area Under the ROC Curve), and TSS (True Skill Statistic). The variable type, scale, and performance for each random forest model iteration is presented in Supplementary Materials 3. To generate a predicted surface of poaching probability we averaged random forest predictions from all 10 bootstrap iterations. Resulting spatial predictions were scaled between 1-100, reflecting probability of mortality for each pixel.

2.3 Expert-based mortality

We developed four separate mortality functions adapted from expert-derived functions from Ash et al. (2020a; ME1, ME2, ME3, and ME4). As described in their paper, this mortality function was developed given three key seemingly ubiquitous relationships between tigers and traits of the local landscape: (1) Tigers have strong positive associations with forest cover (Walston et al. 2010; Sunarto et al. 2012; Reddy et al. 2017); (2) Tigers have negative associations with areas of high road density (Kerley et al. 2002; Hebblewhite et al. 2014); and (3) Tigers are often restricted to protected or undisturbed areas (Walston et al. 2010) and evidence suggests mortality rates of dispersing tigers outside protected areas are high

Table 2 Variables included in the random forest poacher model and data sources. Focal statistics were generated in ArcGIS 10.3.1 (ESRI 2015). The response variable for this model was binomial poacher presence (Ash et al. 2020b).

Variable	ID	Source
Standard deviation of digital elevation model (16km)	DEMSD_16000	Jarvis et al. 2008
Distance to park (private) road	DISTROAD.C2	Royal Forestry Department 2000
% Cropland (16km)	LC1_PLAND_16000	European Space Agency 2015
% Natural vegetation (16km)	LC3_PLAND_16000	European Space Agency 2015
Focal mean of terrain roughness index (16km)	TRI_FM_16000	Jarvis et al. 2008; Evans et al. 2014
Focal mean of terrain roughness index (8km)	TRI_FM_8000	Jarvis et al. 2008; Evans et al. 2014
Standard deviation of terrain roughness index (16km)	TRI_SD_16000	Jarvis et al. 2008; Evans et al. 2014
Standard deviation of terrain roughness index (8km)	TRI_SD_8000	Jarvis et al. 2008; Evans et al. 2014
Settlement density (16km kernel width)	SettlementDensity	2018 Google, US Dept of State
Standard deviation of slope position (16km)	SLOPE_SD_16000	Jarvis et al. 2008; Evans et al. 2014
Focal mean of streams/rivers (16km)	STRC1_FM_16000	Royal Forestry Department 2000
Focal mean of streams/rivers (8km)	STRC1_FM_8000	Royal Forestry Department 2000
% Non-forest (16km)	TC1_PLAND_16000	Hansen et al. 2013
% Closed forest (16km)	TC3_PLAND_16000	Hansen et al. 2013
X coordinate	X	-

(Smith 1993; Goodrich et al. 2008). Thus, these functions act as a simplified model of spatially differential mortality risk based on available tree cover (Hansen et al. 2013), protected area coverage (UNEP-WCMC and IUCN 2019), and road presence (OpenStreetMap 2019). Functions ME1 and ME2 were developed as the inverse of survival surfaces in Ash et al. (2020a), with a mortality probability floor of 20% in fully forested protected areas with a road density of 0 within a 20km window, increasing with decreasing forest cover and increasing road density. Mortality probability outside PAs was increased by a factor of 10 in ME1 and by a factor of two for ME2. The formulae for these functions are as follows, adapted from functions originally described in Ash et al. (2020a):

$$ME1 = \left(1 - \left(\frac{\begin{matrix} Tree\ Cover\ Layer \\ [0\ to\ 1] \end{matrix}}{\begin{matrix} Protected\ Area\ Layer \\ [PA = 1.25\ ; NonPA = 10] \end{matrix}} \times (1 - \ Road\ Density\ Focal\ Mean\ at\ 20km\ [0\ to\ 1])\right)\right) \times 100$$

$$ME2 = \left(1 - \left(\frac{\begin{matrix} Tree\ Cover\ Layer \\ [0\ to\ 1] \end{matrix}}{\begin{matrix} Protected\ Area\ Layer \\ [PA = 1.25\ ; NonPA = 5] \end{matrix}} \times (1 - \ Road\ Density\ Focal\ Mean\ at\ 20km\ [0\ to\ 1])\right)\right) \times 100$$

To investigate potential differences in the effect of roads, Functions ME3 and ME4 were derived from the same approach of ME2, but, in lieu of road density, incorporated increased mortality probability as a function of decreasing distance to public roads. In these functions, additional mortality probability increases from 0% to 66% as distance to road decreases from 17,400m to 570m (based on Ash et al. (2020c). A Euclidean distance to public road raster was generated in ArcGIS 10.3.1 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011). All values greater than 17,400m were assigned a value of 17,400 and all values lower than 570m were assigned a value of 570. This layer was then transformed by 0.25 power for function ME3 and 0.50 power for ME4, then rescaled between 0.33 and 1. In function ME3, this transformation results in an exponential increase in probability of mortality with decreasing distance to roads. In function ME4, this transformation produces a more gradual change in probability of mortality, strengthening the effect of roads at greater distances. Formulae for these functions are as follows:

$$ME3 = \left(1 - \left(\frac{\substack{Tree\ Cover\ Layer \\ [0\ to\ 1]}}{\substack{Protected\ Area\ Layer \\ [PA = 1.25\ ;NonPA = 5]}} \times \left(\frac{Distance\ to\ Road\ Layer\ [570m\ to\ 17400m]^{0.25} - 570^{0.25}}{17400^{0.25} - 570^{0.25}} \times (1 - 0.33) + 0.33\right)\right)\right) \times 100$$

$$ME4 = \left(1 - \left(\frac{\substack{Tree\ Cover\ Layer \\ [0\ to\ 1]}}{\substack{Protected\ Area\ Layer \\ [PA = 1.25\ ;NonPA = 5]}} \times \left(\frac{Distance\ to\ Road\ Layer\ [570m\ to\ 17400m]^{0.5} - 570^{0.5}}{17400^{0.5} - 570^{0.5}} \times (1 - 0.33) + 0.33\right)\right)\right) \times 100$$

2.4 Mortality based on effective population size model

We also generated two mortality functions also used in Ash et al. (2020a; MR1 and MR2), derived from an India-based effective tiger population model in Reddy et al. (2017), generated from local geographic information data. Effective population size in this model was determined as a function of the focal mean of protected area coverage within a 45-km radius, mean forest cover within a 45-km radius, and mean landscape resistance within a 42.5km radius. The local model prediction was inversed and rescaled between 0-1, representing high mortality risk where predicted potential effective population size was low (function MR1). As in Ash et al. (2020a), we also tested a modified version of this model (MR2) in which we calculated the square root of MR1 which mitigated the effect of mortality, particularly in poor-quality habitat. Both functions were multiplied by 100 to reflect percentage probability of mortality.

Table 3 Summary of the effective tiger population size model from Reddy et al. (2017), developed in central India, with coefficients (β), standard error (SE), z-value (*z*) and variable significance (Pr(>|*z*|)). This model was applied in Ash et al. (2020a) and our study with local covariates to generate predicted effective population size in DPKY, rescaled [0-1], and inversed to reflect estimated probability of mortality.

Variable	**β**	**SE**	***z***	**Pr(>|*z*|)**
(Intercept)	61.45	11.48	15.18	5.13E-05
Proportion of landscape within 45km radius covered by protected areas	20.91	9.97	14.12	0.139
Mean landscape resistance within a 42.5km radius	-20.27	10.3	14.59	0.165
Mean forest cover within a 45km radius	20.06	10.4	14.73	0.173

3. CDPOP Setup File Parameters

Table 4 Parameters used in CDPOP setup file for simulations.

Setup File		
Parameter Name	**Parameter Value**	**Comment**
xyfilename	SOURCEPOINTFILE	This is a reference to the folder xyfiles and the name of the source points xy file.
agefilename	AGEVARSFILE	See parameters for agevars file below.
mcruns	1	We incorporate 10 source points to account for stochasticity and unknowns. Each set of source points are run once, producing 10 MC simulations.
looptime	20	
output_years	1	
gridformat	cdpop	
cdclimgentime	0	
matecdmat	CDMATRIXFILE	CDMatrix file generated for each pair of available points, resistance surface, and resolution
dispcdmat	CDMATRIXFILE	As Above
matemoveno	2	2 = Inverse Square (1 / (Cost Distance^2)). This function gets rescaled to the min and threshold of the inverse square cost distance.
matemoveparA	1	
matemoveparB	1	
matemoveparC	1	
matemovethresh	12000 x Mean Resistance	Mate movement threshold adjusted by multiplying 12000m (as per Thatte et al. (2018) by mean resistance per unit area. This value was adjusted for each resistance surface scenario (SCN) and resistance transformation (RST).
output_matedistance	N	
sexans	Y	
Freplace	N	
Mreplace	Y	
philopatry	N	
multiple_paternity	N	
selfans	N	
Fdispmoveno	5	5 = Negative Exponential (parA * 10^(-parB * Cost Distance)). This function gets rescaled to the min and threshold of the negative exponential cost distance.
FdispmoveparA	0.4	
FdispmoveparB	1.59E-06	
FdispmoveparC	1	
Fdispmovethresh	2000000	
Mdispmoveno	5	5 = Negative Exponential (parA * 10^(-parB * Cost Distance)). This function gets rescaled to the min and threshold of the negative exponential cost distance.
MdispmoveparA	0.4	
MdispmoveparB	5.62E-07	
MdispmoveparC	1	
Mdispmovethresh	6000000	
offno	5	Normal distribution draw with mean and sigma for fecundity given in the Agevars file (See below).

Parameter Name	Parameter Value	Comment
offno	5	Normal distribution draw with mean and sigma for fecundity given in the Agevars file (See below).
Femalepercent	50	
EqualsexratioBirth	N	
TwinningPercent	0	
popModel	exp	'exp' – or exponential growth where n(t+1) = birth-rate * n(t) – death-rate * n(t). Population numbers can reach the set carrying capacity of the number of individuals in the XY file, but not exceed this number.
R	1	
K_env	5000	
subpopmortperc	0|0|0|0	
muterate	0.0001	Mutation rate used from Thatte et al. (2018).
mutationtype	forwardbackward	Used from Thatte et al. (2018).
loci	32	
intgenesans	file	
allefreqfilename	ALLELEFREQUENCYFILE	
alleles	2;2;3;3;3;4;4;4;4;4;4;4;5;5;6;6;6;6;6;6;6;6;7;7;7;7;8;9;9;10;10;11	
Mtdna	N	
startGenes	0	
Cdevolveans	N OR 1	N for M0 (non-mortality function) scenarios; 1 for mortality scenarios.
startSelection	0	
betaFile_selection	N	
Epigeneans	N	
startEpigene	0	
betaFile_epigene	N	
Cdinfect	N	
Transmissionprob	0.5	

Table 5 Agevars parameters file for CDPOP simulation setup.

AgeVars			
Age class	0	1	
Distribution	0	1	
Male Mortality	0	100	
Female Mortality	0	100	
Mean Fecundity	0	3	Mean young per female – Used from Thatte et al. (2018).
Std Fecundity	0	2	Standard deviation of young per female – Used from Thatte et al. (2018).
Male Maturation	0	1	
Female Maturation	0	1	

References

Ash E (2015) Thap Lan National Park - Threat and Needs Assessment (Unpublished). Freeland Foundation, Bangkok

Ash E, Cushman SA, Macdonald DW, et al (2020a) How Important Are Resistance, Dispersal Ability, Population Density and

Mortality in Temporally Dynamic Simulations of Population Connectivity? A Case Study of Tigers in Southeast Asia. Land 9:415. https://doi.org/10.3390/land9110415

Ash E, Kaszta Ż, Noochdumrong A, et al (2020b) Opportunity for Thailand's Forgotten Tigers: Assessment of Indochinese tiger Panthera tigris corbetti and prey from camera-trap surveys in Eastern Thailand. Oryx 55:204–211. https://doi.org/10.1017/S0030605319000589

Ash E, Kaszta Ż, Redford T, et al (2020c) Environmental factors, human presence, and prey interact to explain patterns of tiger presence in Eastern Thailand. Anim Conserv 24:268–279. https://doi.org/10.1111/acv.12631

Ash E, Macdonald DW, Cushman SA, et al (2021) Optimization of spatial scale, but not functional shape, affects the performance of habitat suitability models: A case study of tigers (Panthera tigris) in Thailand. Landsc Ecol 36:455–474. https://doi.org/10.1007/s10980-020-01105-6

Coffin AW (2007) From roadkill to road ecology: a review of the ecological effects of roads. J Transp Geogr 15:396–406. https://doi.org/10.1016/j.jtrangeo.2006.11.006

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biol Conserv 128:231–240. https://doi.org/10.1016/j.biocon.2005.09.031

Cushman SA, Elliot NB, Macdonald DW, Loveridge AJ (2016) A multi-scale assessment of population connectivity in African lions (Panthera leo) in response to landscape change. Landsc Ecol 31:1337–1353. https://doi.org/10.1007/s10980-015-0292-3

Dang VL, Yeo GT (2017) A Competitive Strategic Position Analysis of Major Container Ports in Southeast Asia. Asian J Shipp Logist 33:19–25. https://doi.org/10.1016/j.ajsl.2017.03.003

Diniz MF, Cushman SA, Machado RB, De Marco Júnior P (2020) Landscape connectivity modeling from the perspective of animal dispersal. Landsc Ecol 35:41–58. https://doi.org/10.1007/s10980-019-00935-3

Duangchantrasiri S, Umponjan M, Simcharoen S, et al (2016) Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. Conserv Biol 30:639–648. https://doi.org/10.1111/cobi.12655

Elliot NB, Cushman SA, Macdonald DW, Loveridge AJ (2014) The devil is in the dispersers: predictions of landscape connectivity change with demography. J Appl Ecol 51:1169–1178. https://doi.org/10.1111/1365-2664.12282

ESRI (2015) ArcGIS Desktop: Release 10.3.1. Environmental Systems Research Institute, Redlands, CA

European Space Agency (2015) 300 m annual global land cover time series from 1992 to 2015. Climate Change Initiative (CCI), European Space Agency (ESA)

Evans J, Murphy M (2018) rfUtilities. Comprehensive R Archive Network (CRAN), version 2.1-3

Evans JS, Cushman SA, Theobald D (2014) An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, version 2.0-0.

