Biodiversity and global land-use change in Bhutan: a model for the Himalayas



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Acknowledgments

As a timid boy from a small hamlet in eastern Bhutan, I could only dream of getting educated at Oxford. But this timid boy dare dreamt of coming to Oxford. There are beautiful quotes on dreams but the most relevant to me is Walt Disney's, "*All our dreams can come true if we have the courage to pursue them*". My journey to Oxford began in 2014. I applied for the globally renowned WildCRU diploma course, but my application was unsuccessful. I redeemed the following year and got accepted and thence started my long journey. It would have been a gamble for David to accept a student who had no prior experience in wildlife. Thank you, David, for taking the risk, I am sure you must be feeling proud at this juncture. The WildCRU diploma changed my life, forever. It was a whole new world for me – I made the right decision to move into conservation from timber management, perhaps a calculated risk. And here I am – presenting the outcome of an arduous but enjoyable journey that started with matriculation in Michaelmas Term of 2018.

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Abstract

The eastern Himalayas are a global biodiversity hotspot with one of the highest rates of species endemism. But a high rate of habitat degradation and loss fuelled by anthropogenic disturbance and climate change is besieging biodiversity. Understanding the interaction between biodiversity and land-use change is particularly important in the context of the eastern Himalayan landscape in the face of global climate change. However, a synthesis of combined impacts of land use and climate change on biodiversity in this landscape is surprisingly rare. This thesis aims to fulfil that gap. In Chapter 2, using multi-scale models for terrestrial mammal communities, I show that protected areas (PA) and forest cover are the two most important variables associated with habitat use of most modelled species. Further, I show that both carnivores and herbivores are equally important umbrella species. The gap analysis shows that existing PAs and areas adjacent to them are crucial for overall species richness protection. Chapter 3 uses two spatially synoptic methods (i.e., resistant kernel density and factorial least cost path) to identify core habitats and corridors for terrestrial mammal communities. I show that Asian elephant (*Elephas maximus*) was the most effective umbrella species for the overall protection of core habitats. In terms of dispersal corridor

protection, muntjac was the most effective umbrella species. Using cluster analysis, I identified six indicator species (Asian elephant, Asiatic black bear [*Ursus thibetanus*], clouded leopard [*Neofelis nebulosa*], dhole [*Cuon alpinus*], sambar deer [*Rusa unicolor*] and tiger [*Panthera tigris*]) for broad core habitat and corridor protection. Here, I show that dispersal is not just limited within PAs and the long-term viability of wildlife populations require habitats and corridors outside the existing PA network. In Chapter 4, I show that the realised functional space of the vertebrate groups (mammals and birds) is clumped around a small number of functional strategies. The loss of species at the edge of functional space is non-random and could result in the loss of irreplaceable traits impacting long-term ecological and evolutionary processes. Further, this study demonstrates the filtering effect of anthropogenic pressure and climate change on vertebrate functional and phylogenetic diversity. Chapter 5 demonstrates the complex effects of human settlement density on large carnivore interactions. I show that space-use patterns are driven by a combination of the behavioural mechanism of each species and its interactions with competing species. The duality of the effect of settlement density on species interactions suggests that the benefits of exploiting anthropogenic environments are a trade-off between ecological opportunity and the risk of conflict with humans. Taken together, this thesis highlights the importance of eastern Himalayan biodiversity and the need for integrated and synthetic research across the Himalayas to better understand the effects of anthropogenic land-use and climate change on distribution, connectivity, and behavioural ecology of terrestrial vertebrates and on the multiple facets of biodiversity *per se*.

Declaration of Authorship

I declare that this thesis is primarily my work. The conception was collaborative and individual author contributions are specified at the end of each chapter. All the analyses and writing are my own. Since each chapter was collaborative, I use the third person plural “we” to indicate the same. The work in part or full has not been submitted to meet the requirements of any degree or professional qualification.

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Table of Contents

Acknowledgments ..... *i*

Abstract ..... *vi*

Declaration of Authorship ..... *viii*

Funding ..... *viii*

Chapter 1 ..... *1*

General Introduction *1*

An overview of the thesis chapters **12**

Chapter 2 ..... *25*

Prioritizing areas for conservation outside the existing protected area network in Bhutan: the use of multi-species, multi-scale habitat suitability models *25*

1 Introduction **27**

2 Materials and Methods **31**

3 Results **44**

4 Discussion **62**

Chapter 3 ..... *82*

Landscape potential for supporting multispecies population connectivity in a Himalayan biodiversity hotspot *82*

1 Introduction **84**

2 Materials and Methods **88**

3 Results **93**

4 Discussion **106**

Chapter 4 ..... *127*

Effects of land-use and climate change on functional and phylogenetic diversity of terrestrial vertebrates in a Himalayan biodiversity hotspot *127*

1 Introduction **129**

2 Methods **132**

3 Results **138**

4 Discussion **143**

Chapter 5 ..... *161*

Contrasting effects of human settlement on the interaction among sympatric apex carnivores *161*

1 Introduction **162**

2 Materials and Methods **166**

3 Results **170**

4 Discussion **178**

Chapter 6 ..... *192*
General Discussion *192*
Main findings and contribution to the knowledge gap **193**
Relevance and implications for conservation across the Himalayas **198**
Appendices *211*
Supplementary Chapter 1 ..... **212**
Vulnerability of mammal communities to the combined impacts of anthropic land use and climate change in the Himalayan conservation landscape of Bhutan **212**
Supplementary Chapter 2 ..... **243**
Anthropogenic land-use change shapes bird diversity along the eastern Himalayan altitudinal gradient **243**
Supplementary material for Chapter 2 ..... **278**
Supplementary material for Chapter 3 ..... **312**
Supplementary material for Chapter 4 ..... **327**
Supplementary material for Chapter 5 ..... **356**
Supplementary material for Supplementary Chapter 1 ..... **373**
Supplementary material for Supplementary Chapter 2 ..... **398**
Other Publications (between 2019 and 2022) *428*
Understanding the environmental and anthropogenic correlates of tiger presence in a montane conservation landscape **429**
Multi-scale habitat modelling identifies spatial conservation priorities for mainland clouded leopards (*Neofelis nebulosa*) **430**
Habitat requirements of the Himalayan red panda (*Ailurus fulgens*) and threat analysis in Jigme Dorji National Park, Bhutan **432**
How effective are tiger conservation areas at managing their sites against the conservation assured| tiger standards (CA|TS)? **433**
Investigating Carnivore Guild Structure: Spatial and Temporal Relationships amongst Threatened Felids in Myanmar **434**
Density and occupancy of leopard cats across different forest types in Cambodia ... **435**

Chapter 1

General Introduction

The global decline of biodiversity erodes the very foundations of our economies, livelihoods, food security, health, and quality of life (Díaz et al., 2019). The current rate of global biodiversity decline will likely trigger the sixth mass extinction (Ceballos et al., 2015). It sounds a little exaggerated but if we look at the current impacts of human activities (deforestation, agricultural land expansion and wildlife poaching), the extinction may be catastrophic and imminent for many species, and the actions to reverse it are urgent. In the last 100 years, more than 400 vertebrate species have become extinct, which is between ten and a hundred times higher than the natural baseline rate (Ceballos et al., 2015). It was the taking over of the natural world and unfettered expansion of the human (*Homo sapiens*) niches that led to the prehistoric extinction of megafauna (Bartlett et al., 2016). The Malthusian growth model predicted that the exponential growth of the human population and the burgeoning demand for resources therewith will outpace supply and gradually reduce the per capita share of global resources (Hardin, 1968). The motivation to consume (or rather exploit) a resource (natural) is thought of as an individual incentive, often at the expense of every other individual but it does not exclude anyone from claiming their share (thus demand outweighs supply). This apparent self-interested act, if performed by everybody, results in harmful over-consumption of a resource (and the resource becomes unavailable for others). This has been well-argued and articulated by an evolutionary biologist, Garrett Hardin in 1968 in his paper entitled “The Tragedy of the Commons”. Although the tragedy of the commons is an economic theory, it has the utmost relevance to nature, natural resources, and the way we treat Earth, particularly relevant to the use of the common resources (Hardin, 1968). Since our ancestors developed agriculture about 11,000 years ago, the natural lands on earth continue to recede and wilderness areas disappear. We were only about a million at that time, today we are close to 8 billion and our preponderance continues to grow as we expand

our niche selfishly, we continuously pose an existential threat to biodiversity and perhaps to human civilisation (i.e., ourselves) because of the intricate relationship we share with nature.

Terrestrial biodiversity loss, throughout recorded history, has been attributed to the pervasive use and conversion of forest and natural landscape to other land use types (Maxwell et al., 2016, Johnson et al., 2017) with human activities accounting for more than 50% of the alteration (McGill et al., 2015). About 1700 species of amphibians, birds, and mammals, inclusive of species with high conservation value and functional importance that are vital to the provisioning of ecosystem services, are predicted to be under serious threat due to habitat contraction or loss (Barlow et al., 2016). Similarly, a recent study showed that 515 terrestrial vertebrate species (1.7% of the global total) are on the brink of extinction (i.e., population with fewer than 1000 remaining individuals in the wild - the size of the population of a species at which the International Union for Conservation of Nature (IUCN) considers as "critically endangered"; Ceballos et al., 2020) implying that most wildlife species are facing extensive extirpation of populations (but this figure does not include invertebrates and plant species that equally face extinction crises). A rather grim finding by the Living Planet Report shows that an average of 68% of mammals, birds, amphibians, reptiles and fish have decreased in their population between 1970 and 2016 (WWF, 2020). In the last 100 years, more than 400 vertebrate species went extinct, otherwise estimated to take up to 10000 years in the normal course of evolution (Ceballos et al., 2015). The consequences are grim; we have yet to measure the true repercussions of losing a species from an ecosystem. A disappearance of a species from an ecosystem is tantamount to the permanent loss of characteristics, from genes and interactions to phenotypes and behaviours and ultimately the services they provide in functional ecosystems (Sodhi et al., 2010, Chaplin-Kramer et al., 2019).