Goodrich JM, Kerley LL, Smirnov EN, et al (2008) Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. J Zool 276:323–329. https://doi.org/10.1111/j.1469-7998.2008.00458.x

Goodrich JM, Lynam A, Miquelle DG, et al (2015) Panthera tigris. IUCN Red List Threat. Species 2015 e.T15955A50659951

Hansen MC, Potapov P V., Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. Science (80-) 342:850–853. https://doi.org/10.1126/science.1244693

Hebblewhite M, Miquelle DG, Robinson H, et al (2014) Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. Biol Conserv 178:50–64. https://doi.org/10.1016/j.biocon.2014.07.013

IUCN World Heritage Outlook (2020) Dong Phayayen-Khao Yai Forest Complex: 2020 Conservation Outlook Assessment. IUCN World Heritage Programme & IUCN World Commission on Protected Areas (WCPA), Gland

Jackson ND, Fahrig L (2011) Relative effects of road mortality and decreased connectivity on population genetic diversity. Biol Conserv 144:3143–3148. https://doi.org/10.1016/j.biocon.2011.09.010

Jarvis A, Reuter HI, Nelson A, Guevara E (2008) Hole-filled seamless SRTM data V4. In: Int. Cent. Trop. Agric. http://srtm.csi.cgiar.org

Joshi A, Vaidyanathan S, Mondol S, et al (2013) Connectivity of Tiger (Panthera tigris) Populations in the Human-Influenced Forest Mosaic of Central India. PLoS One 8:e77980. https://doi.org/10.1371/journal.pone.0077980

Kanagaraj R, Wiegand T, Kramer-Schadt S, et al (2011) Assessing habitat suitability for tiger in the fragmented Terai Arc Landscape of India and Nepal. Ecography (Cop) 34:970–981. https://doi.org/10.1111/j.1600-0587.2010.06482.x

Kaszta Ż, Cushman SA, Hearn AJ, et al (2019) Integrating Sunda clouded leopard (Neofelis diardi) conservation into development and restoration planning in Sabah (Borneo). Biol Conserv 235:63–76. https://doi.org/10.1016/j.biocon.2019.04.001

Kaszta Ż, Cushman SA, Htun S, et al (2020) Simulating the impact of Belt and Road initiative and other major developments in Myanmar on an ambassador felid, the clouded leopard, Neofelis nebulosa. Landsc Ecol 35:727–746. https://doi.org/10.1007/s10980-020-00976-z

Kerley LI, Goodrich JM, Miquelle DG, et al (2002) Effects of Roads and Human Disturbance on Amur Tigers. Conserv Biol 16:97–108. https://doi.org/10.1046/j.1523-1739.2002.99290.x

Kobayashi K, Rashid KA, Furuichi M, Anderson WP (2017) Economic integration and regional development: the ASEAN economic community. Routledge, Abingdon, United Kingdom

Kramer-Schadt S, Revilla E, Wiegand T, Breitenmoser U (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. J Appl Ecol 41:711–723. https://doi.org/10.1111/j.0021-8901.2004.00933.x

Krishnamurthy R, Cushman SA, Sarkar MS, et al (2016) Multi-scale prediction of landscape resistance for tiger dispersal in central India. Landsc Ecol 31:1355–1368. https://doi.org/10.1007/s10980-016-0363-0

Liaw A, Wiener M (2002) Classification and Regression by randomForest. R News 2:18–22

Limanond T, Jomnonkwao S, Srikaew A (2011) Projection of future transport energy demand of Thailand. Energy Policy 39:2754–2763. https://doi.org/10.1016/j.enpol.2011.02.045

Manorom K (2020) Thailand’s Big Water Challenge. In: Dipl. 23 March 2020. https://thediplomat.com/2020/03/thailands-big-water-challenge/. Accessed 8 Mar 2021

Marks D (2011) Climate Change and Thailand: Impact and Response. Contemp Southeast Asia 33:229–258. https://doi.org/10.1355/cs33-2d

OpenStreetMap (2019) OpenStreetMap. www.openstreetmap.org. Accessed 10 Jun 2019

R Development Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing. v.3.6.1. Vienna

Reddy PA, Cushman SA, Srivastava A, et al (2017) Tiger abundance and gene flow in Central India are driven by disparate combinations of topography and land cover. Divers Distrib 23:863–874. https://doi.org/10.1111/ddi.12580

Royal Forestry Department (2000) Study of the Status and Database Design of Natural Resources in Khao Yai, Thap Lan, Pang Sida, and Ta Phraya National Parks [Thai]. Royal Forestry Department, Government of Thailand and Geo Asia Co. Ltd., Bangkok, Thailand

Seeboonruang U (2016) Impact assessment of climate change on groundwater and vulnerability to drought of areas in Eastern Thailand. Environ Earth Sci 75:42. https://doi.org/10.1007/s12665-015-4896-3

SERVIR-Mekong (2018) SERVIR–Mekong Regional Land Cover Monitoring System (RLCMS). SERVIR-Mekong/USAID/NASA/ADPC/ICIMOD, Asian Disaster Preparedness Center (ADPC), Bangkok, Thailand

Smith JLD (1993) The Role of Dispersal in Structuring the Chitwan Tiger Population. Behaviour 124:165–195. https://doi.org/10.1163/156853993X00560

Sunarto S, Kelly MJ, Parakkasi K, et al (2012) Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS One 7:e30859. https://doi.org/10.1371/journal.pone.0030859

Thatte P, Joshi A, Vaidyanathan S, et al (2018) Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations. Biol Conserv 218:181–191. https://doi.org/10.1016/j.biocon.2017.12.022

UNEP-WCMC, IUCN (2019) Protected Planet. The World Database on Protected Areas (WDPA), UNEP-WCMC, Cambridge, U.K., www.protectedplanet.net

Walston J, Robinson JG, Bennett EL, et al (2010) Bringing the tiger back from the brink-the six percent solution. PLoS Biol 8:6–9. https://doi.org/10.1371/journal.pbio.1000485

Wongwuttiwat J, Lawanna A (2018) The digital Thailand strategy and the ASEAN community. Electron J Inf Syst Dev Ctries 84:e12024. https://doi.org/10.1002/isd2.12024

Yu H (2017) Motivation behind China's 'One Belt, One Road' Initiatives and Establishment of the Asian Infrastructure Investment Bank. J Contemp China 26:353–368. https://doi.org/10.1080/10670564.2016.1245894

Supplementary Materials 2

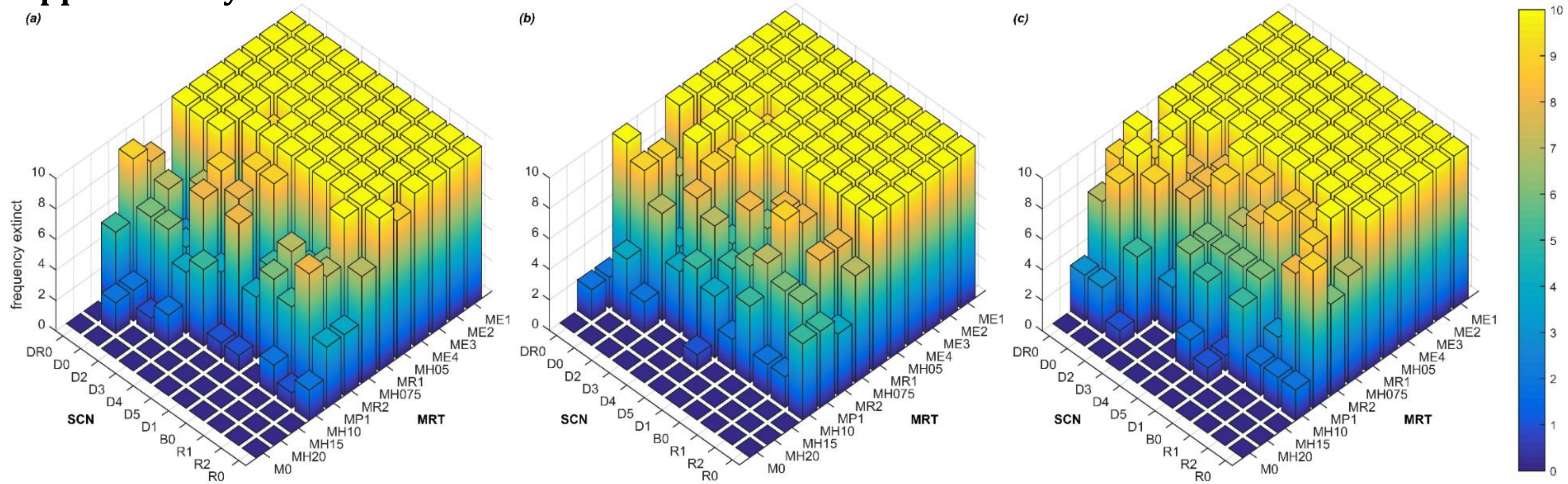

Fig. 1 Summary of number of simulations resulting in population extinction by landscape change scenario (SCN) and mortality function (MRT) under 6km density (DEN) and resistance transformed by (a) 0.5 power function (RST05), (b) 1.0 power function (RST10), and (c) 2.0 power function (RST20).

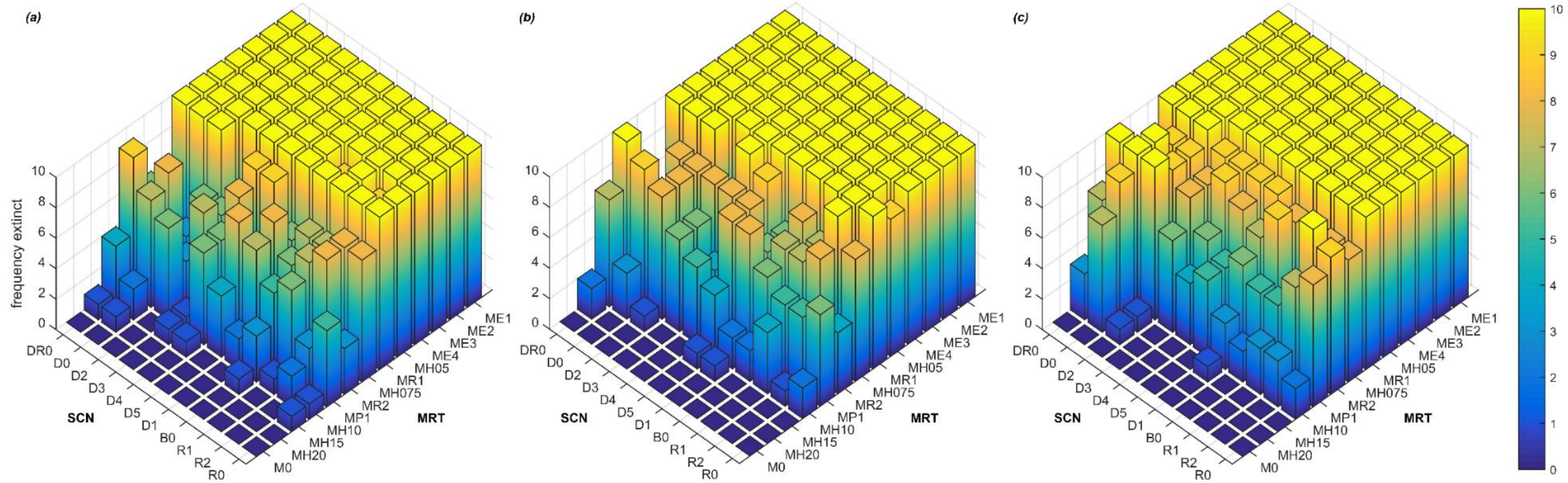

Fig. 2 Summary of number of simulations resulting in population extinction by landscape change scenario (SCN) and mortality function (MRT) under 7.5km density (DEN) and resistance transformed by (a) 0.5 power function (RST05), (b) 1.0 power function (RST10), and (c) 2.0 power function (RST20).

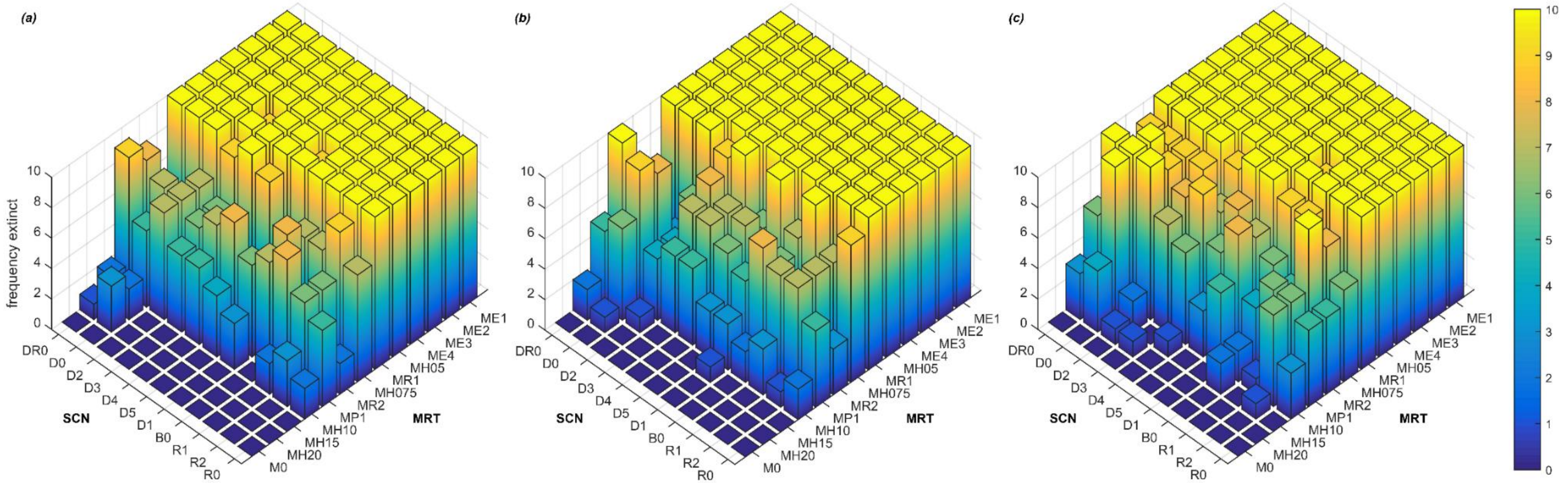

Fig. 3 Summary of number of simulations resulting in population extinction by landscape change scenario (SCN) and mortality function (MRT) under 10km density (DEN) and resistance transformed by (a) 0.5 power function (RST05), (b) 1.0 power function (RST10), and (c) 2.0 power function (RST20).

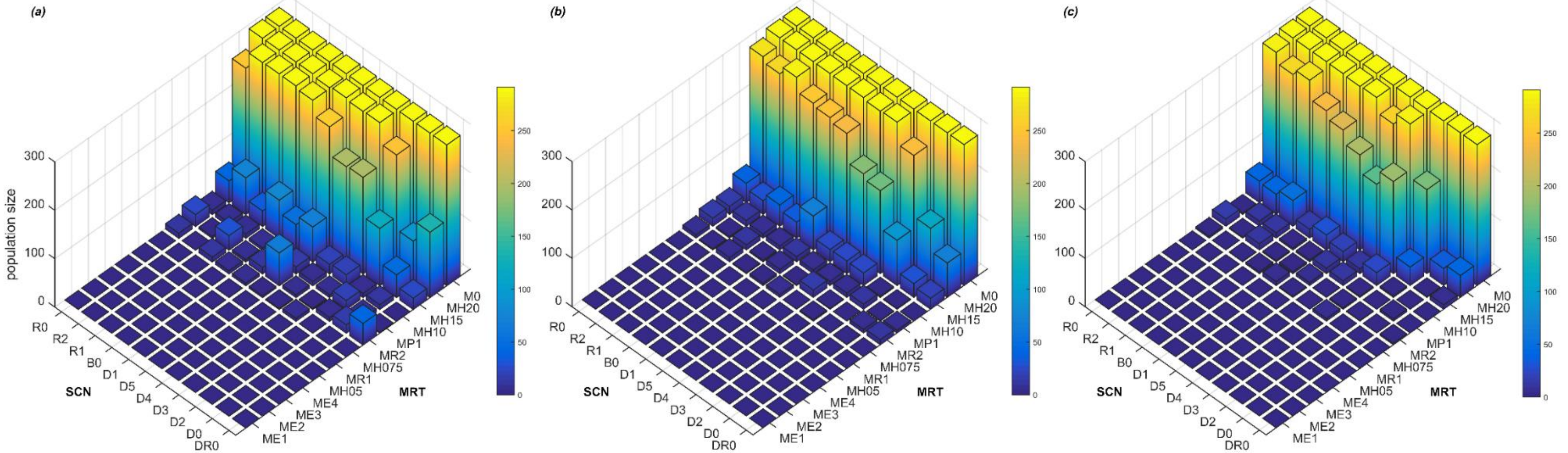

Fig. 4 Summary of simulated population at generation 20 by landscape change scenario (SCN) and mortality function (MRT) under 6km density (DEN) and resistance transformed by (a) 0.5 power function (RST05), (b) 1.0 power function (RST10), and (c) 2.0 power function (RST20).

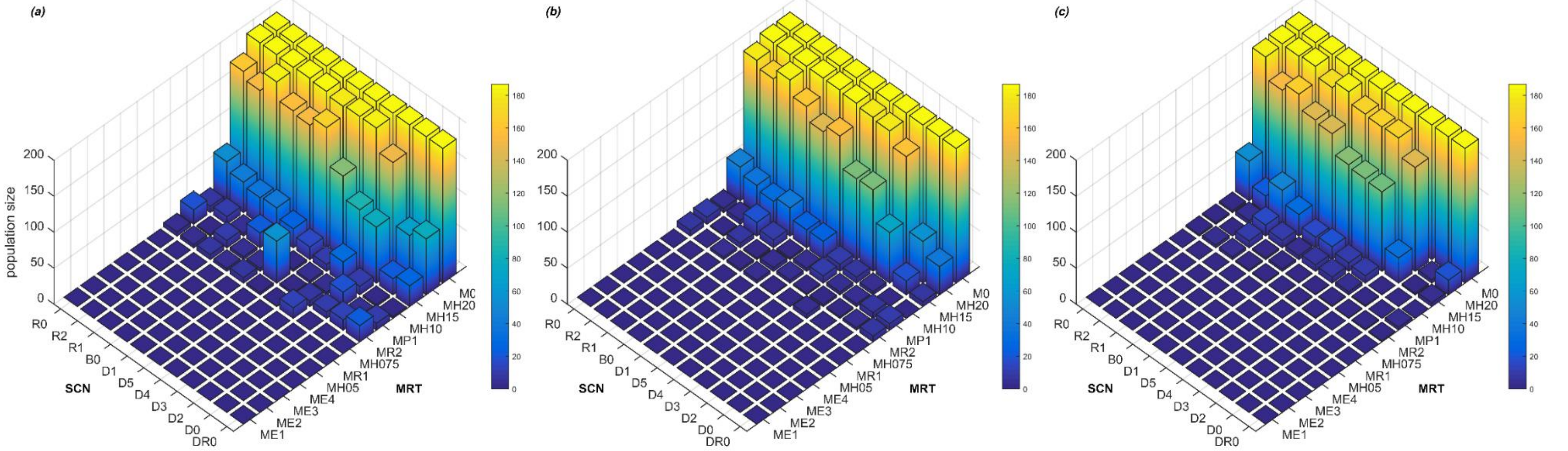

Fig. 5 Summary of simulated population at generation 20 by landscape change scenario (SCN) and mortality function (MRT) under 7.5km density (DEN) and resistance transformed by (a) 0.5 power function (RST05), (b) 1.0 power function (RST10), and (c) 2.0 power function (RST20).

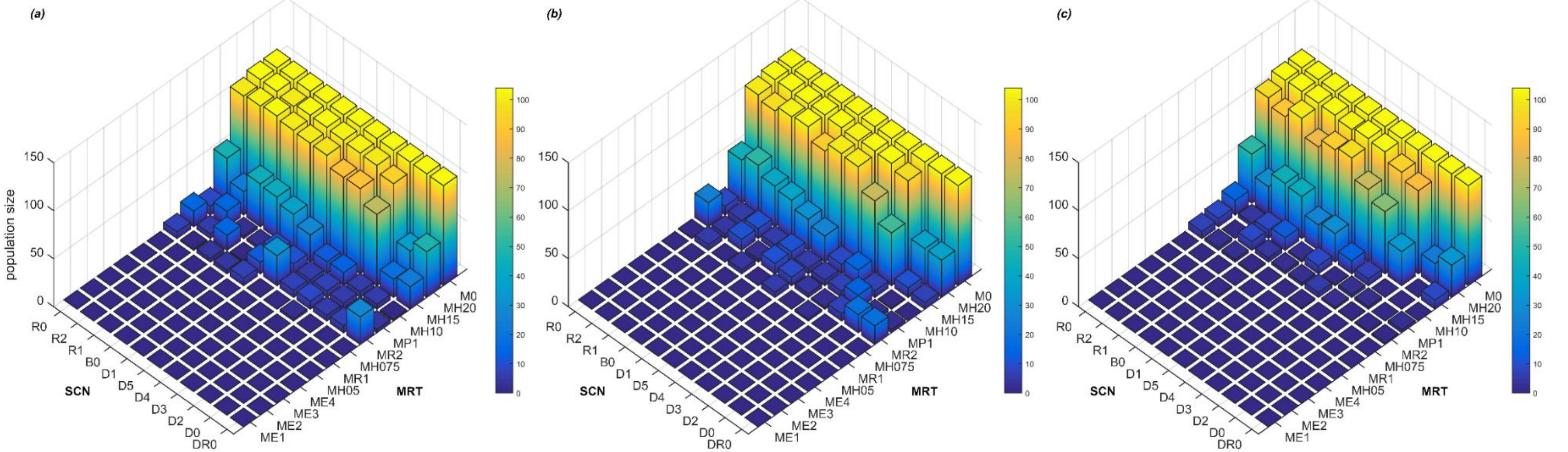

Fig. 6 Summary of simulated population at generation 20 by landscape change scenario (SCN) and mortality function (MRT) under 10km density (DEN) and resistance transformed by (a) 0.5 power function (RST05), (b) 1.0 power function (RST10), and (c) 2.0 power function (RST20).

Table 1 Summary of factorial analysis of variance (ANOVA) between simulated population at generation 20 (N_{20}) between main effects and interactions of land change scenario (SCN), population density (DEN), resistance transformation (RST), and mortality function (MRT) for all simulations. Significant differences in observed means (Pr(>*F*)) are highlighted in bold with *** denoting very highly significant differences.

	Df	Sum Sq	Mean Sq	F value	Pr(>*F*)
SCN	10	1277304	127730	402.057	**< 2e-16 *** **
DEN	2	2770172	1385086	4359.828	**< 2e-16 *** **
RST	2	43658	21829	68.71	**< 2e-16 *** **
MRT	12	58934576	4911215	15459.007	**< 2e-16 *** **
SCN:DEN	20	184456	9223	29.031	**< 2e-16 *** **
SCN:RST	20	23047	1152	3.627	**7.42e-08 *** **
SCN:MRT	120	5511488	45929	144.571	**< 2e-16 *** **
DEN:RST	4	8632	2158	6.793	**1.86e-05 *** **
DEN:MRT	24	9211790	383825	1208.163	**< 2e-16 *** **
RST:MRT	24	99587	4149	13.061	**< 2e-16 *** **
SCN:DEN:RST	40	10808	270	0.851	0.735
SCN:DEN:MRT	240	1040174	4334	13.642	**< 2e-16 *** **
SCN:RST:MRT	240	177837	741	2.332	**< 2e-16 *** **
DEN:RST:MRT	48	30849	643	2.023	**3.76e-05 *** **
SCN:DEN:RST:MRT	480	133262	278	0.874	0.976
Residuals	11583	3679835	318		

Table 2 Summary of factorial analysis of variance (ANOVA) between simulated population at generation 20 (N_{20}) between main effects and interactions of land change scenario (SCN), population density (DEN), and resistance transformation (RST), holding mortality (MRT) constant at moderate levels (MH10). Significant differences in observed means (Pr(>*F*)) are highlighted in bold with *** denoting very highly significant differences.

	Df	Sum Sq	Mean Sq	F value	Pr(>*F*)
SCN	10	275417	27542	30.083	**< 2e-16 *** **
DEN	2	10098	5049	5.515	**0.00417 ** **
RST	2	9706	4853	5.301	**0.00515 ** **
SCN:DEN	20	18828	941	1.028	0.42492
SCN:RST	20	18325	916	1.001	0.45833
DEN:RST	4	6656	1664	1.818	0.12331
SCN:DEN:RST	40	41538	1038	1.134	0.26413
Residuals	891	815744	916		

Table 3 Summary of simulated population at generation 20 for population density (DEN) and resistance transformation (RST), holding mortality function constant at moderate levels (MH10). Values include mean ($\overline{N}_{20}$), median ($\widetilde{N}_{20}$), percentage of simulations resulting in extinctions ($\%N_{20}=0$), population declines (not including extinctions; $\%N_{20\downarrow}$), and stable/increasing populations ($\%N_{20\rightarrow\uparrow}$).

		$\overline{N}_{20}$	$\widetilde{N}_{20}$	$\%N_{20}=0$	$\%N_{20\downarrow}$	$\%N_{20\rightarrow\uparrow}$
DEN	10KM	23.6	6	47.0%	21.8%	31.2%
	7.5KM	21.4	7	46.4%	25.8%	27.9%
	6KM	29.0	10	44.2%	23.0%	32.7%
RST	RST05	28.8	15.5	37.6%	26.4%	36.1%
	RST10	24.0	6	47.0%	21.8%	31.2%
	RST20	21.2	0	53.0%	22.4%	24.5%

Table 4 Summary of Tukey HSD tests on density (DEN) and resistance transformation (RST) holding mortality constant at moderate levels (MH10), showing difference in observed $\overline{N}_{20}$ (Diff), lower confidence interval (lwr), upper confidence interval (upr), and significance (*p*).

		Diff	lwr	upr	*p*
DEN	75KM-6KM	**-7.6**	-13.1	-2.1	**0.0037***
	6KM-10KM	5.4	-0.1	10.9	0.0565
	75KM-10KM	-2.2	-7.7	3.3	0.6238
RST	RST20-RST05	**-7.6**	-13.1	-2.1	**0.0038***
	RST10-RST05	-4.8	-10.3	0.7	0.1045
	RST20-RST10	-2.8	-8.3	2.7	0.4633

Table 5 Summary of notable interactions from Tukey HSD between land change scenario (SCN), density (DEN), and resistance transformation (RST), holding mortality constant at moderate levels (MH10). Results include difference in observed $\overline{N}_{20}$ (*Diff*), lower confidence interval (*lwr*), upper confidence interval (*upr*), and significance (*p*).

	Diff	lwr	upr	*p*
B0:6KM:RST20-B0:6KM:RST05	**-61.2**	-119.6	-2.8	**0.0224***
D1:75KM:RST20-B0:6KM:RST05	**-64.1**	-122.5	-5.7	**0.0091***
D5:75KM:RST05-B0:6KM:RST05	**-61.5**	-119.9	-3.1	**0.0205***
D5:75KM:RST20-B0:6KM:RST05	**-61.2**	-119.6	-2.8	**0.0224***
D5:RST20-B0:RST05	**-30.9**	-60.7	-1.2	**0.0294***
D1:RST20-B0:RST05	**-29.8**	-59.6	0.0	**0.0490***

Supplementary Materials 3

Poacher-based mortality model

Table 1 Summary of variables included in poacher-based mortality model bootstrap iterations, including the optimal scale at which the variable was included in each iteration (1-10).