Agricultural land expansion and encroachment (in the form of infrastructure development such as human settlement, roads, mining and logging) into natural and wilderness areas have been the driving force of global biodiversity loss (Pereira et al., 2010, Cardinale et al., 2012, Venter et al., 2016), accelerating the extinction rates as much as 1000 times the background rate in the fossil record (Johnson et al., 2017). This increasingly threatens the overall natural ecosystem and accelerates the risk of species extinction and corresponding loss of vital ecosystem services such seed dispersal (birds and mammals), carrion removal (birds and mammals), pollination (birds and arboreal mammals) (Flynn et al., 2009a). Although agriculture is the backbone of socio-economic development, it often comes at a cost of biodiversity and ecosystem services (Kiffner et al., 2015, Newbold et al., 2015a, Usubiaga-Liaño et al., 2019). The drivers of biodiversity decline in an agricultural landscape are, for example, monoculture crops, intensive use of pesticides, and fragmentation of natural forests or protected areas (and edge habitats) due to increasing field size (Sirami et al., 2019). Human modification of natural landscapes results in altered ecological community structure (Malhi et al., 2016, Thorn et al., 2016, Cadotte and Tucker, 2017) and often leads to functional and/or phylogenetic homogenisation (Devictor et al., 2007, Ibáñez-Álamo et al., 2017). This makes an ecological community inefficient in ecosystem functioning (Clavel et al., 2011). Ironically, human wellbeing is at stake because biodiversity loss disrupts ecosystem services vital to human survival and recreation (Frishkoff et al., 2014, Mendenhall et al., 2014). Sustainable agricultural production depends on fertile soils and ecosystem services provided and regulated by biodiversity (Mupepele et al., 2021). Therefore, it is imperative to amend the way agricultural farming and infrastructure development is practised and to make it inclusive (e.g., integrating farm production and biodiversity conservation) (Bull et al., 2020).

Another overwhelmingly growing consensus is the threat humanity and global biodiversity are facing from climate emergencies (Ripple et al., 2021). The rapid alteration of global climate caused largely by anthropogenic activities (greenhouse gas emission) may further imperil terrestrial, aquatic, and aerial biodiversity (Radchuk et al., 2019b, Turvey and Crees, 2019). Akin to the threat posed by human land-use change, one in every six species are threatened by climate change (e.g., increase in temperature or erratic rainfall pattern), and about 20-30% of the species are at risk of extinction (Warren et al., 2013, Urban, 2015). At the current rate of global greenhouse gas emission and forest loss (the so-called 'business as usual' scenario), about 34% of species with moderate dispersal ability and about 42% of species with limited dispersal ability, respectively, would lose more than 50% of their range by 2080 (Warren et al., 2013). This has an immense impact on species with high endemism due to disappearing local climate and habitat because most endemic species are confined to small geographical areas and have a specialised niche (Jackson and Overpeck, 2000, Beever et al., 2016). Although some species could track climate shifts (Chen et al., 2011), others would lose most of their ranges and become constricted in a small geographical space ultimately succumbing to the vulnerability of inbreeding and depression. The synergy between land use and climate change is expected to prompt a more profoundly negative impact on biodiversity than a single driver or additive combination (Brodie, 2016, Newbold, 2018). As the human population is expected to double by the end of the century, human-induced land use and climate change will likely interact to repeat the mass extinction of wildlife of geological past (Barnosky et al., 2011, Williams et al., 2007). These impacts are amplified in geographically dynamic and geologically unstable montane landscapes like the Himalayas and, therefore, need a better understanding to discern the changes in the mechanism.

Two international conventions (the Convention on Biological Diversity [CBD] and the United Nations Framework Convention on Climate Change [UNFCCC]) have attempted to halt the dual crises of biodiversity decline and climate emergency. Global initiatives to address the extinction crisis, reverse species loss, and improve biodiversity conservation have produced ambitious visions. Of the ambitious strategies, the Aichi Biodiversity Targets 2020 aimed not only to reduce species loss and protect at least 17% of terrestrial areas but also to safeguard habitat and acknowledge ecosystem services, while also improving the management and sustainable use of natural resources (Tittensor et al., 2014a). Despite such efforts, the rate of global biodiversity loss has likely accelerated, substantially in some ecoregions, in recent decades (Tittensor et al., 2014a). Prioritisation of protected areas as climate refugia and ensuring increased connectivity between protected areas have lagged despite the global effort to expand the overall protected area network in the realisation of the Aichi Target 11 of at least 17% (Carrasco et al., 2021). And despite considerable progress to bring a substantial portion of the earth under protection (16.64% achieved thus far), some terrestrial and marine systems have already experienced local extinctions (Ceballos et al., 2020, Albano et al., 2021). Therefore, more effective and pragmatic conservation programs that optimise the protection of critical habitats to stem biodiversity loss and enhance species recovery are essential (Venter et al., 2014a).

Asia is a biodiverse continent but also has high rates of habitat loss and is a global conservation priority (Allan et al., 2019). A striking paradox is that Asia is home to many of the biodiverse regions on Earth (10 out of 35 global biodiversity hotspots) (Mittermeier et al., 2011) and more than half of the world's population and contributes to almost 40% of global carbon emissions (Zhu et al., 2021and references therein) but only around 9% of the land area

is protected (Bingham et al., 2019). The developing countries in Asia are heavily populated and have some of the highest rates of forest conversion and degradation (Sodhi et al., 2004, Miettinen et al., 2011). The biodiversity in this region is under siege from the threats of human land use and climate change (Tilman et al., 2017), though some countries (e.g., Bhutan) contribute the least to the global greenhouse gas emission or deforestation. Further, tropical Asia harbours some of the highest number of species on the brink of extinction, where the major ongoing biodiversity losses are well known (Ceballos et al., 2015, Ceballos et al., 2020). Asia has the highest number of mammals species (22) on the brink of extinction (Ceballos et al., 2020). The Indo-Malay realm experiences a high rate of deforestation and hydropower damming, as well as a strong overharvest of both terrestrial and aquatic vertebrate faunas (Allan et al., 2019, Rija et al., 2020, Tilker et al., 2019). Therefore, the Indo-Malay and Palearctic realms are at high risk of species and functional diversity loss (Toussaint et al., 2021). Additionally, the fate of Himalayan species faces significant disruptions from a combined impact of habitat loss and climate change and could perhaps serve as a global bellwether for how biodiversity may fare in an increasingly warm and degraded world.

The Himalayas are amongst the most biodiverse terrestrial ecoregions on Earth (Grenyer et al., 2006). The Eastern Himalaya is a biodiversity hotspot (Myers et al., 2000) and a critical part of Asia's water sources and glacier ice repository outside the Poles (Sharma et al., 2019). Mean temperatures in the eastern Himalayas are rising swiftly (about 0.32°C per decade), as are both the magnitude and frequency of exceptionally warm events (Krishnan et al., 2019) and the average rate of glacier/ice loss (Maurer et al., 2020). This increases the risk of flooding and landslides due to glacial lake outbursts which is an imminent threat to communities living in the downstream valley. The Eastern Himalaya has

one of the world's highest rates of species endemism but is under pressure from a high rate of habitat loss driven largely by anthropogenic disturbance, hence aptly called 'biodiversity hotspot' (Myers et al., 2000).

Bhutan lies at the intersection of two biogeographic realms: the Indo-Malayan and the Palearctic (Olson et al., 2001). Bhutan currently has over 70% of land area under forest cover and more than 50% of the total land area receives official protection, supporting a broad spectrum of species and ecosystems (DoFPS, 2011b). Much to the awe of the global leaders present at COP 21 in Paris, Bhutan committed to remaining carbon neutral. This meant that Bhutan would continue to preserve forests and cut emissions employing environment-friendly policies and practices. Bhutan has a longstanding history of revering nature. Before the advent of Vajrayana Buddhism, the erstwhile people of Bhutan (predating the eighth century) practised Bon Shamanism and worshipped natural elements (trees, lakes, rocks, mountains, and wild animals) and some rural communities continue to believe to this day. The belief beheld that every rock and brook was an abode of a deity or a spirit that blessed them with good health, fortune, and longevity. The contamination of a stream or cutting down of a tree would be tantamount to dishonouring the deity and consequently inviting upon them ailment and poverty. Further, Buddhism that supplanted Bon, values all living beings and perceives the interdependence between all things and events (the causal effect or also known as 'Karma') – one would be born as the other when this life or an event comes to an end. Such was the belief that protected Bhutan's natural environment when no environmental legislation was developed. Just as Buddhism ascribed sentience to other living beings, so did the world's most celebrated biologist, Charles Darwin and noted that "*the love for all living creatures is the most noble attribute of man*". So, we see that Western science has a similar

viewpoint as Eastern metaphysics, and certainly not far from Bhutanese ethics for compassionate conservation – that all life forms must be valued.

The leadership and success of conservation in Bhutan can be attributed to the visionary monarchs who championed environmental protection and thus enshrined it into the constitution of the Kingdom of Bhutan to preserve more than half of the land as forests. The love and reverence for nature are apparent in our national interest as we begin our National Anthem as '*Dru tsendhen kepä gäkhap na*…' which translates to 'In the Kingdom adorned with cypress trees…'. Further, under the benevolence and guidance of the Fourth King, His Majesty Jigme Singye Wangchuck, Bhutan embarked on a unique development philosophy that enshrined environment protection as one of the foundations of development and that began as early as the 1970s (known as the pillars of the Gross National Happiness) (Ura et al., 2012). Environmental sustainability, in Bhutan, is both the primary objective and the starting point for national development. The 2008 national constitution mandates to conserve and improve its pristine environment, safeguard biodiversity and further entrusts stewardship to every Bhutanese citizen (the right to utilise as well as the responsibility to protect). Thus, the protection of the environment is deemed as a fundamental duty in Bhutan.

Bhutan's under a million population (~760,000, population growth rate of 1.1%) (NSB, 2020) is largely agrarian and more than 60% depend on agriculture and farming for subsistence. However, less than 4% of the land is cultivable. As a developing country, Bhutan is beset with challenges to biodiversity conservation, including road development, urban expansion, human-wildlife conflict, wildlife poaching and depletion of natural resources. The link between human development and wildlife conservation in a mountainous country like Bhutan is intricate and delicate. Agriculture and infrastructure developments are

necessary, yet the fragility of the landscape (erosion-prone landscape, melting glaciers and flood risk) makes biodiversity in this region susceptible to environmental change and vulnerable to the challenges of the Anthropocene (Chettri et al., 2010, Penjor et al., 2020). Thus, understanding the interaction between biodiversity and land-use change is particularly important in the context of the eastern Himalayan landscape in the face of global climate change.