		Scale									
Variable	**ID**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Focal mean of PA boundary	BOUNDFM	2000	250	4000	16000	250	16000	16000	16000	500	250
Focal mean of elevation	DEMFM	2000	16000	500	8000	500	16000	250	2000	250	500
Standard deviation of elevation	DEMSD	8000	1000	8000	16000	500	1000	1000	2000	2000	16000
Distance to park substation	DIST.SS	-	-	-	-	-	-	-	-	-	-
Distance to all roads	DISTROAD.	-	-	-	-	-	-	-	-	-	-
Distance to public roads	DISTROAD.	-	-	-	-	-	-	-	-	-	-
Distance to park roads	DISTROAD.	-	-	-	-	-	-	-	-	-	-
% Evergreen forest	FTpland1	4000	250	2000	16000	8000	2000	1000	16000	16000	1000
% Dry dipterocarp forest	FTpland3	250	8000	4000	250	250	250	4000	250	250	250
% Reforested areas	FTpland4	1000	16000	16000	16000	4000	8000	16000	16000	8000	500
%Bamboo forest	FTpland5	16000	4000	8000	8000	4000	16000	4000	16000	8000	250
% Secondary forest/old clearing	FTpland6	8000	8000	4000	8000	4000	1000	8000	8000	16000	8000
Human influence index	HII	-	-	-	-	-	-	-	-	-	-
Aggregation index of land cover	LCai	2000	4000	8000	4000	500	500	2000	16000	4000	16000
Contrast weighted edge-density of land cover	LCcwed	16000	8000	1000	8000	8000	16000	8000	8000	250	16000
Patch density of land cover	LCpd	8000	2000	2000	8000	250	1000	4000	8000	8000	8000
% Cropland	LCpland1	2000	16000	16000	500	1000	1000	16000	4000	16000	8000
% Mosaic cropland	LCpland2	16000	500	16000	16000	8000	4000	250	2000	8000	8000
% Forest/natural vegetation	LCpland3	16000	4000	16000	16000	2000	2000	8000	8000	8000	8000
% Shrubland/grassland	LCpland4	8000	16000	8000	4000	4000	16000	1000	16000	2000	16000
% Sparse vegetation & bare areas	LCpland5	250	250	250	250	250	250	250	250	250	16000
		1000	1000	1000	1000	1000	1000	1000	1000	1000	1000
% Urban areas	LCpland6	16000	250	250	8000	16000	250	250	250	250	250
Focal mean of terrain roughness	ROUGHFM	4000	2000	4000	8000	8000	8000	8000	1000	2000	16000
Standard deviation of terrain roughness index	ROUGHSD	8000	16000	16000	4000	4000	8000	16000	16000	1000	4000
Point density of settlements	Settlement	-	-	-	-	-	-	-	-	-	-
Focal mean of slope position	SLOPEFM	8000	250	4000	2000	250	16000	8000	16000	8000	8000
Standard deviation of slope position	SLOPESD	2000	1000	1000	8000	16000	16000	1000	2000	16000	8000
Focal mean of streams/rivers	STRC1FM	16000	16000	500	4000	8000	1000	250	500	250	250
% Non-forest	TCpland1	8000	1000	8000	4000	16000	2000	4000	16000	2000	8000
% Open forest	TCpland2	4000	250	8000	4000	4000	16000	8000	4000	250	8000
% Closed canopy forest	TCpland3	4000	8000	1000	16000	250	2000	4000	16000	8000	4000
X Coordinate	X	-	-	-	-	-	-	-	-	-	-
Y Coordinate	Y	-	-	-	-	-	-	-	-	-	-

Table 2 Summary of variables included in poacher-based mortality model bootstrap iterations (1-10) and variable importance.

		Variable Importance									
Variable	**ID**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Focal mean of PA boundary	BOUNDFM	0.04	0.04	0.11	0.40	0.04	0.35	0.36	0.39	0.07	0.02
Focal mean of elevation	DEMFM	0.29	0.45	0.27	0.59	0.23	0.43	0.28	0.29	0.33	0.25
Standard deviation of elevation	DEMSD	0.46	0.37	0.47	0.72	0.29	0.30	0.33	0.28	0.32	0.64
Distance to park substation	DIST.SS	0.39	0.41	0.40	0.35	0.41	0.36	0.39	0.38	0.42	0.41
Distance to all roads	DISTROAD.ALL	0.37	0.44	0.45	0.41	0.42	0.35	0.41	0.45	0.44	0.43
Distance to public roads	DISTROAD.C1	0.39	0.36	0.37	0.42	0.33	0.32	0.34	0.41	0.36	0.35
Distance to park roads	DISTROAD.C2	0.69	0.74	0.71	0.68	0.65	0.64	0.62	0.70	0.75	0.64
% Evergreen forest	FTpland1	0.22	0.04	0.16	0.54	0.31	0.16	0.11	0.59	0.58	0.12
% Dry dipterocarp forest	FTpland3	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
% Reforested areas	FTpland4	0.03	0.48	0.52	0.52	0.05	0.14	0.45	0.49	0.18	0.01
%Bamboo forest	FTpland5	0.30	0.16	0.23	0.27	0.19	0.33	0.18	0.42	0.23	0.02
% Secondary forest/old clearing	FTpland6	0.44	0.47	0.20	0.48	0.19	0.02	0.43	0.48	0.35	0.47
Human influence index	HII	0.32	0.36	0.32	0.30	0.31	0.28	0.33	0.36	0.32	0.30
Aggregation index of land cover	LCai	0.17	0.29	0.38	0.30	0.01	0.01	0.17	0.36	0.29	0.33
Contrast weighted edge-density of land	LCcwed	0.36	0.53	0.07	0.46	0.45	0.33	0.45	0.44	0.00	0.39
Patch density of land cover	LCpd	0.32	0.12	0.10	0.31	0.02	0.05	0.20	0.33	0.38	0.35
% Cropland	LCpland1	0.04	0.62	0.57	0.01	0.03	0.02	0.58	0.10	0.59	0.45
% Mosaic cropland	LCpland2	0.32	0.01	0.35	0.34	0.28	0.17	0.01	0.11	0.29	0.25
% Forest/natural vegetation	LCpland3	0.60	0.32	0.60	0.61	0.22	0.22	0.42	0.44	0.43	0.43
% Shrubland/grassland	LCpland4	0.38	0.38	0.44	0.33	0.28	0.38	0.06	0.41	0.20	0.42
% Sparse vegetation & bare areas	LCpland5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
% Urban areas	LCpland6	0.23	0.00	0.00	0.01	0.20	0.00	0.00	0.00	0.00	0.00
Focal mean of terrain roughness	ROUGHFM	0.35	0.40	0.39	0.62	0.65	0.62	0.59	0.34	0.37	0.75
Standard deviation of terrain roughness	ROUGHSD	0.62	0.73	0.72	0.35	0.36	0.66	0.70	0.71	0.25	0.33
Point density of settlements	Settlement	0.51	0.54	0.58	0.58	0.48	0.48	0.55	0.63	0.54	0.58
Focal mean of slope position	SLOPEFM	0.16	0.08	0.12	0.04	0.06	0.06	0.20	0.08	0.21	0.16
Standard deviation of slope position	SLOPESD	0.46	0.43	0.42	0.59	0.69	0.67	0.34	0.48	0.72	0.56
Focal mean of streams/rivers	STRC1FM	0.75	0.77	0.53	0.57	0.70	0.55	0.50	0.48	0.52	0.49
% Non-forest	TCpland1	0.40	0.20	0.43	0.29	0.61	0.25	0.31	0.66	0.22	0.43
% Open forest	TCpland2	0.31	0.05	0.52	0.30	0.33	0.40	0.49	0.29	0.03	0.51
% Closed canopy forest	TCpland3	0.26	0.47	0.19	0.63	0.05	0.29	0.30	0.66	0.46	0.26
X Coordinate	X	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Y Coordinate	Y	0.35	0.38	0.35	0.40	0.34	0.34	0.32	0.36	0.35	0.36

Table 3 Summary of performance statistics for poacher-based mortality model bootstrap iterations including OOB (Out-of-Bag error), PCC (Percent Correctly Classified), AUC (Area Under the ROC Curve) and TSS (True Skill Statistic).

Iteration	OOB	Sensitivity	Specificity	Kappa	PCC	AUC	TSS
1	0.2275	0.8892	0.4653	0.3833	77.2467	0.6772	0.4287
2	0.2084	0.9156	0.4653	0.4217	79.1587	0.6904	0.4952
3	0.2275	0.9050	0.4236	0.3656	77.2467	0.6643	0.4340
4	0.2409	0.8865	0.4236	0.3394	75.9082	0.6551	0.3884
5	0.2218	0.9050	0.4444	0.3860	77.8203	0.6747	0.4509
6	0.2371	0.8865	0.4375	0.3529	76.2906	0.6620	0.4001
7	0.2275	0.9050	0.4236	0.3656	77.2467	0.6643	0.4340
8	0.2333	0.9024	0.4097	0.3481	76.6730	0.6560	0.4155
9	0.2333	0.8892	0.4444	0.3634	76.6730	0.6668	0.4119
10	0.2467	0.8839	0.4097	0.3221	75.3346	0.6468	0.3704

Table 4 Summary of variables included in the final poacher-based mortality model by presence in each bootstrap iteration.

Variable	ID	1	2	3	4	5	6	7	8	9	10
Standard deviation of digital elevation model (16km)	DEMSD_16000				•						•
Distance to park (private) road	DISTROAD.C2	•	•	•	•	•	•	•	•	•	•
% Cropland (16km)	LC1_PLAND_16000		•								
% Natural vegetation (16km)	LC3_PLAND_16000	•			•						
Focal mean of terrain roughness index (16km)	TRI_FM_16000										•
Focal mean of terrain roughness index (8km)	TRI_FM_8000				•	•	•				
Standard deviation of terrain roughness index (16km)	TRI_SD_16000		•	•				•	•		
Standard deviation of terrain roughness index (8km)	TRI_SD_8000	•					•				
Settlement density (16km kernel width)	SettlementDensity								•		
Standard deviation of slope position (16km)	SLOPE_SD_16000					•	•			•	
Focal mean of streams/rivers (16km)	STRC1_FM_16000	•	•								
Focal mean of streams/rivers (8km)	STRC1_FM_8000					•					
% Non-forest (16km)	TC1_PLAND_16000					•			•		
% Closed forest (16km)	TC3_PLAND_16000				•				•		
X Coordinate	X	•	•	•	•	•	•	•	•	•	•

Chapter 8

Discussion

Discussion

The alarming downward trajectory of tiger populations throughout their range, particularly in Southeast Asia, underscores the necessity of reviews on the status, ecology, and importance of populations that remain. In essence, this thesis represents a timely and comprehensive assessment on the status and ecology of tigers in the Dong Phayayen-Khao Yai Forest Complex (DPKY) in eastern Thailand. Through this thesis, I improve understanding of DPKY's role in national and regional tiger conservation paradigms to aid in the development of management strategies. Concurrently, this thesis provides novel insight into methods commonly used in ecological research, which may aid in similar studies of tigers and other species. In this concluding chapter, I (1) summarize and synthesize the most important results from this research, (2) provide recommendations for future management actions, and (3) contextualize results within tiger conservation and research more broadly.

1. Tigers in the Dong Phayayen-Khao Yai Forest Complex

1.1 Assessing the population of tigers in DPKY

The results from long-term camera-trap surveys described in ***Chapter 2*** represent the first dedicated tiger surveys across all protected areas in this landscape and among the most expansive and longest-running surveys of tigers in Southeast Asia. This provided the foundation for a broad assessment of the population in this landscape. Specifically, there were three key findings about this population of particular significance. First, records of at least 16 adults, some of which had long-term persistence, imply a larger population is present in DPKY than previously suggested (Lynam 2010). Second, variation in detections imply a heterogeneity in tiger presence across the landscape. Higher detection rates strongly infer greater abundance in Thap Lan and Pang Sida national parks, just to an unknown degree, and the lack of detections in Khao Yai National Park reinforces evidence that tigers have been extirpated from the park. Third, and most importantly, surveys documented several cases of successful breeding, establishing DPKY as one of the few remaining breeding sites for Indochinese tigers globally. In effect, results demonstrate that DPKY is one of the most important extant tiger populations remaining in mainland Southeast Asia.

Results from ***Chapter 2*** were well-suited for providing a broad assessment of tigers in, what had previously been, an understudied landscape and further defined its conservation significance. However, reliable assessments of tiger population trends over time require specific and repeated estimations of more rigorous indicators of population status such as population density (Karanth et al. 2017; Royle et al. 2017). ***Chapter 5*** serves to address this by generating a reliable baseline estimate of density for this population. Using a model incorporating variation in sex for parameters *g0* and σ, this study produced a density estimate of 0.63 ± SE0.22 (0.32–1.21) tigers per 100km^2 and a population estimate of 20 (14–33). Importantly, this density estimate is considerably lower than estimates from elsewhere in Thailand (Duangchantrasiri et al. 2016) and among the lowest estimates in the tiger's global range (Harihar et al. 2018). In the study, I speculated that this may be due to a complex history of anthropogenic pressure from which this population may still be recovering. Importantly, evaluation of future population changes will be well-served by the baseline metrics generated by this study.

1.2 Patterns of tiger habitat selection

Differences in patterns of detection documented in ***Chapter 2*** suggest that tiger presence across DPKY is considerably heterogeneous. Understanding the factors and patterns driving this heterogeneity is a crucial step toward developing landscape-specific management strategies. In ***Chapter 3***, I utilized scale- and functional form (shape) optimized models to define the influence of key environmental covariates and generate predictions of tiger presence. Models developed in this chapter highlighted three key patterns of tiger habitat selection in this landscape. First, tiger habitat selection is highly scale-dependent and is influenced by covariates at large spatial scales. Second, the study documented positive associations between tigers and percentage of bamboo forest, moderate topographic heterogeneity, and reforested areas, and negative associations with secondary and open forest. Third, predictions of tiger presence suggest the presence of a core area of mid- to high-quality habitat in central DPKY within a large-scale block of intact forest, notably, far from human habitation. These results are consistent with literature highlighting the importance of large protected areas and low human disturbance for tiger populations (Trisurat et al. 2010;

Sunarto et al. 2012; Ngoprasert et al. 2012; Hebblewhite et al. 2014; Reddy et al. 2017).

1.3 Tiger prey in DPKY

In tiger studies elsewhere in their range, prey emerges as the strongest, or among the strongest, predictors of tiger presence (Karanth et al. 2011; Harihar and Pandav 2012; Ngoprasert et al. 2012; Barber-Meyer et al. 2013). In ***Chapter 2***, I identified six potential prey species in DPKY: gaur (*Bos gaurus*), banteng (*Bos javanicus*), Chinese serow (*Capricornis milneedwardsii*), northern red muntjac (*Muntiacus vaginalis*), sambar (*Rusa unicolor*) and wild boar (*Sus scrofa*). All but one potential prey species (banteng) were documented in all five protected areas, though detection rates of prey varied considerably by park.

Notably in ***Chapter 2***, two species – wild boar and sambar deer – were identified as having higher relative rates of detection that could explain differences in detections of tigers. In ***Chapter 4***, I sought to model and test the potential influence of these and other prey species on tiger presence. Contrary to the study's hypothesis that tigers would have the strongest associations with the largest prey species (i.e., sambar and gaur), models described strong, positive associations with wild boar presence and prey richness, while positive or negative relationships could not be determined for sambar and gaur. This study suggests wild boar and prey rich areas underpin tiger presence in this landscape, necessitating careful consideration in conservation management strategies.

1.4 Anthropogenic factors explaining tiger presence

In contrast to the presence of prey, studies from elsewhere in the tiger's range report strong negative associations between tiger presence and anthropogenic disturbance, such as roads (Kerley et al. 2002) and proximity to settlements (Sunarto et al. 2012), though these relationships may be complex (Carter et al. 2012). Given the high degree of human influence in defining the tiger's present range overall (Goodrich et al. 2015), understanding the specific anthropogenic factors that may affect tigers in DPKY is critically important. In ***Chapter 4***, I investigated the degree to which anthropogenic factors explain patterns of tiger presence, hypothesizing that tiger presence would be strongly, and negatively associated with human habitation and, to a lesser degree, human presence overall. Results were consistent with this hypothesis. Notably, the model described strong, negative associations with human settlement density, public roads, and presence of poachers. Such associations are almost universal across the tiger's range (Kerley et al. 2002; Kanagaraj et al. 2011; Hebblewhite et al. 2012; Sunarto et al. 2012; Barber-Meyer et al. 2013) and appear to be a potentially major influence in tiger distribution in DPKY.

1.5 Comparing environment, prey, and human factors explaining tiger presence

Given DPKY's complex history, the interaction of environmental, prey, and human factors on recent tiger distribution is likely also complex. Above, I described how these factors explain patterns of heterogeneity in tiger presence in DPKY independently. However, understanding the degree to which these factors explain tiger presence when confounded could further aid in the development of management strategies in the complex. In ***Chapter 4***, I assessed the relative contribution of environment (using the multi scale- and functional shape-optimized model [MSSO] from ***Chapter 3***), prey, and human factors to explaining the degree of variance in tiger detections in DPKY using variance partitioning. Specifically, I hypothesized that prey would better explain tiger presence compared to human presence or environmental characteristics, given the established importance of prey as a major limiting factor in tiger presence (Karanth and Stith 1999; Karanth et al. 2004). Surprisingly, results were not consistent with this hypothesis, with environmental factors explaining the greatest overall proportion of variance (19.6%), especially when confounded with human factors (31.1%). The results in this study suggest that explanatory factors for tiger presence in the Dong Phayayen–Khao Yai Forest Complex are more nuanced than initially hypothesized. Importantly, the environmental (MSSO) model from ***Chapter 3***, may have been a more comprehensive predictor of tiger presence than prey or human factors on their own. Specifically, this model described strong positive associations with habitat suitable for important prey species highlighted in this chapter, strong positive associations with core habitat away from human habituation, and strong negative associations with habitat near settlements and, thus, heavily impacted by human activity. This suggests that, in some cases, an environmental model, especially coupled with anthropogenic factors, could be used to model tiger occurrence where other data may be lacking. However, this approach would merit a high degree of caution since, regardless of environmental characteristics, poaching and prey depletion can eradicate tigers and other species from otherwise intact habitat (Benítez-López et al. 2019).

1.6 Tiger range expansion and habitat connectivity

Tigers are wide-ranging and the long-term dynamics of their populations is shaped considerably by dispersal and landscape configuration (Vasudev et al. 2017; Thapa et al. 2017; Thatte et al. 2018). Further, the potential extirpation of tigers from Khao Yai National Park and likely limited presence in other areas identified in ***Chapter 2*** suggest it may be possible for tigers to expand their range in this complex. In addition, given DPKY is likely to be the eastern-most remaining breeding population of tigers in Southeast Asia (Lynam and Nowell 2011) understanding the potential for DPKY to act as a source site for recolonization of former tiger range countries Cambodia and southern Lao PDR, could have important implications for the conservation of tigers at a regional level. In ***Chapter 6***, I utilized a spatially- and temporally-dynamic resistance kernel modelling approach and sensitivity analysis to evaluate predicted tiger population size, distribution, and connectivity across a relatively contiguous section of Thailand, Cambodia, and southern Lao PDR. In this study, a number of strong patterns were apparent. First, a majority of simulations resulted in dispersal to Khao Yai National Park, though successful colonization where populations persisted was less frequent. Second, there was a low frequency of dispersal to areas of Cambodia and, in fewer cases, Lao PDR, with successful colonization extremely rare and in cases where parameters were largely biologically unrealistic (i.e., no spatial mortality risk). Third, mortality was a key factor in the study and would potentially act as a considerable obstacle not only for long-range dispersal and re-colonization, but may also considerably undermine long-term persistence, a finding reinforced in ***Chapter 7***. Overall results from this study suggest that this population is likely effectively isolated from other large areas of potential habitat and limited in its capacity for large-scale range expansion.

1.7 Long-term tiger population dynamics

While records of breeding from ***Chapter 2*** suggest tiger population recovery may be possible in DPKY, the low population estimate generated in ***Chapter 5*** reinforces that concerted efforts must be made if this population is to be spared from extinction. A key part of these efforts is understanding key factors, such as landscape change, which may affect population viability in the future. The effects of broad-scale human pressure on DPKY have been the subject of growing concern (IUCN World Heritage Outlook 2020). Among potential landscape changes of note are the potential of expansion of human presence in the area, given its location along economic corridors (Wongwuttiwat and Lawanna 2018), expansion and intensification of roads, and growing pressure to construct dams due to water insecurity (Marks 2011; IUCN World Heritage Outlook 2020; Manorom 2020). Concurrently, there may be opportunities to expand or augment tiger habitat through reforestation, protected area expansion, or the addition of wildlife crossing structures along major highways.

In ***Chapter 7***, I utilized an individual-based, spatially-explicit population modelling approach to evaluate the relative effects of landscape change scenarios, mortality risk, and other factors on predictions of tiger population dynamics in DPKY over 20 generations. This study produced a number of important results relevant for the conservation of tigers in this landscape in the future. First, mortality risk overwhelmingly dominated predictions of population persistence with predictions highly sensitive to mortality functional form and definition. Introduction of mortality risk frequently resulted in population declines/extinction, consistent with evidence that even marginal increases in mortality, such as from poaching, can drive disproportionately higher predicted extinction risk (Kenney et al. 1995; Linkie et al. 2006; Chapron et al. 2008). Second, there were significant differences in population trajectories depending on landscape change scenario with particularly strong negative effects predicted in scenarios incorporating road expansion and construction of dams. Third, strong negative effects of combined development persisted even when habitat restoration measures were applied, suggesting efforts to mitigate the effects of infrastructure may fall short, particularly with synergistic effects of increased mortality risk. Importantly, the high sensitivity to mortality risk and high variability in population trajectories suggest this population is on a proverbial knife’s edge.

1.8 Other findings of importance

Long-term camera-trap surveys described in ***Chapter 2*** not only produced a considerably large database of tiger records, but also documented a number of species of conservation and research interest. In addition to tigers, surveys documented four other species of felids - Asiatic golden cat (*Catopuma temminckii*; 35 detections), mainland clouded leopard (*Neofelis nebulosa;* 158), marbled cat (*Pardofelis marmorata*; 30) and leopard cat (*Prionailurus bengalensis*; 724). Notably, leopard (*Panthera pardus*) were not detected in surveys though the reasons for its absence are unknown. The Indochinese leopard (*Panthera pardus delacouri*) has not been detected recently in other parts of Southeast Asia, suggesting a severe decline in its population and range (Rostro-García et al. 2016a; Rasphone et al. 2019). Overall, surveys documented 37 mammal species in total, including one Critically Endangered, five Endangered, 10 Vulnerable, three Near Threatened, and 18 Least Concern species. These results further reinforce the importance of this site not only for tigers, but as a refuge for other species of conservation priority.

2. Methodological Insights

While the primary focus of this thesis was to investigate the status and ecology of tigers in the Dong Phayayen-Khao Yai Forest Complex, this thesis also provided opportunities to explore additional methodological questions pertaining to the use of tools used in ecological research on tigers and other species. I believe these methodological investigations have complemented and strengthened the scientific merit of the studies in this thesis and provided insights of broad academic appeal. Specifically, I explored the effect of spatial scale- and functional shape-optimization in habitat selection modelling. I also investigated the extent to which simulations can guide study design for population density surveys. Lastly, I evaluated the sensitivity of population connectivity and viability models to parametric variation and assessed the effect of their interactions on model predictions. Here, I discuss methodological insights which have emerged organically from the work in this thesis.

2.1 Use of targeted, non-systematic surveys in large carnivore research

Methodologically-rigorous study designs should be employed wherever possible in monitoring wildlife populations, but if resources are constrained a targeted, non-systematic study design (referred to as "opportunistic" in previous chapters) may be appropriate (Harihar et al. 2007; Stein et al. 2008; Johnson et al. 2016). Prior to the work described in ***Chapter 2***, tigers were believed to have disappeared from Khao Yai National Park (Lynam 2001; Lynam et al. 2006; Jenks et al. 2011), information was lacking for other areas of DPKY, and resources for further research were limited. In these circumstances, a targeted, non-systematic study design was suitable to address fundamental research questions, particularly, to confirm tiger, prey, and other species presence in the landscape. Early findings suggested tigers were present in the area, results which helped to secure further funding and improved access to resources such as camera traps that were later used for tiger density and population estimates. In addition, results from these surveys, notably records of tiger and prey presence, greatly benefitted the development of survey designs for generating population density estimates in ***Chapter 5***. This previous knowledge enabled effective placement of camera-traps, which generated a sufficient number of detections necessary for producing a reliable population density estimate. Additional funding generated from survey results also enabled investments in law enforcement, patrol-based monitoring, and local community outreach programs (***Chapter 2***). Although the conclusions that can be drawn from such targeted, non-systematic studies are limited, they can contribute timely and important insights into species presence in poorly studied areas (Stein et al. 2008; Jenks et al. 2011) and could be an effective vehicle through which greater conservation and research investment can be directed. Importantly, given the uncertain status of the tiger in many areas of Southeast Asia, this approach could be a cost-effective way to assess potential tiger presence in other understudied landscapes.

2.2 Scale- and functional shape-optimization in habitat selection modelling

There are a number of aspects of tiger ecology that are of potential relevance when planning for the development of habitat selection models. First and foremost, tigers are wide-ranging species, can disperse large distances (Smith 1993; Sunquist 2010), and can be affected by variation in the environment at broad scales (Krishnamurthy et al. 2016; Reddy et al. 2017). Conclusions regarding tiger habitat can be highly dependent on the spatial scales in which variables are included in models (Krishnamurthy et al. 2016; Rostro-García et al. 2016b; Reddy et al. 2017). Further, tigers may exhibit strong negative relationships with habitat affected by human presence and activity (Hebblewhite et al. 2014; Sarkar et al. 2017), a response which may be non-linear.

Given species-habitat relationships can be influenced by both fine- and broad-scale environmental attributes (Wiens 1976; Johnson et al. 1992; Levin 1992) investigations into habitat selection should be conducted at multiple, ecologically-relevant spatial scales (Wiens 1989; Goodwin and Fahrig 1998; McGarigal et al. 2016). The assumption is that, by incorporating variables at optimal scales, this may produce more robust and ecologically informative models. The degree to which similar improvements can be achieved by accounting for optimal functional form and non-linearity in a species' response to its environment (Austin et al. 1990) has largely been untested.

Given these considerations, the development of tiger habitat selection models in ***Chapter 3*** provided the opportunity not only to evaluate key factors and predictions in tiger habitat selection in DPKY, but also to assess (1) the degree of scale-dependency in tiger-habitat relationships, and (2) the degree to which optimization for spatial-scale and functional form improves model performance over non-optimized models. Therefore, in ***Chapter 3***, concurrent to assessments of tiger habitat selection, I provided the first formal assessment of the relative impacts of both spatial scale-optimization and functional shape-optimization on habitat suitability model performance and predictions. Four model approaches were developed: (1) single-scale optimized models (SSO); (2) a multi-scale optimized model (MSO); (3) single-scale shape-optimized models (SSSO) and (4) a multi-scale- and shape-optimized model (MSSO).

Evaluation of model performance and the efficacy of each approach revealed four results of particular note. First, results suggested that tiger occurrence probability is highly scale dependent with strong differences in the univariate strength of relationship between most variables across scale. Second, a majority of variables were most strongly associated with tiger occurrence at the broadest spatial scales. Third, the multi-scale optimized and the best single-scale optimized model (16km SSO/SSSO) performed exceptionally and equivalently well, suggesting that a single-scale model may sometimes perform as well as a multi-scale optimized model (though requiring explicit assessment). Fourth, despite the hypothesis that optimization of functional form (shape) would improve model performance, this was not the case in our study. However, it did allow for the expression of potentially important and nuanced relationships between tigers and covariates not apparent in models assuming linear forms. Importantly, this study clearly reinforced findings in previous studies (McGarigal and Cushman 2002; McGarigal et al. 2016) which highlight the importance of accounting for scale when modelling habitat selection and other ecological relationships, particularly for wide-ranging species such as tigers.

2.3 Using simulations in population density estimation

In the early stages of development for the population density survey design for tigers in DPKY (***Chapter 5***), a number of potential challenges became evident. Spatially-explicit capture-recapture (SECR) surveys on large carnivores like tigers are inherently challenging, given the requirement of detecting a rare and elusive species, often ranging over large areas of remote and difficult terrain (Karanth and Nichols 2010). Second, reliable estimates of population density under this framework require meeting the assumption of population closure, among others, necessitating a sufficient sample of detections in a short period of time (White et al. 1982; Karanth and Nichols 1998). Consequently, decisions on the spatial arrangement of camera-traps to generate data for population density estimates can significantly influence the reliability of survey results (Royle et al. 2014). Previous evidence suggested that the tiger population in DPKY was of relatively low density (DNP et al. 2014, *unpublished*), introducing the risk that a corresponding low number of detections could lead to a broad range of error, undermining its use in population monitoring. It was clear that great care was required in developing such a study. The prospect of simulations, which could enable insights into likely results emerging from different spatial arrangements of camera traps (Obbard et al. 2010; Tobler and Powell 2013), emerged as a potentially effective method in addressing these challenges.