Global approaches to conservation planning are diverse and equivocal and when used in isolation often produce mixed results. Several approaches have been proposed and implemented: (i) efficiency-based approach that focuses on maximising the number of endemic and extinction-risk species and ecosystems (Venter et al., 2014a); (ii) threshold-based approach in which sites of global conservation significance (relating to the occurrence of threatened or geographically restricted species or ecosystems, intact ecological communities or biological processes) are identified and protected as, for example, Key Biodiversity Area (KBA), (Allan et al., 2021); and (iii) proactive approach to conserve the most ecologically intact and pristine places for long-term ecological and evolutionary processes and species persistence before they are degraded or severed (Di Marco et al., 2018, Watson et al., 2018). These approaches are complementary and overlapping but often produce distinct science-based suggestions, and advised to use in conjunction rather than in isolation (Kullberg et al., 2019). A blanket focus on proactively conserving ecologically intact ecosystems may fail to meet the conservation need of threatened species (Di Marco et al., 2018) or a species-based focus might fail to protect large intact ecosystems needed for biodiversity persistence (Watson et al., 2018). Taken together, successful conservation would require combining these approaches through a unified and inclusive framework that strives to conserve species, ecosystems and remaining intact wilderness areas (Allan et al., 2021).

Keeping the nuances of different approaches in mind, this thesis seeks to produce a better scientific basis (and evidence) for conservation planning in Bhutan and perhaps in the eastern Himalayas by unifying species- (Chapter 2, 3 and 5) and ecosystem-based (Chapter 2 and 3) approaches and identifying functional traits and phylogenetic relationships (Chapter 4) that underpin ecosystem functioning and provisioning of ecosystem services.

Bhutan's rugged terrain and harsh climate pose an immense logistical challenge to conducting field surveys. The repeated observation would not have been possible had it not been for the advent of the revolutionary camera trapping techniques. Compared with African savannah and plains, however, fieldwork in mountainous Bhutan remains a challenge. In 2009, Wang and Macdonald conducted the first camera trap survey in central Bhutan to study tigers and leopards. Since then, wildlife and biodiversity monitoring using camera traps have grown progressively in number and spatial coverage across Bhutan. Bhutan's 2014-15 nationwide camera trap survey to revalidate tiger number was a landmark step in utilising camera traps at a national scale to monitor wildlife and perhaps the first in the world at the country level to survey large carnivores. Documenting more than 50 terrestrial mammal species as a by-catch, this survey formed the basis for many ecological studies that yielded important scientific evidence for conservation management in Bhutan (DoFPS, 2015b, Penjor et al., 2018, Tempa et al., 2019, Penjor et al., 2019, Dorji et al., 2019, Penjor et al., 2020, Thinley et al., 2021). However, a synthesis of combined impacts of land use and climate change on biodiversity in the Eastern Himalayas and Bhutan is rare. This thesis, thus, aims to fulfil that gap. The main foci of this thesis are: (i) to investigate the impacts of land-use change on biodiversity and identify potential conservation areas outside the existing protected area network and propose key conservation priority areas; (ii) assess functional connectivity of the existing protected areas and biological corridors and propose realignments based on

spatial predictions; (iii) to examine the response of functional and phylogenetic diversity of terrestrial mammals and birds to anthropogenic land use and climate change; and finally (iv) to investigate the how the anthropogenic disturbances influence spatial interaction among threatened large carnivores. This thesis thus aims to fulfil a knowledge gap that stymies the current conservation effort due to the paucity of evidence of the impacts of land use and climate change on biodiversity at a landscape scale.

An overview of the thesis chapters

This thesis follows an integrated format where some chapters are published, and others are in review (although all are submitted). Chapters 1 and 6 are general introduction and synthesis (general discussion and conclusions), respectively and Chapters 2 – 5 are data chapters. I briefly present the literature review in the general introduction chapter and rather delve deeper into the subject matter in each data chapter's introduction section. The data chapters are formatted as journal articles with figures and tables embedded within the main text and supplemented by additional materials in support of the chapter. I have also appended eight published papers (three as a lead author and co-author in the rest) that I worked on simultaneously alongside my thesis and that I believe will complement this thesis and provide support to some of the data chapters.

With the overall scene set in the introduction (Chapter 1), I now funnel down the problems and research questions in the context of the Eastern Himalayan landscape and particularly focus on the biodiversity of Bhutan to answer them. The central premise of this thesis revolves around four broad themes each forming a data chapter on its own as follows: (i) land-use change and impact on species distribution (ecology, Chapter 2); (ii) core areas

and corridors (connectivity, Chapter 3); (iii) functional and phylogenetic diversity in response to land use and climate change (community ecology, Chapter 4); and (iv) spatial interaction among large carnivores in human-dominated landscape (behaviour, Chapter 5). I used a dataset from a non-invasive camera trap survey for mammals (Chapters 2, 3, and 5) and point-count transect surveys for birds (Chapter 4). Since this study did not handle live animals, no ethical approval was required. The details of the survey protocol, data collation and preparation are provided in the data chapters.

Chapter 2

I used large-scale camera trap data from 849 paired stations established across Bhutan in 2014-15 to investigate the effects of multiple scales of environmental and anthropogenic variables and landscape metrics on habitat suitability of terrestrial mammals in Chapter 2. In this chapter, first I developed habitat suitability models for 16 terrestrial mammal species (please see Chapter 2 for the list of species) of conservation concern, second, I identified potential umbrella and indicator species, third, assessed the effectiveness of the current protected area network (and beyond) in protecting the 16 focal species and finally, evaluated the potential effectiveness of indicator and umbrella species for conservation planning. This chapter highlights three important findings: (i) the importance of a multi-scale and multi-species approach to identifying important habitats and conservation areas, (ii) the need to optimally protect species-rich areas outside of the current protected areas, and (iii) the importance of ungulates and smaller carnivores as potential umbrella and indicator species. This work has been published in the Landscape Ecology journal.

Chapter 3

In Chapter 3, I used the outputs (species distribution models) developed in Chapter 2 to model landscape connectivity of the same 16 terrestrial mammals (as in Chapter 2). I employed spatially synoptic methods (namely resistant kernel density and factorial least cost path) to identify core habitats and dispersal corridors. I used correlation and cluster analyses to identify focal umbrella and indicator species and performed quantitative ranking to prioritise core areas and corridors for the focal species. The take-home messages of this chapter are (i) the importance of multi-species consideration in core habitat and corridor planning, and (ii) species movement and dispersal can be facilitated outside of the protected area and (iii) the need for transboundary collaboration to allow smooth movement and dispersal of species between countries sharing a porous border. This Chapter is under review by the Landscape Ecology journal.

Chapter 4

Using data comprising 45 mammal species and 336 bird species from the camera trap and transect survey, respectively, I investigated the response of functional and phylogenetic diversity to land use and climate variables in Chapter 4. I used a novel approach that corrects for imperfect detection in functional and phylogenetic diversity estimates (Jarzyna and Jetz, 2016, Si et al., 2018, Palacio et al., 2020) and regressed the facets of biodiversity against land use and climate variables. Further, I present the first picture of the functional trait space of mammals and birds in Bhutan and use this concept to identify important functional traits to answer questions about community structure and ecosystem services. This study also highlights the differences in the response of mammal and bird communities to anthropogenic land use and climate change and provides evidence that land use and climate shape local and perhaps regional patterns of biodiversity of terrestrial vertebrates. Conservation thus requires an integrated approach to biodiversity management that not only incorporates species

richness but also the distribution of traits and evolutionary history. The minor revision of this chapter has just been submitted to the Diversity and Distributions jounal.

Chapter 5

The final data chapter (Chapter 5) looks at the interspecific interaction among threatened large carnivores across human land-use gradients. I analysed spatial interaction among large carnivore guild comprising tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) using capture history data obtained from 849 camera traps stations. I used a state-of-the-art multispecies occupancy model for two or more interacting species to examine the effects of environmental and anthropogenic variables on interspecific interaction while accounting for detection probability. This study suggests that multi-carnivore communities across human land-use gradients are spatially structured and mediated also by human presence and/or the availability of natural prey. The duality of the effect of human settlement density on species interaction suggests that species that perceive anthropogenic environments as ecological opportunities may need to trade off with the risk of escalating conflict with humans. This chapter has been published in the Proceedings of the Royal Society B journal.

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Chapter 2

Prioritizing areas for conservation outside the existing protected area network in Bhutan: the use of multi-species, multi-scale habitat suitability models

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Abstract

Context

Understanding the environmental and anthropogenic factors influencing habitat selection of multiple species is a foundation for quantifying human impacts on biodiversity and developing effective conservation measures.

Objectives

To determine the effect of multiple scales of environmental/topographic and anthropogenic variables and landscape patterns on habitat suitability of terrestrial mammals in Bhutan, assess the effectiveness of the current protected area network, identify areas of high species richness, and evaluate the conservation effectiveness of indicator and umbrella species.

Methods

We modelled habitat suitability of sixteen mammal species using camera trap data and used the predicted distribution maps to assess existing protected area effectiveness. We performed simulations to identify high priority areas. We used correlation and cluster analyses to identify indicator species. We assessed how optimally protected areas for one species would protect habitat for other species to evaluate umbrella effectiveness.

Results

Protected areas and forest cover were strongly associated with habitat use of most modelled species. Topographical features contributed to habitat selection of multiple species, but often in different ways. Environmental and topographical variables were mostly selected at medium to broad scales. Anthropogenic variables were negatively associated with habitat suitability of most species at both fine and broad scales. Protected areas in south-central

Bhutan were effective in mean and total richness protection. Biological corridors in the south-central region offered high mean richness protection. Optimal areas for additional protection were mostly in southern Bhutan. Muntjac, wild pig, serow, sambar and Asian golden cat were the effective umbrella species while tiger, gaur, dhole, clouded leopard and common leopard were effective indicator species.