In ***Chapter 5***, I used simulations to assess the suitability of different trap arrays and survey lengths to develop a robust study design and, in turn, generate a reliable density estimate for this population. This provided an opportunity to assess the utility of simulations in evaluating survey design. A clustered, field-based trap configuration (based on previous tiger and prey detections and landscape features) was compared with the simulated performance of a regular camera trapping array, over 45-day and 60-day sampling occasions. Simulation results (i.e., number of individuals, detections, relative standard error, and relative bias) suggested that this non-regular trapping array, deployed for 60 sampling days, would generate reliable density estimates. Following survey deployment, simulations closely reflected actual results under the null model and the selected survey design performed well, generating a sufficient number of detections and individuals to estimate density within a reasonable range of error. This study produced two key methodological findings. First, results suggested that such comparative simulations could be particularly beneficial for areas with low species density where the need for a sufficient number of detections for a robust estimate is particularly challenging. Second, the study demonstrated the utility and ease of implementation of non-uniform trapping arrays, particularly those informed by previous data. This suggests SECR surveys to generate tiger density and population estimates may be reasonably flexible in their design and implementation, which may also be useful in low density populations.

2.4 Sensitivity of population connectivity and viability models

In both ***Chapter 6*** and ***Chapter 7***, I sought to identify potential population growth and range expansion scenarios for tigers along with key factors relevant to their long-term management. These chapters addressed two related, but distinct drivers of long-term population dynamics. The former evaluated large-scale landscape connectivity, largely under current conditions, and the latter investigated the potential effects of landscape change scenarios on the probability of persistence of this source population. Both of these spatially-explicit assessments required inputs defining the form and strength of the relationship between tigers and landscape features, movement ability, spatial patterns of mortality risk, and potential population density. Notably, model predictions may be particularly sensitive to how these factors are parameterized and their interactions could drastically affect results (Dunning Jr et al. 1995; McCarthy et al. 1995).

While ***Chapter 3*** provided locally-suitable habitat selection predictions, such predictions for habitat types not present in DPKY in areas such as Cambodia or Lao PDR were uncertain, as was the degree of potential mortality risk. Further, resistance surfaces, which define step-wise cost to movement in a landscape, and species movement parameters, are ideally developed via empirical data (Cushman 2006; Vasudev et al. 2017). Such data can be rare, especially for understudied or endangered species (Zeller et al. 2012). While this thesis addressed a number of knowledge gaps for tigers in this landscape, these landscape studies did not have access to reliable empirical data on these factors, particularly across a large study area. Nonetheless, the importance of this population requires proactive assessments of potential population dynamics, particularly in relation to landscape connectivity and landscape change, to understand key factors likely to affect the population's trajectory. In these circumstances, such as for our study population, it is advisable and advantageous to test a range of realistic parameters to account for uncertainty and to discern potential sensitivity of results to factors and their interactions.

In ***Chapter 6*** and ***Chapter 7***, I incorporated sensitivity analysis in which I evaluated the sensitivity of model predictions on population connectivity (CH6), distribution (CH6), abundance (CH6/CH7), and likelihood of persistence (CH7) to variations in key factors. These included variations of resistance surface, population density, and mortality in both chapters, dispersal ability in ***Chapter 6***, and landscape change scenarios in ***Chapter 7***. In ***Chapter 6***, I employed a temporally dynamic cumulative resistance kernel approach via UNICOR (Landguth et al. 2012) to assess landscape connectivity across parameter combinations. In ***Chapter 7***, simulations were conducted using CDPOP (Landguth and Cushman 2010), an individual-based, spatially-explicit framework to model mating, dispersal, and mortality through space and time.

Both chapters provided valuable insight for the development of spatially-explicit population connectivity and viability models. First, and perhaps most importantly, models were highly sensitive to spatially-differential mortality risk which dominated predictions. Incorporation of mortality risk resulted in dramatically lower predicted connectivity and population, often to a highly significant degree and often resulting in simulated population extinction. In ***Chapter 7***, marginal adjustments in the form of mortality risk led to dramatic differences in predicted extinction rates. These studies demonstrate that the application of mortality risk, often unaccounted for, can produce strong and highly divergent conclusions on the degree of landscape connectivity and population trajectory. Second, in both studies, when mortality risk and ability to move through the landscape were both high (due to high dispersal ability [CH6] or low resistance to movement [CH7]), these factors interacted to result in elevated mortality and declining populations. For highly vagile organisms, reduced ability to navigate through the landscape when mortality risk is high may produce more viable and larger populations than when movement ability is unconstrained. Third, in both studies, the effect of resistance transformation independently was low relative to other factors, which may suggest optimization of resistance surfaces may be less important than other factors, such as mortality or dispersal ability. Fourth, in ***Chapter 6***, the relative importance of factors differed depending on whether the assessment was based on divergence among scenarios or displacement of scenarios from initial conditions. Further, the relative effects of different factors varied depending on timestep. This suggests that temporally-explicit analysis may be important for these kinds of assessments and could help discern nuanced differences in the relative effect of factors over time. Fifth, the relative effect of varying population density differed somewhat between studies with intermediate effects on connectivity predictions in ***Chapter 6*** and limited effect in ***Chapter 7***. It is possible this factor may have more of an effect in connectivity simulations over large areas compared to simulations on population persistence where evaluations are across a smaller, more constrained block of habitat. Lastly, in both studies, wildlife crossing structures had little effect on predictions of landscape connectivity or population persistence. This may be attributed to both the small-scale nature of these simulated changes relative to the size of the landscape and the overwhelming effect of other factors such as mortality, which was not measurably reduced by these structures. Overall, in the absence of empirical data to parameterize models more reliably, the approach of evaluating model sensitivity in these studies was particularly beneficial and produced insightful conclusions on the differential effects of various factors and their interactions.

2.5 Contribution to other studies

The work underpinning this thesis also partially contributed to additional peer-reviewed studies including a range-wide, scale-optimized assessment on habitat-selection of mainland clouded leopards

(*Neofelis nebulosa*; Macdonald et al. 2019) and a regional assessment on biodiversity (Macdonald et al. 2020). Contributions to these studies included the processing and provision of species presence data and assisting in the writing of resulting publications. These studies are included in the Appendix of this thesis.

3. General Limitations and Future Research Directions

It is worth emphasizing that, although this thesis aimed to comprehensively assess the status and ecology of tigers in DPKY, as well as the key factors affecting their conservation, it is not intended to provide answers to all questions related to tiger ecology and conservation in the DPKY complex. In addition to providing key insight into this population, this thesis may also act as a springboard upon which further academic inquiries can be launched. This is especially important given that, in any scientific pursuit, the state of knowledge is constantly changing and, for a vulnerable species in a dynamic landscape, this is particularly apt.

A significant portion of this thesis is based primarily on an extensive dataset generated from targeted, non-systematic camera-trap surveys (***Chapter 2***) to assess fundamental questions on tiger presence rather than to generate data with a specific analytical framework in mind. This inherently introduced limitations in the types of analyses that could be implemented. For example, there was considerable interest in applying an occupancy framework to the dataset. However, the strict assumptions of the method, particularly those pertaining to independence and population closure necessary for calculating reliable estimates of detection probability, precluded application of this framework to such spatially- and temporally-variable data (Welsh et al. 2013). In contrast, the study outlined in ***Chapter 5*** was specifically designed for the analytical methods used. Ideally, studies should be designed in order to address specific research questions *a priori*, with particular care given to generation of data and application of analytical methods that can effectively answer those questions. Concurrently, the intuitiveness, flexibility, and wide-spread use of generalized linear models (McGarigal et al. 2016), such as within an optimized framework, was well-suited to understanding broad patterns of associations with environment, prey, and human factors. Occupancy modelling in particular has been used for assessing tigers and prey species in Western Thailand (Duangchatrasiri et al. 2019). Additional, dedicated occupancy studies in DPKY could be useful for establishing baseline metrics for evaluation over time and comparison with estimates elsewhere in the country.

Evidence from other studies suggest a strong relationship between tiger densities and prey abundance, which are likely to influence population persistence and range expansion (Karanth and Stith 1999; Karanth et al. 2004). This thesis provided broad assessments on the presence of prey (***Chapter 2***) and the degree to which prey may explain patterns of tiger presence (***Chapter 4***). However, these assessments should be distinguished from prey selection, which require specific studies on diet analysis (Karanth and Nichols 1998; Andheria et al. 2007). Effective management of tigers in DPKY could be bolstered by targeted studies on prey species, particularly in validating species of notable importance, estimating prey abundance or occupancy (Karanth et al. 2004; Duangchatrasiri et al. 2019), and discerning patterns of prey habitat selection (Hebblewhite et al. 2014).

In ***Chapter 6*** and ***Chapter 7***, wildlife crossing structures along highways did not measurably affect predictions of tiger population connectivity or persistence. Overall, there has been a paucity of studies formally investigating the effect of highway crossing structures on tiger population connectivity. However, studies on other wide-ranging carnivores have documented the use of such structures, which could facilitate movement at a landscape scale (Gloyne and Clevenger 2001; Ford et al. 2017; González-Gallina et al. 2018). It will be important to conduct further, dedicated research at finer scales to determine the local effect of existing structures on tigers and other wildlife in the area (Paansri et al. 2021). Such research can determine if tigers are using these structures and if they are likely to facilitate recolonization of tigers in Khao Yai National Park.

Lastly, there are two notable long-term factors that could affect tiger persistence in DPKY that I did not address in this thesis. First, I did not simulate the long-term genetic trajectories of this population. Given the small population size and vulnerability of tigers in DPKY (***Chapter 7***), this too will likely be a factor in population persistence, which can be severely undermined by inbreeding depression (van Noordwijk 1994; Vasudev et al. 2017). Future directions for related research could include investigating the potential genetic effect of translocations of tigers into DPKY, notably, to determine what measures, if any, could mitigate the genetic risks associated with this population. Second, I did not conduct investigations into the potentially strong and pervasive effects of climate change, which may also threaten population persistence across landscapes (Rudnick et al. 2012; Wasserman et al. 2012; Dar et al. 2021). Given the specific objectives and methodological assessments conducted in this thesis, adding additional complicating factors – particularly one as complicated as climate change – would render these studies exceedingly complex and undermine their clarity. However, understanding the potential effects of climate change on tigers in DPKY and elsewhere in their range will be critically important to developing adaptation strategies. Utilizing some of the approaches used and advanced in this thesis, such as scale- and functional shape-optimization, could provide a sound foundation for such assessments.

4. Management Recommendations

While this thesis primarily serves an academic purpose, given the lack of previous information on tigers in the DPKY landscape, this collection of studies is well-suited and well-timed to aid in the development of management and conservation strategies. While these works do not address all aspects of management, a number of key findings have emerged that necessitate careful consideration.

4.1 Mitigation of threats

First and foremost, based on findings throughout this thesis, I strongly recommend investment in measures for detecting and mitigating sources of elevated mortality, disturbance, and poaching of prey, particularly in core areas. This will be crucial for providing a foundation for long-term recovery of tigers in this landscape. Simulations of population trajectories in ***Chapter 7*** suggest that this population may be extremely vulnerable, situated on a proverbial knife's edge. Predictions of population trajectory and persistence in this study were highly sensitive, particularly to mortality risk and certain development scenarios. Importantly, marginal shifts in mortality, particularly combined with landscape change, drastically shifted predictions. These results are supported by strong, negative associations with human settlements, public roads, and poachers reported in ***Chapter 4***. Evidence from these studies, consistent with others on tigers (Kenney et al. 1995; Linkie et al. 2006; Chapron et al. 2008), reinforces the point that preventing mortality, whether from poaching, development in tiger habitat, or other factors, is likely the most critical measure to be considered in developing management and conservation strategies. The increased use of snaring as a poaching tool is a particular cause for concern, given its role in the extirpation of tigers from elsewhere in Southeast Asia (Johnson et al. 2016; Gray et al. 2017b; Rasphone et al. 2019). In particular, the core high-quality habitat predicted in ***Chapter 3*** should be designated as a zone of critical protection priority within which greater investments in protection and monitoring should be made.

In addition, given the small size of this population and its inherent vulnerability, concerted efforts must be made to detect and prevent potential disease outbreaks. In camera-trap surveys described in ***Chapter 2***, spatial overlap of humans and domestic animals with tigers and prey species was common. Domestic dogs were commonly detected along park boundaries and, in some cases, deep within protected areas. Notably, canine distemper virus (CDV) has emerged as a disease of particular concern for tigers and other big cats (Roelke-Parker et al. 1996; Goodrich et al. 2011; Terio and Craft 2013; Gilbert et al. 2014). Transmission of CDV and other diseases to tigers could be catastrophic for DPKY, particularly given its current state as a single contiguous population. Diseases with the potential to affect tiger prey species (Guberti et al. 2019) should also be closely monitored.

Results from ***Chapter 4*** and ***Chapter 7***, which documented strong negative associations with human presence and infrastructure, reinforce recommendations in Thailand's national tiger action plan (Pisdamkam et al. 2010) and IUCN World Heritage Outlook (2020) against the development of infrastructure in tiger habitat (Pisdamkam et al. 2010). Infrastructure development, specifically expansion and intensification of roads and dam construction, were associated with profoundly negative effects on predicted tiger population persistence and was notably synergistic with elevated mortality. Predicted negative effects of dams in ***Chapter 7*** merits targeted research on the potential effects of dams on tigers and other terrestrial mammals. Further, efforts to mitigate the effects of infrastructure, such as wildlife crossing structures along roads should be planned carefully, given that use of these structures may vary due to complex factors and by species (Clevenger and Waltho 2000; Caldwell and Klip 2020). Specific research on the use and effect of current structures on tigers is also recommended.

Like many other tiger populations across Asia, DPKY's tiger population may be smaller than recommended for long-term viability (Wikramanayake et al. 2011; Kenney et al. 2014). For DPKY, active population management measures, such as translocations, may be an option to prevent or mitigate the effects of inbreeding depression (Kenney et al. 2014). Additional research investigating the potential effect of such measures and its viability as a management strategy may be warranted.

4.2 Population monitoring

Given the vulnerability of this population and the necessity of detecting sources of mortality outlined in the previous section, efforts to conserve and effectively manage this population should be underpinned by high-standard and regular monitoring of the tiger population, prey, and threats. Tigers are a conservation-dependent species (Sanderson et al. 2010) and require active management and monitoring in order to ensure population persistence. This is particularly relevant for this small and vulnerable population (***Chapter 6***). Work in this thesis has generated a reliable estimate of population density (***Chapter 5***) which can be used as a baseline for evaluating tiger population trends over time. Importantly, these evaluations could be useful in evaluating the overall efficacy of management interventions.

Tigers may be vulnerable to extirpation even in seemingly well-secured protected areas. This was underscored dramatically by the extirpation of tigers in two high-profile tiger reserves in India - Sariska Tiger Reserve in 2004 and Panna Tiger Reserve in 2009 (Narain et al. 2005; Gopal et al. 2010; Wright 2010). The efficiency with which poachers targeted and removed tigers from these protected areas, the inaccuracy of population estimates, and the delay in management's detection and response to the threat, are often cited as an important case study for tigers (Wright 2010; Karanth 2011; Kopnina 2015). This demonstrates the degree to which threats to tigers can emerge undetected, highlighting the need for vigilance and regular assessments of tiger populations and threats. Indeed, the silent extirpation of tigers from much of their former range, particularly Southeast Asia, provides a stark reminder of the need for proactive, science-driven management for remaining populations. DPKY's recently established Dong Phayayen-Khao Yai Wildlife Research Station could serve as an effective foundation for these efforts, especially for providing a centralized, landscape-wide monitoring location and acting as a local training centre for methods of wildlife research.

4.3 Protection of habitat

I recommend prioritization of core habitat in central DPKY as an area of critical conservation priority for tigers and their prey as well as investigation of measures to facilitate unconstrained movement to other available habitat. Specifically, results from habitat-selection modelling in this thesis (***Chapter 3***) indicated that central DPKY, notably areas of closed forest cover containing bamboo forest patches within a 16km window, is most appropriate for increased investments in protection and monitoring. Such efforts will likely be critical to the long-term recovery of this population. Predictions from habitat-selection modelling reinforce the importance of accounting for spatial scale not only in the development of models, but also in the development of tiger population management and recovery strategies. This may be particularly helpful considering the strong patterns of scale-dependence of tigers in this landscape and the importance of broad-scale habitat patterns. These models reinforced the importance of protecting surrounding broad-scale (8 to 16km) forest within these protected areas and ensuring low human impact as part of a landscape-scale management strategy. Future habitat modelling studies in the landscape should incorporate a robust, ecologically-relevant scale-optimization framework and consider the inclusion, and evaluation of, functional shape-optimization in model development.

4.4 Protection and monitoring of prey

Given the importance of prey in the presence and persistence of tigers (Karanth and Stith 1999; Karanth et al. 2004), I strongly recommended that specific, targeted efforts be dedicated to the research, monitoring, and recovery of prey populations in DPKY. Results from habitat-selection modelling in ***Chapter 3***, and evaluations in ***Chapter 4***, imply that key habitat for tigers in this landscape is associated with habitat potentially beneficial for key prey species, reinforcing the importance of protecting core, high-quality habitat predicted by these models. In particular, results suggest that wild boar may be a prey species of particular importance for tigers and that protection efforts should prioritize habitat supporting high prey richness.

Active management of habitat to bolster prey abundance could be a means by which tiger density could be increased (Karanth et al. 2004), though scientifically-rigorous methods of assessment should underpin any exploration of this kind of intervention.

5. Conclusion

Three guiding problem statements formed the foundation of this thesis. First, the status, ecology, and conservation importance of the tiger population in the Dong Phayayen-Khao Yai Forest Complex (DPKY), up until this point, had been unclear. Second, for tigers and other species, such a lack of clarity could undermine management effectiveness. Third, while efforts to generate necessary information on this population have been extensive, data generated from these efforts have largely been under-utilized and unavailable to the greater scientific community.

I believe this thesis, in answering my research questions, effectively addresses each of these problem statements. In essence, this thesis explored the past, present, and potential future of tigers in DPKY. Utilizing data from expansive camera-trap surveys, I discerned key patterns in the presence of tigers in the landscape and interpreted these patterns to firmly establish its conservation importance. Further, models generated from these data were used to identify key environmental, prey, and anthropogenic factors explaining the heterogeneity of tiger distribution in the complex. This thesis also generated a population density estimate of tigers in the complex, representing a key metric for future assessment of population trends. Next, the potential role of this population in regional conservation planning was explored via an investigation into the extent of population connectivity with potential habitat in former tiger range countries. This thesis also used spatially-explicit modelling to investigate the potential long-term viability of this population and ascertain the key factors likely to influence its trajectory into the future. This represents a substantial contribution to the body of knowledge regarding tigers in this landscape while concurrently exploring important methodological questions relevant to ecological research on other species.

Notably, these works addressed a number of goals, objectives, and strategies outlined in Thailand's national tiger action plan (2010-2022). Specifically, the plan calls for increased understanding of tiger ecology in priority landscapes in order to guide management. This includes monitoring of tigers in priority landscapes, research on long-term tiger and ecology, and generation of information for strategic planning.

The Indochinese tiger is one of the least understood extant subspecies of tiger (Lynam and Nowell 2011; Goodrich et al. 2015). Comprehensive investigations of this subspecies in Southeast Asia are urgently needed to generate a more accurate picture of their status. This thesis provided additional clarity on the status and regional importance of tigers in DPKY relevant for future assessments of tigers in Southeast Asia (e.g., Lynam and Nowell, 2011). Given the likely extirpation of tigers from Cambodia, Lao PDR, Southern China, Vietnam, and other parts of Thailand (Lynam and Nowell 2011; DNP 2016; Gray et al. 2017a; Rasphone et al. 2019), DPKY represents one of the most important populations remaining in the region.

While this thesis provided much needed clarity on tigers in DPKY, the future of tigers in this landscape and in remaining populations in Southeast Asia remains uncertain. This thesis provides a degree of optimism. Previously understudied and relatively unknown, surveys revealed a population larger than previously thought, recorded long-term persistence of individuals, and documented multiple instances of successful breeding and cub-rearing which could underpin population recovery. However, results from this work also reinforce the high degree of vulnerability of this population. DPKY remains entrenched in a human-dominated, ever-changing landscape in a rapidly developing region. It is likely this population is at a conservation crossroads. Concerted efforts are required in order to ensure this population persists into the future. It is my hope that this thesis, rather than serving as a tiger population's epitaph, can instead help serve as a road-map for successful conservation.

References

Andheria AP, Karanth KU, Kumar NS (2007) Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. J Zool 273:169–175. https://doi.org/10.1111/j.1469-7998.2007.00310.x

Austin MP, Nicholls AO, Margules CR (1990) Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. Ecol Monogr 60:161–177. https://doi.org/doi:10.2307/1943043

Barber-Meyer SM, Jnawali SR, Karki JB, et al (2013) Influence of prey depletion and human disturbance on tiger occupancy in Nepal. J Zool 289:10–18. https://doi.org/10.1111/j.1469-7998.2012.00956.x

Benítez-López A, Santini L, Schipper AM, et al (2019) Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. PLoS Biol 17:e3000247–e3000247. https://doi.org/10.1371/journal.pbio.3000247

Caldwell MR, Klip JMK (2020) Wildlife Interactions within Highway Underpasses. J Wildl Manage 84:227–236. https://doi.org/10.1002/jwmg.21801

Carter NH, Shrestha BK, Karki JB, et al (2012) Coexistence between wildlife and humans at fine spatial scales. Proc Natl Acad Sci 109:15360–15365. https://doi.org/10.1073/pnas.1210490109

Chapron G, Miquelle DG, Lambert A, et al (2008) The impact on tigers of poaching versus prey depletion. J Appl Ecol 45:1667–1674. https://doi.org/10.1111/j.1365-2664.2008.01538.x

Clevenger AP, Waltho N (2000) Factors Influencing the Effectiveness of Wildlife Underpasses in Banff National Park, Alberta, Canada. Conserv Biol 14:47–56. https://doi.org/10.1046/j.1523-1739.2000.00099-085.x

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biol Conserv 128:231–240. https://doi.org/10.1016/j.biocon.2005.09.031

Dar SA, Singh SK, Wan HY, et al (2021) Projected climate change threatens Himalayan brown bear habitat more than human land use. Anim Conserv. https://doi.org/10.1111/acv.12671

DNP (2016) Practical Plan to Improve Tiger Population 2015-2035 (20 Years). Department of National Parks, Wildlife and Plant Conservation (DNP), Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

Duangchantrasiri S, Umponjan M, Simcharoen S, et al (2016) Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. Conserv Biol 30:639–648. https://doi.org/10.1111/cobi.12655

Duangchatrasiri S, Jornburom P, Jinamoy S, et al (2019) Impact of prey occupancy and other ecological and anthropogenic factors on tiger distribution in Thailand’s western forest complex. Ecol Evol 9:2449–2458. https://doi.org/10.1002/ece3.4845

Dunning Jr JB, Stewart DJ, Danielson BJ, et al (1995) Spatially explicit population models: current forms and future uses. Ecol Appl 5:3–11. https://doi.org/10.2307/1942045

Ford AT, Barrueto M, Clevenger AP (2017) Road mitigation is a demographic filter for grizzly bears. Wildl Soc Bull 41:712–719. https://doi.org/10.1002/wsb.828

Gilbert M, Miquelle DG, Goodrich JM, et al (2014) Estimating the Potential Impact of Canine Distemper Virus on the Amur Tiger Population (Panthera tigris altaica) in Russia. PLoS One 9:e110811. https://doi.org/10.1371/journal.pone.0110811

Gloyne CC, Clevenger AP (2001) Cougar Puma concolor use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. Wildlife Biol 7:117–124. https://doi.org/10.2981/wlb.2001.009

González-Gallina A, Hidalgo-Mihart MG, Castelazo-Calva V (2018) Conservation implications for jaguars and other neotropical mammals using highway underpasses. PLoS One 13:e0206614. https://doi.org/10.1371/journal.pone.0206614

Goodrich JM, Lynam A, Miquelle DG, et al (2015) Panthera tigris. IUCN Red List Threat. Species 2015 e.T15955A50659951

Goodrich JM, Seryodkin I V, Miquelle DG, et al (2011) Effects of canine breakage on tiger survival, reproduction and human-tiger conflict. J Zool 285:93–98. https://doi.org/10.1111/j.1469-7998.2011.00819.x

Goodwin BJ, Fahrig L (1998) Spatial scaling and animal population dynamics. In: Peterson DL, Parker VT (eds) Ecological Scale: Theory and Applications. Columbia University Press, New York, pp 193–206

Gopal R, Qureshi Q, Bhardwaj M, et al (2010) Evaluating the status of the endangered tiger Panthera tigris and its prey in Panna Tiger Reserve, Madhya Pradesh, India. Oryx 44:383–389

Gray TNE, Crouthers R, Ramesh K, et al (2017a) A framework for assessing readiness for tiger Panthera tigris reintroduction: a case study from eastern Cambodia. Biodivers Conserv 26:2383–2399. https://doi.org/10.1007/s10531-017-1365-1

Gray TNE, Lynam AJ, Seng T, et al (2017b) Wildlife-snaring crisis in Asian forests. Science 355:255–256. https://doi.org/10.1126/science.aal4463

Guberti V, Khomenko S, Masiulis M, Kerba S (2019) African Swine Fever in Wild Boar Ecology and Biosecurity. FAO Animal Production and Health Manual No. 22, FAO, OIE and EC, Rome

Harihar A, Chanchani P, Borah J, et al (2018) Recovery planning towards doubling wild tiger Panthera tigris numbers: Detailing 18 recovery sites from across the range. PLoS One 13:e0207114. https://doi.org/10.1371/journal.pone.0207114

Harihar A, Pandav B (2012) Influence of connectivity, wild prey and disturbance on occupancy of tigers in the human-dominated western Terai Arc landscape. PLoS One 7:e40105. https://doi.org/10.1371/journal.pone.0040105

Harihar A, Prasad DL, Ri C, et al (2007) Status of tiger and its prey species in Rajaji National Park. In: Harihar A, Kurien AJ, Pandev B, Goyal S. (eds) Response of tiger population to habitat, wild ungulate prey and human disturbance in Rajaji National Park, Uttarakhand. Wildlife Institute of India, Dehradun, pp 87–110

Hebblewhite M, Miquelle DG, Robinson H, et al (2014) Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. Biol Conserv 178:50–64. https://doi.org/10.1016/j.biocon.2014.07.013

Hebblewhite M, Zimmermann F, Li Z, et al (2012) Is there a future for Amur tigers in a restored tiger conservation landscape in Northeast China? Anim Conserv 15:579–592. https://doi.org/10.1111/j.1469-1795.2012.00552.x

IUCN World Heritage Outlook (2020) Dong Phayayen-Khao Yai Forest Complex: 2020 Conservation Outlook Assessment. IUCN World Heritage Programme & IUCN World Commission on Protected Areas (WCPA), Gland

Jenks K, Chanteap P, Damrongchainarony K, et al (2011) Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses - an example from Khao Yai National Park, Thailand. Trop Conserv Sci 4:113–131. https://doi.org/10.1177/194008291100400203

Johnson A, Goodrich J, Hansel T, et al (2016) To protect or neglect? Design, monitoring, and evaluation of a law enforcement strategy to recover small populations of wild tigers and their prey. Biol Conserv 202:99–109. https://doi.org/10.1016/j.biocon.2016.08.018

Johnson AR, Wiens JA, Milne BT, Crist TO (1992) Animal Movements and Population-Dynamics in Heterogeneous Landscapes. Landsc Ecol 7:63–75. https://doi.org/10.1007/bf02573958

Kanagaraj R, Wiegand T, Kramer-Schadt S, et al (2011) Assessing habitat suitability for tiger in the fragmented Terai Arc Landscape of India and Nepal. Ecography (Cop) 34:970–981. https://doi.org/10.1111/j.1600-0587.2010.06482.x

Karanth K., Nichols JD (2010) Non-invasive Survey Methods for Assessing Tiger Populations. In: Tilson R, Nyhus PJ (eds) Tigers of the World, Second Edition. Elsevier Inc., New York, pp 241–261

Karanth KU (2011) India's tiger counts: the long march to reliable science. Econ Polit Wkly 46:22–25

Karanth KU, Gopalaswamy AM, Kumar NS, et al (2011) Monitoring carnivore populations at the landscape scale: Occupancy modelling of tigers from sign surveys. J Appl Ecol 48:1048–1056. https://doi.org/10.1111/j.1365-2664.2011.02002.x

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862. https://doi.org/10.2307/176521

Karanth KU, Nichols JD, Harihar A, et al (2017) Field practices: Assessing tiger population dynamics using photographic captures. In: Karanth KU, Nichols JD (eds) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore, pp 191–224

Karanth KU, Nichols JD, Kumar NS, et al (2004) Tigers and their prey: Predicting carnivore densities from prey abundance. Proc Natl Acad Sci U S A 101:4854–4858. https://doi.org/10.1073/pnas.0306210101