Conclusions

This study highlights the need to protect optimally located species-rich areas outside the current protected areas. This kind of multi-species habitat assessment provides important information to optimize future conservation and development plans at national and regional scales.

Keywords: habitat suitability, indicator species, multi-scale, multi-species, priority conservation areas, umbrella species

1 Introduction

Humans have impacted biodiversity for millennia and are linked to the decline of megafauna and prehistoric extinctions (Bartlett et al., 2016). However, the recent explosion in human populations, coupled with increasing per capita resource consumption, has accelerated these impacts, with more than 50% of global land cover now altered by human activities (McGill et al., 2015). These rapid land-use changes have driven large declines in wildlife populations worldwide (WWF, 2016). As a result, it is estimated that current extinction rates are as much as 1000 times the background rate in the fossil record (Johnson et al., 2017).

Global initiatives to address the extinction crisis and improve biodiversity conservation have produced ambitious visions. Amongst them, the Aichi Biodiversity Targets 2020 aims not only to reduce species loss but also to safeguard habitat and acknowledge ecosystem services, while also improving the management and sustainable use of natural resources (Tittensor et al., 2014b). Despite such efforts, the rate of global biodiversity loss has likely accelerated substantially in recent decades (Tittensor et al., 2014b). Therefore, more effective conservation programs that optimize protection of critical habitat are essential to stem biodiversity loss and enhance species recovery (Venter et al., 2014b).

Animals have varied requirements for habitat extents, patterns and characteristics (Finlayson et al., 2008, Kelt et al., 1999, Torres-Contreras et al., 1997) and their habitat use and distribution are influenced by biotic and abiotic factors, such as food availability, predation, guild interaction and competition (Falkenberg and Clarke, 1998). Thus, knowledge of factors influencing species habitat use is a prerequisite to habitat protection, conservation and management. Further, species respond to environmental, topographical and anthropogenic features at different scales (Wiens, 1989, Collingham et al., 2000, McGarigal et al., 2016). Specifically, scale plays an important role in resource and space use of organisms in heterogeneous landscapes (Kotliar and Wiens, 1990b, Holling, 1992). Different species select habitat at different scales (Roland and Taylor, 1997), and a given species may select different resources at different scales (Grand et al., 2004, Wasserman et al., 2012b). Therefore, it is critical to incorporate the effects of scale in species-habitat relationships and more importantly in planning and designing reserves (Thompson and McGarigal, 2002).

To stem species loss and habitat conversion, global protected area (PA) designations have increased in extent and number in the last few decades (Watson et al., 2014). However, PAs

have often been designated without sufficient strategic planning, and as a result, existing PAs are often inadequate or inefficient in their protection of critical biodiversity and their habitats (Jenkins et al., 2015, Chundawat et al., 2016, Johansson et al., 2016). Assessment of the biodiversity effectiveness of existing PAs is often lacking (Chape et al., 2005). It is largely unknown whether PAs adequately represent biodiversity and ensure sustainable protection (Margules et al., 2002). Pragmatically, it is impossible to protect all wilderness areas; hence, it is important to identify critical biodiversity areas and prioritize them for intensive conservation (Waldron et al., 2013).

When prioritizing land use and protected area establishment, past studies have frequently intersected connectivity models with protected areas and prioritized areas for protection based on the strength, centrality or connectedness of areas outside the existing connectivity network (Cushman et al., 2018, Kaszta et al., 2020, Ahmadi et al., 2020, Ashrafzadeh et al., 2020). These approaches, however, do not use formal optimization to select or prioritize new areas for protection and often have been limited to one (Cushman et al., 2018) or a few (Cushman et al., 2013a) species. Formal optimization approaches, such as MARXAN (Ball et al., 2009), have the advantage of being objective, stochastic and replicable, which can improve the efficacy and robustness of predictions. However, past optimization approaches have been limited for use in connectivity analyses as they typically are zonal-based and do not formally include connectivity or spread algorithms within them. In this study, therefore, we wrote a new simulation model to select areas of the highest priority for multiple species based on their habitat quality, their proximity to existing protected areas, and their overall connectivity within the full predicted distribution of the species across Bhutan.

The Eastern Himalaya is a global biodiversity hotspot, with one of the world's highest rates of species endemism but is under pressure from habitat loss driven by anthropogenic disturbance (Myers et al., 2000, Dorji et al., 2018). Bhutan, within the Eastern Himalayan biodiversity hotspot (Myers et al., 2000), currently has over 70% of land area under forest cover and more than 50% of the total land area receives official protection, supporting a broad spectrum of species and ecosystems (DoFPS, 2011a). However, as a developing country, Bhutan is beset with challenges to biodiversity conservation, including road development, urban expansion, human-wildlife conflict, wildlife poaching and depletion of natural resources (DoFPS, 2011). Hence, validating the effectiveness of PAs in the face of human land-use change and climate warming is imperative. Additionally, Bhutan has a constitutional mandate of protecting 60% of the total land as forest cover.

Although the current protected area and biological corridor network in Bhutan (hereafter PAN) is extensive (constituting 51% of the national area, 19,581 km^2), the efficacy of the protected area network in protecting wildlife, particularly megafauna, is largely unknown. Further, rapid human infrastructure development calls for identification and urgent protection of key biodiversity areas outside the PAN for the sustainability of conservation efforts. Lastly, there is a general interest in the conservation and scientific community regarding the use of indicator and umbrella species in conservation planning (Dufrêne and Legendre, 1997, Roberge and Angelstam, 2004). In this paper, we define indicator species as those whose presence indicates (by high correlation with) the presence of other species, and umbrella species as those whose protection would simultaneously protect optimal habitat for many other species.

To address these knowledge gaps and management needs, this study aims to: (1) investigate the multiple scale habitat relationships of 16 terrestrial mammal species of conservation importance and predict their distribution across Bhutan, (2) evaluate the effectiveness of the existing PAN based on the amount of total species richness protected, (3) identify areas of conservation importance outside of the existing PAN that could be chosen to optimally expand the protected area network, and (4) evaluate the efficacy of each of the 16 focal species as conservation umbrella and indicator species. Our models are replicable, enabling incorporation into long-term monitoring of critical biodiversity areas by governments and conservation agencies.

2 Materials and Methods

2.1 Study area

This study was conducted in Bhutan as a part of the nation-wide tiger survey in 2014-15. Bhutan, with an area of 38,394 km^2, is a small country in the eastern Himalayas between India and China (Figure 1). About 70% of the total geographical area is covered by forest and another ~10% is a natural shrub and alpine scrub cover (FRMD, 2017b). Vegetation varies with elevation; lower foothills are characterized by broadleaved forest, the temperate zone by conifer-broadleaved mixed forest and higher elevations by alpine and sub-alpine scrub and shrub. The altitude ranges from 100m in the south to above 7,500m in the north. The wet season (monsoon) occurs between July and September, with annual precipitation ranging between 300mm and 6,000mm (NCHM, 2017). The topography is rugged, with steep terrain, narrow river valleys and deep gorges. Bhutan has ~120 species of mammals, ~700 birds and ~5,000 plants (Gyeltshen et al., 2020).

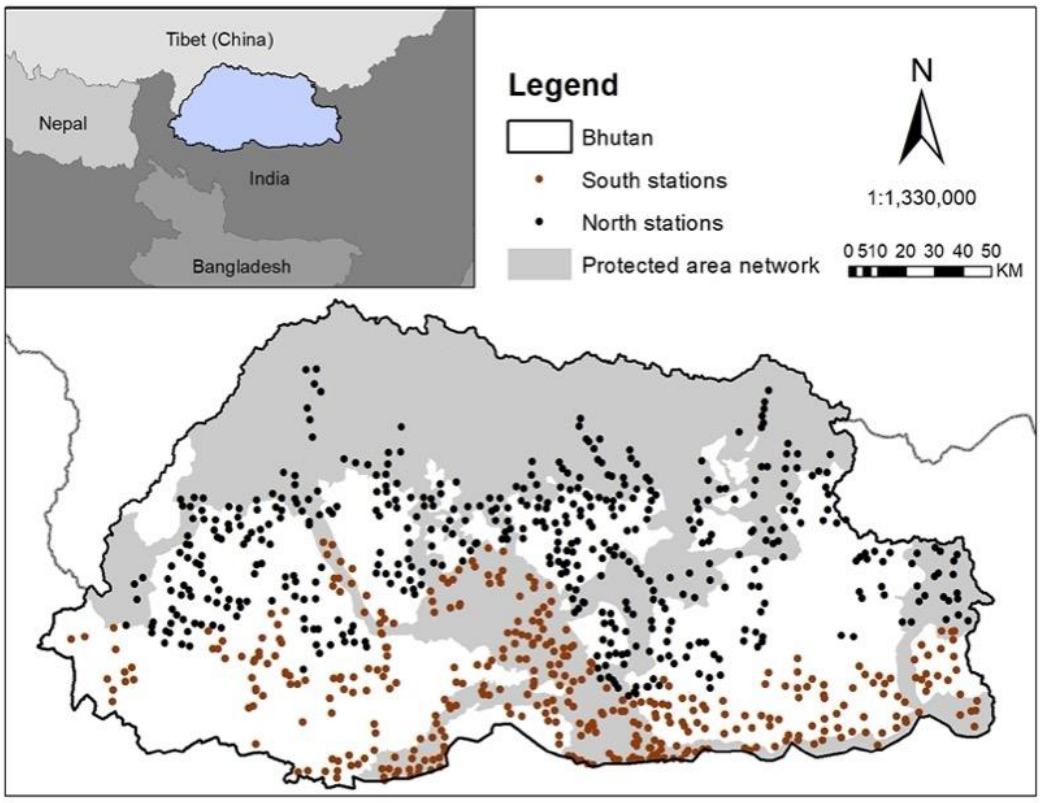


Figure 1. Study area with camera trap locations from the national tiger survey.

2.2 Field survey

The nation-wide camera-trap survey was conducted between March 2014 and March 2015 with a break during the intervening rainy season. For logistical reasons, the country was divided into two blocks: north (n=681) and south (n=448), (Table S1). Five different camera models were deployed (Reconyx, HCO Scoutguard, Cuddeback, U-Way, Bushnell). All stations had paired cameras, and none was baited. The deployment followed a 25km^2 grid based on the size of a female tiger home range (Karanth et al., 2002) and excluded settlements and areas above 4500m (DoFPS, 2015a). The minimum distance between stations was 2km. The monitoring team checked camera stations for battery drain, cleared bushes obstructing the camera lens and downloaded memory cards every month.

We used data for 16 species of mammals, each captured in more than 10% of the total camera stations. Many of these species are regarded as charismatic, flagship or umbrella species. Of the 16 species, five are listed as Least Concern (LC), five as Vulnerable (VU), three as Near Threatened (NT) and three as Endangered (EN) in the International Union for Conservation of Nature (IUCN) Red List (Table S2; IUCN, 2020). The study species are Asiatic black bear (*Ursus thibetanus*), Asiatic golden cat (*Catopuma timminckii*), clouded leopard (*Neofelis nebulosa*), dhole (*Cuon alpinus*), Asian elephant (*Elephas maximas*), gaur (*Bos gaurus*), masked palm civet (*Paguma larvata*), common leopard (*Panthera pardus*), leopard cat (*Prionailurus bengalensis*), marbled cat (*Pardofelis marmorata*), muntjac (*Muntiacus muntjac*), sambar deer (*Rusa unicolor*), Himalayan serow (*Capricornis thar*), tiger (*Panthera tigris*), wild pig (*Sus scrofa*), and yellow-throated marten (*Martes flavigula*).

2.3 Predictor variables

Resource use by a species is influenced by natural and anthropogenic factors. While topographical factors impose physical constraints and drive major patterns of climate and vegetation, human land use often perturbs ecological systems, altering their structure, composition and suitability for many species (Magioli et al., 2019, Macdonald et al., 2020). We selected 20 predictor variables reflecting environmental, topographical and anthropogenic conditions that we hypothesized would affect habitat suitability of the 16 studied species (Table 1). These variables, as described below, were further used to calculate six landscape metrics, which quantify the composition and configuration of environmental patterns, (McGarigal et al., 2012) (Table 1).

Table 1. Predictor variables

Predictor variable	Category	Original Resolution (m)	Metrics calculated	Scale (km)	Tool	Source
Agriculture	Anthropic	vector	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	Landcover Mapping project (LCMP) 2017
Bare area	Topographic	vector	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	LCMP 2017
Broadleaved forest	Environmental	vector	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	LCMP 2017
Built-up area	Anthropic	vector	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	LCMP 2017
Conifer forest	Environmental	vector	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	LCMP 2017
Meadow/shrub	Environmental	vector	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	LCMP 2017
Snow cover	Topographic	vector	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	LCMP 2017
Non-forest (<20%)	Environmental	30	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	Hansen et al., 2013, Global Forest Change (GFC)
Open forest (21-40%)	Environmental	30	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	Hansen et al., 2013, Global Forest Change (GFC)
Closed forest (41%<)	Environmental	30	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	Hansen et al., 2013, Global Forest Change (GFC)
Digital Elevation Model (DEM)	Topographic	90	FM	0.5, 1, 2, 4, 8, 16, 32	ArcGIS 10.6.1	Jarvis et al., 2008, Shuttle Radar Topography Mission (SRTM)
Compound topographic index (CTI)	Topographic	90	FM	0.5, 1, 2, 4, 8, 16, 32	ArcGIS 10.6.1	Derived from SRTM

Protected area	Environmental	vector	FM	0.5, 1, 2, 4, 8, 16, 32	ArcGIS 10.6.1	Department of Forests and Park Services (DoFPS)
River density	Environmental	vector	FM	0.5, 1, 2, 4, 8, 16, 32	ArcGIS 10.6.1	DoFPS
Road density	Anthropic	vector	FM	0.5, 1, 2, 4, 8, 16, 32	ArcGIS 10.6.1	DoFPS
Roughness	Topographic	90	FM	0.5, 1, 2, 4, 8, 16, 32	ArcGIS 10.6.1	Derived from SRTM
Settlement density	Anthropic	vector	FM	0.5, 1, 2, 4, 8, 16, 32	ArcGIS 10.6.1	DoFPS
Slope position	Topographic	90	FM	0.5, 1, 2, 4, 8, 16, 32	ArcGIS 10.6.1	Derived from SRTM
Landcover	Topographic	vector	CWED, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	LCMP 2017
Tree canopy cover	Environmental	30	PLAND, GYRATE_AM, PD	0.5, 1, 2, 4, 8, 16, 32	FRAGSTATS 4.2, ArcGIS 10.6.1	Hansen et al., 2013, Global Forest Change (GFC)

PLAND - Percentage of landscape; GYRATE_AM - Radius of Gyration Area weighted mean, PD - Patch density; CWED - Contrast weighted edge density; FM – focal mean

Each metric for each predictor variable was calculated at seven spatial scales (500m, 1km, 2km, 4km, 8km, 16km, 32km). Twelve variables had three metrics (PLAND/CWED, GYRATE_AM and PD) and each metric had seven scales resulting in 12 x 21 = 252 predictor variables, and eight variables had one metric (FM) at seven spatial scales resulting in 8 x 7 = 56 variables. The total variables initially tested were 308

To predict effects of topography on habitat selection, the Shuttle Radar Topography Mission (STRM) digital elevation model (Jarvis et al., 2008) was transformed into topographical roughness (which measures the complexity of the terrain), slope position (measuring the relative position of a location from valley bottom to ridge top) and compound topographic index (CTI) using the Geomorphometry and gradient metrics toolbox (Evans et al., 2014) in ArcGIS 10.6.1 (ESRI, 2018). CTI measures the flow accumulation (wetness index) such that broad valleys with large drainage areas have high CTI and steep mountain ridges have low CTI values (Beven and Kirkby, 1979, Macdonald et al., 2018b). Forest cover (Hansen et al., 2013) was classified into three classes: non-forest (0-20% tree cover), open-forest (20-40% tree cover) and closed forest (>40% tree cover) to enable an analysis of the spatial pattern of forest density and canopy closure on species occurrence patterns. Land cover (FRMD, 2017b) was classified into eight categories: agriculture, bare, broadleaved forest, built-up, conifer forest, meadow-shrub, water bodies and snow-glacier areas. We also included the spatial layers of settlement, road, river densities and the extent of protected areas (Table 1).

To identify spatial extents at which habitat components and anthropogenic factors most strongly affect species presence, we calculated each predictor variable for each species at seven spatial scales: 500m, 1km, 2km, 4km, 8km, 16km and 32km. This scale range was chosen to bracket the range of expected optimal scales for each species' response to each variable (e.g. Macdonald et al., 2019a, Macdonald et al., 2018b, McGarigal et al., 2016, Mateo Sánchez et al., 2014) and is consistent with the range of scales in other multi-scale studies of wide-ranging species in Asia (Macdonald et al., 2018b, Macdonald et al., 2019a). We categorize these scales as fine-scale (500m, 1km, 2km), medium-scale (4km, 8km) and broad-scale (16km, 32km).

For settlements, rivers, roads and protected areas we ran a focal mean (FM) analysis in ArcGIS 10.6 (ESRI REF) by applying a circular moving window of a radius equal to each of the seven investigated scales. To investigate the effects of spatial configuration and composition of the landscape mosaic at different scales on habitat use, we calculated landscape metrics on the reclassified land cover layer described above and the three classes of forest cover (McGarigal et al., 2012). These metrics included: PLAND-percentage of the landscape of a particular habitat class; CWED-contrast-weighted edge density which is a measure of edge effect of similar or contrasting habitats; GYRATE_AM-correlation length which measures the expected value of the distance from a random location in a cover type to the edge of that cover type moving in a random direction and is an effective measure of patch extensiveness; and PD – patch density. These metrics were chosen based on past research showing them to be among the metrics that most strongly and consistently affect wildlife habitat selection (e.g. Grand et al., 2004, Chambers et al., 2016). The metrics were calculated for all forest cover and land cover classes within a circular moving window of a radius corresponding to the chosen seven scales (Table 1), using FRAGSTATS (McGarigal et al., 2012).

All initial rasters were re-sampled to 90m resolution. The value for each predictor variable at each focal scale was then extracted at each camera station. All 308 predictor variables were standardized to mean 0 and standard deviation 1 before analysis. After removing variables which lacked sufficient information due to small coverage (e.g., unvarying in > 95% of stations), the final number of variables used in the multi-scale modelling was 291.

2.4 Multi-scale habitat suitability models

Multi-scale habitat suitability models (sensu McGarigal et al., 2016) were used to identify key environmental and anthropogenic variables that were predictive of the occurrence of each species, and the optimal scale of species-habitat relationship for each variable (Macdonald et al., 2018b, Macdonald et al., 2019a). The species detection data at each camera site were collated into binary form, with 1 for detection and 0 for non-detection. We then employed a three-step modelling approach to optimize scale and assess species-habitat relationships, as suggested by (McGarigal et al., 2016). All analyses were performed in R (R Core Team, 2019).

In the first step, we fit univariate generalized linear models (GLM) with a binomial link function for each species as a response variable and each variable at each scale as the predictor variable. The best scale for each variable for each species was selected based on the lowest AICc score (Akaike Information Criterion corrected for small sample size) (Burnham and Anderson, 2002).

In the second step of the modeling process, we screened predictor variables for multi-collinearity (Dormann et al., 2013). We used Pearson's correlation coefficient threshold of $|r| \geq 0.6$ to screen out correlated predictors. We ran univariate GLM for each correlated pair and retained one with lower AIC value. We also assessed spatial autocorrelation using Moran's I statistic in the spdep R package (Bivand and Wong, 2018). When significant spatial autocorrelation was found, we added an auto-covariate term with a distance threshold of the mean distance between camera traps in the final multivariate model.