Karanth KU, Stith BM (1999) Prey depletion as a critical determinant of tiger population viability. In: Seidensticker J, Jackson P, Christie S (eds) Riding the Tiger: Tiger Conservation in Human-Dominated Landscapes. Cambridge University Press, Cambridge, pp 100–113

Kenney J, Allendorf FW, McDougal C, Smith JLD (2014) How much gene flow is needed to avoid inbreeding depression in wild tiger populations? Proc R Soc B Biol Sci 281:20133337–20133337. https://doi.org/10.1098/rspb.2013.3337

Kenney JS, Smith JLD, Starfield AM, McDougal CW (1995) The Long-Term Effects of Tiger Poaching on Population Viability. Conserv Biol 9:1127–1133. https://doi.org/10.1046/j.1523-1739.1995.9051116.x-i1

Kerley LI, Goodrich JM, Miquelle DG, et al (2002) Effects of Roads and Human Disturbance on Amur Tigers. Conserv Biol 16:97–108. https://doi.org/10.1046/j.1523-1739.2002.99290.x

Kopnina H (2015) Of Tigers and Humans: The Question of Democratic Deliberation and Biodiversity Conservation. In: Wuerthner G, Crist E, Butler T (eds) Protecting the Wild: Parks and Wilderness, the Foundation for Conservation. Island Press/Center for Resource Economics, Washington, DC, pp 63–71

Krishnamurthy R, Cushman SA, Sarkar MS, et al (2016) Multi-scale prediction of landscape resistance for tiger dispersal in central India. Landsc Ecol 31:1355–1368. https://doi.org/10.1007/s10980-016-0363-0

Landguth EL, Hand BK, Glassy J, et al (2012) UNICOR: a species connectivity and corridor network simulator. Ecography (Cop) 35:9–14. https://doi.org/10.1111/j.1600-0587.2011.07149.x

Landguth LE, Cushman SA (2010) cdpop: A spatially explicit cost distance population genetics program. Mol Ecol Resour 10:156–161. https://doi.org/10.1111/j.1755-0998.2009.02719.x

Levin SA (1992) The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology 73:1943–1967. https://doi.org/10.2307/1941447

Linkie M, Chapron G, Martyr DJ, et al (2006) Assessing the viability of tiger subpopulations in a fragmented landscape. J Appl Ecol 43:576–586. https://doi.org/10.1111/j.1365-2664.2006.01153.x

Lynam A (2001) Status, Ecology, and Conservation of Tigers in their Critical Habitats in Thailand, September 2001. Wildlife Conservation Society, Bangkok

Lynam A, Nowell K (2011) Panthera tigris ssp. corbetti. IUCN Red List Threat. Species 2011 e.T136853A4346984

Lynam A, Round P, Brockelman W (2006) Status of Birds and Large Mammals in Thailand’s Dong Phayayen - Khao Yai Forest Complex. Wildlife Conservation Society and Biodiversity Research Training (BRT) Programme, Bangkok

Lynam AJ (2010) Securing a future for wild Indochinese tigers: Transforming tiger vacuums into tiger source sites. Integr Zool 5:324–334. https://doi.org/10.1111/j.1749-4877.2010.00220.x

Macdonald DW, Bothwell HM, Kaszta Ż, et al (2019) Multi-scale habitat modelling identifies spatial conservation priorities for mainland clouded leopards (Neofelis nebulosa). Divers Distrib 25:1639–1654. https://doi.org/10.1111/ddi.12967

Macdonald DW, Chiaverini L, Bothwell HM, et al (2020) Predicting biodiversity richness in rapidly changing landscapes: climate, low human pressure or protection as salvation? Biodivers Conserv 29:4035–4057. https://doi.org/10.1007/s10531-020-02062-x

Manorom K (2020) Thailand’s Big Water Challenge. In: Dipl. 23 March 2020. https://thediplomat.com/2020/03/thailands-big-water-challenge/. Accessed 8 Mar 2021

Marks D (2011) Climate Change and Thailand: Impact and Response. Contemp Southeast Asia 33:229–258. https://doi.org/10.1355/cs33-2d

McCarthy MA, Burgman MA, Ferson S (1995) Sensitivity analysis for models of population viability. Biol Conserv 73:93–100. https://doi.org/10.1016/0006-3207(95)90029-2

McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12:335–345. https://doi.org/10.1890/1051-0761(2002)012[0335:CEOEAT]2.0.CO;2

McGarigal K, Wan HY, Zeller KA, et al (2016) Multi-scale habitat selection modeling: a review and outlook. Landsc Ecol 31:1161–1175. https://doi.org/10.1007/s10980-016-0374-x

Narain S, Panwar HS, Gadgil M, Singh S (2005) Joining the Dots – Tiger Task Force Report. Union Ministry of Environment and Forests (Project Tiger), Government of India, New Delhi

Ngoprasert D, Lynam AJ, Sukmasuang R, et al (2012) Occurrence of Three Felids across a Network of Protected Areas in Thailand: Prey, Intraguild, and Habitat Associations. Biotropica 44:810–817. https://doi.org/10.1111/j.1744-7429.2012.00878.x

Obbard ME, Howe EJ, Kyle CJ (2010) Empirical comparison of density estimators for large carnivores. J Appl Ecol 47:76–84.

https://doi.org/10.1111/j.1365-2664.2009.01758.x

Paansri P, Sangprom N, Suksavate W, et al (2021) Spatial Modeling of Forage Crops for Tiger Prey Species in the Area Surrounding Highway 304 in the Dong Phayayen-Khao Yai Forest Complex. Environ Nat Resour J 19:220–229. https://doi.org/10.32526/ennrj/19/2020234

Pisdamkam C, Prayurasiddhi T, Kanchanasaka B, et al (2010) Thailand Tiger Action Plan - 2010-2012. Ministry of Natural Resources and Environment, Royal Government of Thailand. Bangkok

Rasphone A, Kéry M, Kamler JF, Macdonald DW (2019) Documenting the demise of tiger and leopard, and the status of other carnivores and prey, in Lao PDR's most prized protected area: Nam Et - Phou Louey. Glob Ecol Conserv 20:e00766. https://doi.org/10.1016/j.gecco.2019.e00766

Reddy PA, Cushman SA, Srivastava A, et al (2017) Tiger abundance and gene flow in Central India are driven by disparate combinations of topography and land cover. Divers Distrib 23:863–874. https://doi.org/10.1111/ddi.12580

Roelke-Parker ME, Munson L, Packer C, et al (1996) A canine distemper virus epidemic in Serengeti lions (Panthera leo). Nature 379:441–445. https://doi.org/10.1038/379441a0

Rostro-García S, Kamler JF, Ash E, et al (2016a) Endangered leopards: Range collapse of the Indochinese leopard (Panthera pardus delacouri) in Southeast Asia. Biol Conserv 201:293–300. https://doi.org/10.1016/j.biocon.2016.07.001

Rostro-García S, Tharchen L, Abade L, et al (2016b) Scale dependence of felid predation risk: identifying predictors of livestock kills by tiger and leopard in Bhutan. Landsc Ecol 31:1277–1298. https://doi.org/10.1007/s10980-015-0335-9

Royle J, Chandler RB, Sollmann R, Gardner B (2014) Spatial Capture-Recapture. Elsevier, Oxford

Royle JA, Gopalaswamy AM, Dorazio RM, et al (2017) Concepts: Assessing Tiger Population Dynamics Using Capture–Recapture Sampling. In: Karanth KU, Nichols JD (eds) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore, pp 163–189

Rudnick DA, Ryan SJ, Beier P, et al (2012) The role of landscape connectivity in planning and implementing conservation and restoration priorities. Ecological Society of America, Washington DC

Sanderson EW, Forrest J, Loucks C, et al (2010) Setting Priorities for Tiger Conservation: 2005-2015. In: Tilson R, Nyhus PJBT-T of the W (Second E (eds) Tigers of the World, Second Edition. Elsevier, New York, pp 143–161

Sarkar MS, Krishnamurthy R, Johnson JA, et al (2017) Assessment of fine-scale resource selection and spatially explicit habitat suitability modelling for a re-introduced tiger (Panthera tigris) population in central India. PeerJ 5:e3920. https://doi.org/10.7717/peerj.3920

Smith JLD (1993) The Role of Dispersal in Structuring the Chitwan Tiger Population. Behaviour 124:165–195. https://doi.org/10.1163/156853993X00560

Stein AB, Fuller TK, Marker LL (2008) Opportunistic use of camera traps to assess habitat-specific mammal and bird diversity in northcentral Namibia. Biodivers Conserv 17:3579–3587. https://doi.org/10.1007/s10531-008-9442-0

Sunarto S, Kelly MJ, Parakkasi K, et al (2012) Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS One 7:e30859. https://doi.org/10.1371/journal.pone.0030859

Sunquist M (2010) What Is a Tiger? Ecology and Behavior. In: Tilson R, Nyhus PJ (eds) Tigers of the World, Second Edition. Elsevier, New York, pp 19–33

Terio KA, Craft ME (2013) Canine distemper virus (CDV) in another big cat: Should CDV be renamed carnivore distemper virus? MBio 4:e00702-13. https://doi.org/10.1128/mBio.00702-13

Thapa K, Wikramanayake E, Malla S, et al (2017) Tigers in the Terai: Strong evidence for meta-population dynamics contributing to tiger recovery and conservation in the Terai Arc Landscape. PLoS One 12:e0177548. https://doi.org/10.1371/journal.pone.0177548

Thatte P, Joshi A, Vaidyanathan S, et al (2018) Maintaining tiger connectivity and minimizing extinction into the next century:

Insights from landscape genetics and spatially-explicit simulations. Biol Conserv 218:181–191. https://doi.org/10.1016/j.biocon.2017.12.022

Tobler MW, Powell GVN (2013) Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. Biol Conserv 159:109–118. https://doi.org/10.1016/j.biocon.2012.12.009

Trisurat Y, Pattanavibool A, Gale GA, Reed DH (2010) Improving the viability of large-mammal populations by using habitat and landscape models to focus conservation planning. Wildl Res 37:401–212. https://doi.org/10.1071/WR09110

van Noordwijk AJ (1994) The interaction of inbreeding depression and environmental stochasticity in the risk of extinction of small populations. In: Loeschcke V, Jain SK, Tomiuk J (eds) Conservation Genetics. Birkhäuser Basel, Basel, pp 131–146

Vasudev D, Nichols JD, Ramakrishnan U, et al (2017) Assessing Landscape Connectivity for Tigers and Prey Species: Concepts and Practice. In: Karanth KU, Nichols JD (eds) Methods For Monitoring Tiger And Prey Populations. Springer Singapore, Singapore, pp 255–288

Wasserman TN, Cushman SA, Shirk AS, et al (2012) Simulating the effects of climate change on population connectivity of American marten (Martes americana) in the northern Rocky Mountains, USA. Landsc Ecol 27:211–225. https://doi.org/10.1007/s10980-011-9653-8

Welsh AH, Lindenmayer DB, Donnelly CF (2013) Fitting and Interpreting Occupancy Models. PLoS One 8:e52015. https://doi.org/10.1371/journal.pone.0052015

White GC, Anderson DR, Burnham KP, Otis DL (1982) Capture-Recapture and Removal Methods for Sampling Closed Populations. Los Alamos National Laboratory, LA 8787-NERP, Los Alamos

Wiens J (1976) Population Responses to Patchy Environments. Annu Rev Ecol Syst 7:81–120. https://doi.org/10.1146/annurev.es.07.110176.000501

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397. https://doi.org/10.2307/2389612

Wikramanayake E, Dinerstein E, Seidensticker J, et al (2011) A landscape-based conservation strategy to double the wild tiger population. Conserv Lett 4:219–227. https://doi.org/10.1111/j.1755-263X.2010.00162.x

Wongwuttiwat J, Lawanna A (2018) The digital Thailand strategy and the ASEAN community. Electron J Inf Syst Dev Ctries 84:e12024. https://doi.org/10.1002/isd2.12024

Wright B (2010) Will the Tiger Survive in India? In: Tilson R, Nyhus PJ (eds) Tigers of the World. Elsevier, New York, pp 87–100

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landsc Ecol 27:777–797. https://doi.org/10.1007/s10980-012-9737-0

Appendix

Contribution to Other Publications

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BIODIVERSITY RESEARCH

Diversity and Distributions WILEY

Multi-scale habitat modelling identifies spatial conservation priorities for mainland clouded leopards (*Neofelis nebulosa*)

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Abstract

Aim: Deforestation is rapidly altering Southeast Asian landscapes, resulting in some of the highest rates of habitat loss worldwide. Among the many species facing declines in this region, clouded leopards rank notably for their ambassadorial potential

David W. Macdonald and Helen M. Bothwell are Joint first authors.

Diversity and Distributions. 2019;25:1639–1654. wileyonlinelibrary.com/journal/ddi | 1639

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ORIGINAL PAPER

Predicting biodiversity richness in rapidly changing landscapes: climate, low human pressure or protection as salvation?

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Abstract

Rates of biodiversity loss in Southeast Asia are among the highest in the world, and the Indo-Burma and South-Central China Biodiversity Hotspots rank among the world's most threatened. Developing robust multi-species conservation models is critical for stemming biodiversity loss both here and globally. We used a large and geographically extensive remote-camera survey and multi-scale, multivariate optimization species distribution modelling to investigate the factors driving biodiversity across these two adjoining biodiversity hotspots. Four major findings emerged from the work. (i) We identified clear spatial patterns of species richness, with two main biodiverse centres in the Thai-Malay Peninsula and in the mountainous region of Southwest China. (ii) Carnivores in particular, and large ungulates to a lesser degree, were the strongest indicators of species richness. (iii) Climate had the largest effect on biodiversity, followed by protected status and human footprint. (iv) Gap analysis between the biodiversity model and the current system of protected areas revealed that the majority of areas supporting the highest predicted biodiversity are not protected. Our results highlighted several key locations that should be prioritized for expanding the protected area network to maximize conservation effectiveness. We demonstrated the importance of switching from single-species to multi-species approaches to highlight areas of high priority for biodiversity conservation. In addition, since these areas mostly occur over multiple countries, we also advocate for a paradigmatic focus on transboundary conservation planning.

Keywords Biodiversity hotspots · Community assembly · Multi-scale · Multi-species · Southeast Asia · Species richness

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