In the third and final step, we ran multivariate GLM with a binomial link on all remaining scale-optimized predictor variables. We then used the 'dredge' function in R package MuMIn (Barton, 2019) to test all possible combinations of predictor variables and ranked models using ΔAICc (the difference between AICc of subsequent models with the top model). The final models were considered competitive if they were within ΔAICc of 2. We employed model averaging based on AIC model weights to produce final coefficient estimates (Burnham and Anderson, 2002), which we then used to map habitat suitability for each species.

We evaluated the performance of the model-averaged predictions using the area under the receiver operating characteristic curve (AUC). The mean habitat suitability of each study species across Bhutan was calculated as the mean of all pixels with suitability value > 0 using the Zonal Statistics tool in ArcGIS 10.6 (ESRI, 2018)

2.5 Conservation effectiveness of existing PAN

To evaluate conservation effectiveness, we calculated the mean predicted relative species richness within each protected area and biological corridor and the proportion of the total sum of richness across Bhutan (percent richness) in each protected area and biological corridor. To calculate species richness, we summed the predicted habitat suitability layers of the 16 species. We then calculated the mean richness value for each protected area and biological corridor and the percentage of the sum of species richness represented by each protected area and corridor. The cumulative layer of the sum of predicted occurrence probability for all 16 species was used to identify hotspots.

2.6 Simulation to identify additional conservation areas

We wrote a new model in Arc Macro Language for ArcInfo Workstation Grid to simulate optimal locations for protected area expansion. The model was written in ArcInfo Workstation Grid given its high efficiency for spatial analysis and functionality of nested and looped spatial functions. We designed the model to optimize the selection of areas outside of the current protected area network that had simultaneously high local habitat quality and had high connectivity to existing protected areas for multiple focal species. We ran the model for each of the 16 focal species and the sum of predicted probability of all focal species (17 simulation scenarios).

The routine consisted of five components, and the simulation works through two nested iterative loops (Figure 2). The basic method is to select additional cells for new protected areas for each species, or all species jointly (as the scenario may be), based on two criteria: (1) habitat suitability for that species or collective total sum suitability across species (as the scenario may be); and (2) cost distance from existing protected areas across the suitability surface. This results in new cells being stochastically selected based on the combination of their quality as habitat and their cost proximity to cells previously selected, which ensures that new protected areas are both high-quality habitat and well connected to current and additionally selected protected area cells.

There are several steps in the iterative simulation process. First, we create a difference raster by subtracting the inverted and rescaled cost distance (between 0 and 1) from protected area cells across the resistance surface (Figure 2 d) and a uniform random raster (Figure 2 e). This creates a stochastic process to select cells of low relative cost distance. This is done by selecting all cells with value >0.75 from the difference raster. A resistance surface, as used in cost distance modelling, reflects the cost of resistance to movement of each cell for the

process being modelled (Spear et al., 2015). In this case, we modelled connectivity for a focal species or for a community of focal species (as the scenario may be), and the resistance layer was defined as the inverse of the predicted occurrence probability layer (or the sum of predicted occurrence probability layers, for the multispecies scenario), rescaled between 1 and 100. In each time step of the iterative model, the algorithm described in the first step above selects all cells that are 75% greater than the random value generated for that cell and results in a small proportion (~0.25% per time step) of the most optimal cells being selected. The choice of a value of 0.75 for this threshold is subjective but was calibrated such that it produced in each time step a selection of cells that was sufficiently large to seed a meaningful optimization but small enough to avoid seeding many suboptimal pixels.

In the next iterative step, these pixels that were stochastically selected from the most well-connected cells in the landscape are then added to the raster of protected areas (Figure 2 c) and the iterative process just described is repeated 50 times, creating additional optimal stochastically selected protected area cells. Once this loop is completed the entire process is repeated in another exterior loop (Figure 2 step 2) 50 times. The choice of 50 iterations for both loops was intended to provide enough Monte Carlo runs to produce a precise estimate while balancing processing time.

At the end of the total simulation, the protected area rasters produced are summed, creating values between 0 (never selected as an optimal new protected area) and 50 (selected as an optimal protected area in each exterior iteration). This provides a quantitative measure of how optimal each cell is for inclusion in a new protected area based jointly on habitat quality and connectivity for each focal species.

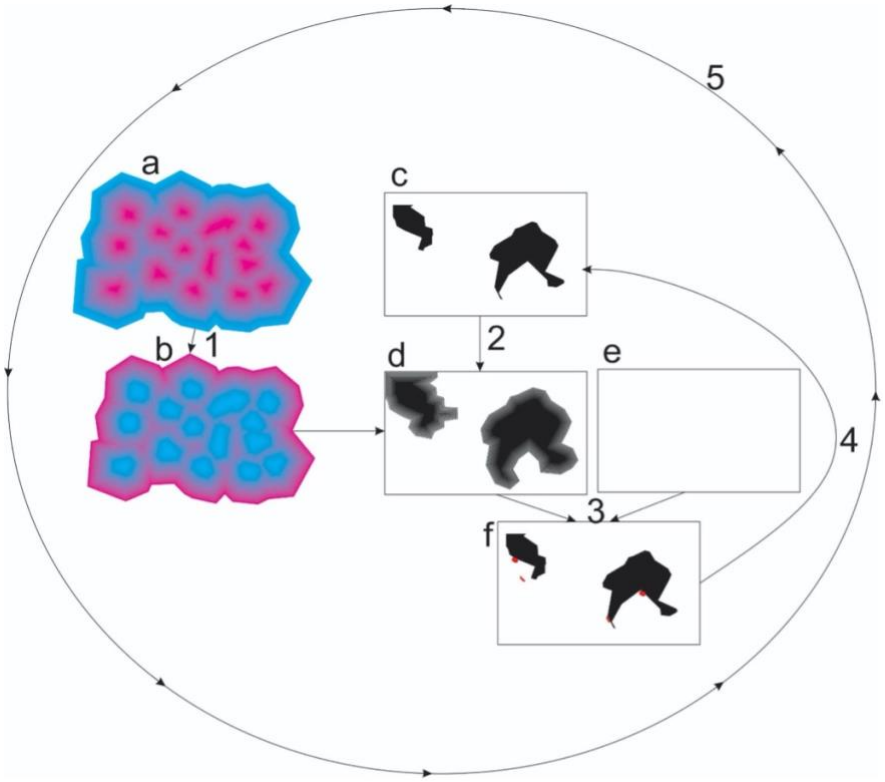


Figure 2. Schematic of the simulation model developed to stochastically optimize new protected areas based on habitat quality, proximity to existing protected areas and connectivity across the population. There are six inputs/outputs (a-f) and five iterative steps (1-5). The inputs/outputs are: a) habitat suitability map, b) resistance map produced from (a), c) existing protected areas, d) cost distance from existing protected areas across the resistance map (b), e) uniform random raster for stochastic simulation, f) selection of new optimal cells for additional protected areas as the difference of (d) and (e). The iterative steps are 1) conversion of habitat suitability to resistance (outside of all iterative loops), 2) calculation of cost distance from protected areas on the resistance surface (inside iterative loops), 3) stochastic selection of new protected areas (inside iterative loops), 4) iterative loop 1, 50 reps of sequential additive selection of new protected area cells, 5) iterative loop 2, repetition of the full selection 50 times

We computed these optimal protected area selections for all 16 species individually, and for all 16 species jointly. The prioritization for all 16 species jointly was done in two ways: (1) based on the sum of their predicted probability maps, (2) based on a weighted sum of predicted probability maps. The weighting reflects the relative conservation priority of each of the 16 species based on their local and global conservation status (Table S2). Specifically, in the first case, we summed the predicted probability of occurrence maps for all 16 species without any transformation, while in the second we weighted the sum such that the species with higher conservation importance (Table S2) received more priority. As noted above, these predicted probability surfaces (for each species scenario) and the sum of predicted probability surfaces (for the two multi-species scenarios), were transformed through inversion and rescaling between 1 and 100 to produce resistance layers for use in the spatial simulation.

For each of these 18 scenarios, we produced the raster of prioritization (0-50) for cells to include in new protected areas. We present all of these rasters in the supplemental material (Figure S22). We include those for several focal species of particular interest and one of the multispecies optimizations as figures in the Results. We also evaluated the relative similarity and overlap of optimal cells for expansion of the protected area network between scenarios (16 species and 2 multispecies) by computing the pixel-wise correlation between values (0-50) in the output prioritization rasters.

2.7 Umbrella and indicator species

We assessed the effectiveness of each species as umbrella species, in which conservation of optimal habitat for that species would simultaneously conserve habitat for the others. The umbrella species analysis was done by (1) computing the average and (2) sum of habitat

suitability for each species within the optimal protected area cell selection raster (from the simulation analysis described in the previous section) for all species sequentially, which quantifies how well the optimal protected area network for each species would protect habitat for the other species. Furthermore, we evaluated the efficacy of the two multi-species prioritization strategies in providing optimal protection for each species, by calculating the mean and sum of habitat suitability for each species within the optimal protected area polygons developed for each of the multispecies selection strategies. We also evaluated the relative ability of each species to serve as an indicator species for the sampled mammalian community using cluster analysis and correlation analysis. Cluster analyses generated groups of species based on the similarity in predicted occurrence probabilities. The pairwise correlations calculated between the predicted occurrence probability rasters produced from the multi-scale habitat modelling among all pairs of species identified which species had the highest average correlation with all other species (Cushman et al., 2010).

3 Results

We retrieved images from 849 camera stations (of 1129 initially installed; Table S1). Fifty-four mammal species were recorded over 73,259 trap days. The overall mean trap nights per camera was 86.7 (21.3). The number of species detected per camera station ranged from 0 to 17. The naïve occupancy (stations with species detection divided by the total number of camera stations) was highly variable among the study species with highest observed for Muntjac *Muntiacus muntjac* (0.58) and lowest for Asian elephant *Elephas maximus* (0.10).

3.1 Habitat suitability models

About 39% of the predictor variables were selected at broad scales while small and medium scales were selected in equal proportions (~31% and 30% respectively) across all species (Table S4). Multi-scale single species habitat suitability models showed that forest-related variables were strong predictors of Asiatic golden cat *Catopuma timminckii*, muntjac *Muntiacus muntjac*, wild pig *Sus scrofa*, yellow-throated marten *Martes flavigula*, clouded leopard *Neofelis nebulosa*, serow *Capricornis thar*, tiger *Panthera tigris* and dhole *Cuon alpinus* habitat suitability. Surprisingly, masked palm civet *Paguma larvata*, Asian elephant *Elephas maximus*, leopard cat *Prionailurus bengalensis*, common leopard *Panthera pardus* and sambar deer *Rusa unicolor* displayed a negative relationship with forest-related variables (Table 2). The density of rivers in a local landscape had significant relationships with tiger, serow and wild pig while having significant negative relationships with smaller carnivores like dhole and marbled cat *Pardofelis marmorata*.

Table 2. Final equations of averaged generalized linear models for 16 studied mammals with standardized β-coefficients, name of the variable/metric, scale and the AUC value of model performance

Species	Model equation	AUC
Asiatic black bear	-0.82 + (**-0.24*Agri_GYRATE_500m**) **+** (**-0.31*CTI_FM_1km**) + (-0.19*Mead_PD_2km) + 0.14*River_FM_32km **+** (**-0.56*NF_PLAND_8km**) + 0.05*Built_PD_32km + 0.03*Rough_FM_32km + (-0.03*Slope_FM_4km)	0.70
Asian elephant	-10.7 + (**-0.66*Agri_PD_8km**) + (**-0.98*BLF_PD_16km**) + (**-2.1*Ele_FM_32km**) + (-0.24*River_FM_16km) + (**-0.68*Rough_FM_2km**) + (-0.29*Slope_FM_2km) + (-12.7*Snow_GYRATE_32km) + (-0.32*PA_FM_500m) + 0.15*OF_GYRATE_4km	0.97
Asiatic golden cat	-0.89 + **0.25*CoF_PD_2km** + **0.31*Rough_FM_16km** + 0.13*Slope_FM_4km + (-0.12*Land_CWED_8km) + (-0.11*Agri_GYRATE_32km) + 0.10*BLF_PD_32km + (-0.07*NF_GYRATE_32km)	0.63
Common leopard	-2.44 + **0.61*CTI_FM_16km** + (**-0.69*Ele_FM_4km**) + **1.05*PA_FM_500m** + (-0.24*River_FM_32km) + 0.26*Rough_FM_32km + (**-0.40*NF_GYRATE_32km**) + 0.20*Tree_PD_16km + 0.22*BLF_PD_32km + 0.17*Settle_FM_16km + 0.18*Agri_PD_8km + 0.12*Road_FM_32km + 0.13*Land_PD_16km + 0.11*Built_PD_32km + 0.05*Slope_FM_32km + (-0.06*OF_GYRATE_4km)	0.83
Clouded leopard	-2.57 + **0.84*BLF_PLAND_32km** + (**-0.36*Land_PD_4km**) + **0.42*PA_FM_4km** + (-0.12*River_FM_8km) + (**-0.35*NF_GYRATE_500m**) + (-0.19*Built_PLAND_8km) + 0.10*Road_FM_8km + (-0.03*BLF_PD_4km) + 0.001*Rough_FM_16km	0.82
Dhole	-1.33 + (-0.17*Agri_GYRATE_1km) + (-0.13*Land_CWED_4km) + (**-0.25*River_FM_2km**) + (**-0.51*Road_FM_1km**) + **0.21*Slope_FM_4km** + **0.21*OF_GYRATE_8km** + 0.14*Land_GYRATE_1km + (-0.12*Bare_GYRATE_2km) + 0.06*BLF_PD_32km + (-0.06*Built_GYRATE_4km)	0.65
Gaur	-3.79 + (**-2.26*Ele_FM_32km**) + **0.36*PA_FM_500m** + (-0.34*Rough_FM_8km) + (-0.44*CF_PD_4km) + (-0.15*River_FM_16km) + 0.18*OF_GYRATE_4km	0.93
Himalayan serow	-0.76 + 0.19*Bare_GYRATE_32km + **0.45*BLF_PD_32km** + (**-0.24*Built_PLAND_8km**) + (**-0.39*CTI_FM_4km**) + (**-0.27*Mead_GYRATE_500m**) + (**-0.17*River_FM_16km**) + 0.15*Rough_FM_32km + (-0.13*Built_GYRATE_4km) + 0.14*BLF_GYRATE_8km + 0.09*Slope_FM_500m + 0.09*Agri_PD_32km + (-0.04*Land_PD_500m) + 0.04*Land_CWED_4km + (-0.03*PA_FM_32km) + 0.02*Tree_CWED_500m	0.69

Leopard cat	-0.97 + (**-0.72*Ele_FM_500m**) **+ 0.30*PA_FM_4km** + (**-0.21*OF_GYRATE_4km**) + 0.10*Settle_FM_1km + 0.07*Rough_FM_8km + 0.03*River_FM_2km + (-0.03*NF_GYRATE_500m)	0.75
Marbled cat	-2.1 + **0.29*Agri_PD_32km** + (**-0.52*Built_PLAND_8km**) + **0.42*PA_FM_4km** + (**-0.39*River_FM_2km**) + **0.48*Rough_FM_4km** + **0.58*Slope_FM_500m** + **0.67*Snow_PLAND_500m** + (**-0.54*Tree_PD_2km**) + (-0.18*BLF_PD_4km) + (-0.13*CF_GYRATE_16km) + 0.06*CF_PD_32km + (-0.03*OF_GYRATE_32km)	0.81
Masked palm civet	-2.24 + (**-1.85*CoF_PLAND_8km**) + 0.06*Road_FM_2km + 0.04*Rough_FM_8km + 0.02*BLF_PD_500m	0.80
Muntjac	0.38 + **0.92*BLF_PLAND_2km** + **0.21*Built_PD_32km** + 0.15*Road_FM_4km + (-0.15*Slope_FM_32km) + (-0.14*OF_GYRATE_500m) + (-0.09*Mead_PD_500m) + 0.11*Agri_PD_32km	0.74
Sambar	-0.43 + **0.19*Built_GYRATE_4km** + (**-0.50*Ele_FM_4km**) + (**-0.26*Mead_PD_500m**) + 0.12*River_FM_32km + 0.11*Settle_FM_2km + 0.14*Road_FM_4km + (-0.11*Slope_FM_32km) + (-0.08*OF_GYRATE_500m) + 0.08*NF_GYRATE_500m + 0.09*Built_PD_32km + (-0.04*Agri_PD_32km)	0.70
Tiger	-2.03 + (**-0.31*Agri_PD_4km**) + (**-0.37*BLF_PD_32km**) + (**-0.34*Mead_PD_16km**) + **0.49*PA_FM_32km** + **0.24*River_FM_32km** + **0.27*OF_GYRATE_16km** + (-0.10*Rough_FM_1km) + 0.07*CTI_FM_2km + (-0.1*Tree_CWED_32km)	0.76
Wild pig	-0.14 + (-0.23*Agri_PD_32km) + (**-0.22*Bare_GYRATE_8km**) + **0.37*BF_GYRATE_2km** + (**-0.25*PA_FM_32km**) + (**-0.29*River_FM_16km**) + **0.30*Road_FM_32km** + **0.30*Rough_FM_32km** + (**-0.31*Slope_FM_32km**) + 0.12*Agri_GYRATE_8km + (-0.07*NF_PD_500m) + (-0.07*OF_GYRATE_500m)	0.70
Yellow-throated marten	-0.57 + (-0.17*Agri_GYRATE_16km) + **0.29*BLF_PLAND_16km** + (**-0.23*CTI_FM_2km**) + (**-0.16*Land_CWED_500m**) + **0.25*Rough_FM_4km** + 0.09*Slope_FM_4km + (-0.11*River_FM_500m) + 0.06*BF_PLAND_500m + 0.08*CF_PLAND_32km + (-0.03*CoF_PD_500m)	0.67

Covariates: Agri = Agriculture, CTI = Compound Topographic Index, Mead = Meadow-Shrub, NF = Non Forest, OF = Open forest, CF = Closed forest, Built = Built-up area, Rough = Roughness, Slope = Slope position, BLF = Broadleaved forest, CoF = Conifer forest, Ele = Elevation, PA = Protected area, Land = Land cover, Tree = Tree canopy cover, Settle = Settlement, Bare = Bare area

Metrics: PLAND = percentage of land, PD = patch density, GYRATE = radius of gyration area weighted mean, CWED = contrast weighted edge density, FM = focal mean

*Equations in **bold** indicate significant relationships (95% confidence intervals do not overlap zero).*

AUC: Area under the receiver operating characteristic curve

Anthropogenic variables were generally negatively associated with most modelled species. Forest obligate species like serow, Asian elephant, marbled cat, tiger, dhole and Asian black bear displayed strong negative response to anthropogenic factors. However, wild pig and sambar deer showed positive associations with anthropogenic variables, suggesting that they may not avoid and may even select areas of relatively higher human impact.

The response of mammals to topographical predictors was highly variable. For example, roughness, CTI and slope position were positively associated with habitat use of Asian golden cat, wild pig, yellow-throated marten, marbled cat, common leopard and dhole but negatively associated with habitat use of Asian elephant, Asiatic black bear, serow, gaur *Bos gaurus*, leopard cat and sambar deer (Table 2). Muntjac had the highest mean habitat suitability across Bhutan (0.53) while clouded leopard had the lowest (0.13, Table 2).

3.2 Effectiveness of existing PAN

Some protected areas, notably Jigme Singye Wangchuck National Park (JSWNP) and Royal Manas National Park (RMNP) had relatively high effectiveness based on both mean and total relative richness protected (Table 3; Figure 3). Others, like Phipsoo Wildlife Sanctuary (PWS) and Jomotshangkha Wildlife Sanctuary (JWS), had high ranking based on mean relative richness per unit area but ranked low based on the total proportion of relative species richness cumulatively protected across Bhutan. Protected areas JWSNP, Jigme Dorji National Park (JDNP), Wangchuck Centennial National Park (WCNP) and RMNP had the highest total proportion of richness protected, while PWS, RMNP and JWS had the highest per unit area richness protection value. Based on both measures, protected areas Sakteng Wildlife Sanctuary (SWS), Jigme Khesar Strict Nature Reserve (JKSNR) and Bumdelling Wildlife

Sanctuary (BWS) had relatively lower values of relative species richness compared to other protected areas.

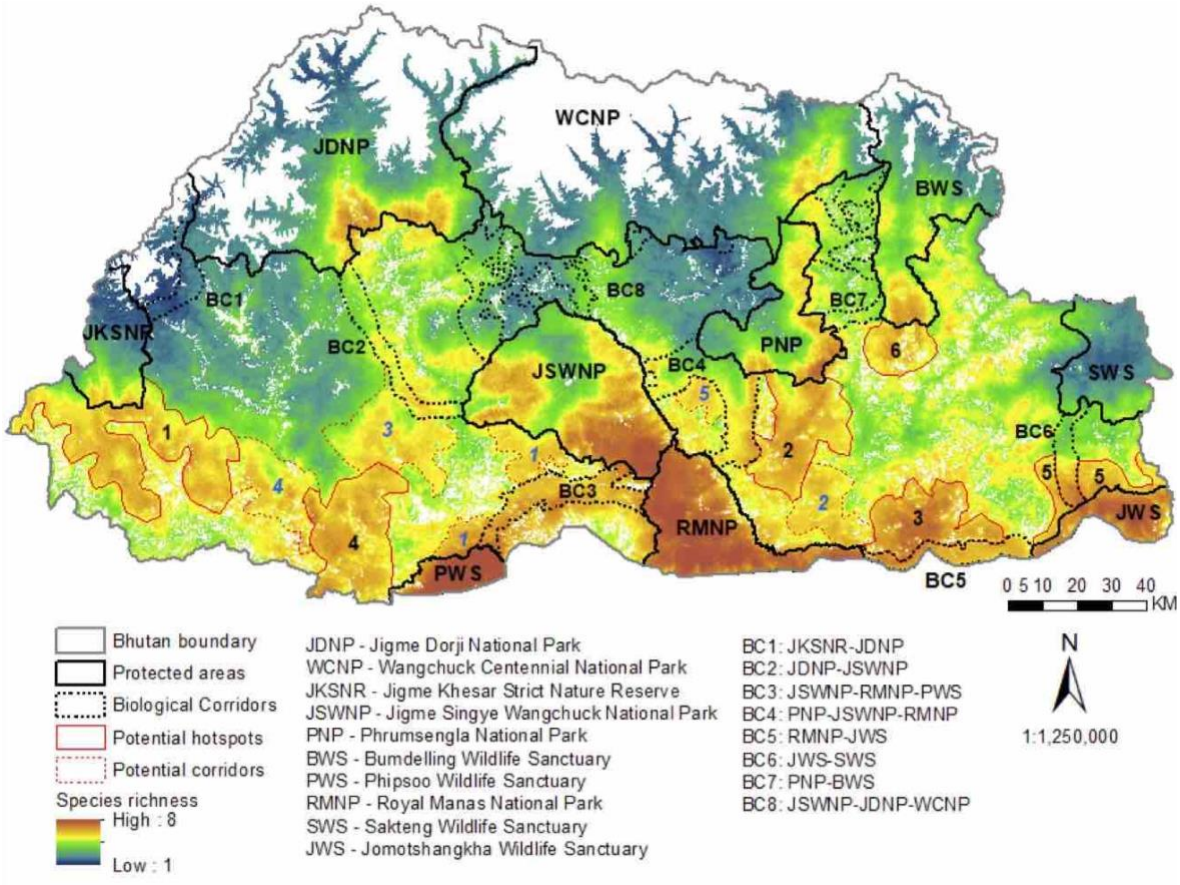


Figure 3. Predicted species richness (16 modelled species) across Bhutan, and identification of focal areas for new conservation areas and corridors. Six priority areas for potential new conservation areas are labelled 1-6 in the black-colored non-Italic font. Five areas for priority consideration as new or realigned corridors are labelled 1-5 in blue-colored Italic font. The areas above 4500m are clipped

3.3 Predicted relative species richness by biological corridors

Biological corridors BC3 (which connects JSWNP, RMNP and PWS), BC5 (connecting RMNP and JWS), BC6 (connecting JWS and SWS), BC4 (connecting PNP, JSWNP and RMNP), BC2 (connecting JSWNP and JDNP) and BC7 (connecting PNP and BWS) had high

overall mean relative predicted species richness (Table 3; Figure 3). BC8 (connecting JSWNP, JDNP and WCNP) was substantially higher than the others in terms of the cumulative proportion of national species richness protected, followed by BC3 and BC4. BC1 (connecting JKSNR and JDNP) had the lowest ranking on both measures.

Table 3. Mean species richness and per cent species richness (%) for 16 species and each protected area and biological corridor

Protected Area Network	Code	Asiatic golden cat		Asiatic black bear		Asian elephant		Clouded leopard		Common leopard		Dhole	
		Mean	%	Mean	%	Mean	%	Mean	%	Mean	%	Mean	%
Protected areas													
Bumdeling Wildlife Sanctuary	BWS	0.347	4.222	0.217	3.007	0.017	0.415	0.106	4.243	0.137	4.785	0.216	4.292
Jigme Dorji National Park	JDNP	0.298	7.326	0.151	4.222	0.009	0.467	0.027	2.215	0.077	5.415	0.171	6.868
Jigme Khesar Strict Nature Reserve	JKSNR	0.312	1.848	0.148	0.997	0.029	0.347	0.054	1.041	0.060	1.012	0.170	1.647
Jigme Singye Wangchuck National Park	JSWNP	0.394	6.813	0.459	9.067	0.112	3.938	0.253	14.405	0.176	8.719	0.248	7.035
Phrumsengla National Park	PNP	0.393	3.607	0.343	3.597	0.036	0.680	0.133	4.026	0.296	7.777	0.255	3.828
Phipsoo Wildlife Sanctuary	PWS	0.140	0.375	0.366	1.120	0.850	4.645	0.332	2.931	0.439	3.372	0.219	0.960
Royal Manas National Park	RMNP	0.186	1.928	0.418	4.935	0.694	14.634	0.418	14.204	0.241	7.134	0.213	3.611
Sakteng Wildlife Sanctuary	SWS	0.351	2.635	0.208	1.781	0.039	0.600	0.056	1.384	0.091	1.950	0.187	2.297
Wangchuck Centennial National Park	WCNP	0.282	7.302	0.133	3.938	0.010	0.520	0.027	2.286	0.061	4.527	0.167	7.072
Jomotshangkha Wildlife Sanctuary	JWS	0.189	0.665	0.288	1.153	0.745	5.329	0.166	1.915	0.407	4.094	0.204	1.173
Corridors													
JDNP-JSWNP	BC2	0.393	1.081	0.418	1.311	0.035	0.198	0.073	0.658	0.063	0.495	0.303	1.367
JKSNR-JDNP	BC1	0.247	0.371	0.056	0.096	0.036	0.109	0.006	0.030	0.006	0.024	0.112	0.275
PNP-JSWNP-RMNP	BC4	0.424	2.152	0.415	2.404	0.170	1.760	0.142	2.366	0.034	0.488	0.241	2.002
JSWNP-RMNP-PWS	BC3	0.244	0.911	0.419	1.787	0.383	2.922	0.243	2.994	0.136	1.460	0.204	1.251
JWS-SWS	BC6	0.376	0.612	0.472	0.878	0.403	1.337	0.122	0.655	0.025	0.115	0.245	0.654
JSWNP-JDNP-WCNP	BC8	0.348	3.243	0.273	2.895	0.023	0.443	0.039	1.202	0.044	1.166	0.244	3.711
RMNP-JWS	BC5	0.142	0.304	0.152	0.370	0.869	3.778	0.069	0.487	0.176	1.074	0.183	0.639
PNP-BWS	BC7	0.442	0.329	0.262	0.223	0.016	0.024	0.062	0.153	0.141	0.300	0.191	0.232

Table contd.

Protected Area Network	Code	Gaur		Himalayan serow		Leopard cat		Marbled cat		Masked palm civet		Muntjac	
		Mean	%	Mean	%	Mean	%	Mean	%	Mean	%	Mean	%
Bumdeling Wildlife Sanctuary	BWS	0.013	0.621	0.461	4.373	0.221	2.774	0.214	6.373	0.075	1.517	0.375	2.571
Jigme Dorji National Park	JDNP	0.001	0.081	0.354	6.797	0.186	4.730	0.186	11.198	0.115	4.726	0.304	4.212
Jigme Khesar Strict Nature Reserve	JKSNR	0.003	0.068	0.485	2.239	0.194	1.188	0.184	2.672	0.062	0.608	0.306	1.019
Jigme Singye Wangchuck National Park	JSWNP	0.049	3.227	0.406	5.480	0.382	6.830	0.233	9.877	0.157	4.527	0.585	5.704
Phrumsengla National Park	PNP	0.015	0.515	0.430	3.084	0.262	2.484	0.138	3.120	0.069	1.057	0.486	2.515
Phipsoo Wildlife Sanctuary	PWS	0.761	7.819	0.267	0.559	0.621	1.720	0.173	1.140	0.385	1.721	0.760	1.147
Royal Manas National Park	RMNP	0.549	21.755	0.252	2.033	0.600	6.414	0.263	6.683	0.386	6.650	0.729	4.248
Sakteng Wildlife Sanctuary	SWS	0.006	0.167	0.284	1.665	0.220	1.708	0.080	1.471	0.025	0.318	0.244	1.033
Wangchuck Centennial National Park	WCNP	0.001	0.083	0.353	7.141	0.181	4.854	0.135	8.590	0.089	3.858	0.268	3.917
Jomotshangkha Wildlife Sanctuary	JWS	0.475	6.390	0.248	0.680	0.583	2.114	0.139	1.197	0.365	2.136	0.670	1.324
JDNP-JSWNP	BC2	0.013	0.139	0.505	1.085	0.213	0.606	0.097	0.653	0.064	0.296	0.707	1.096
JKSNR-JDNP	BC1	0.000	0.001	0.282	0.331	0.117	0.182	0.081	0.297	0.043	0.107	0.263	0.222
PNP-JSWNP-RMNP	BC4	0.017	0.330	0.381	1.509	0.241	1.263	0.161	2.002	0.198	1.671	0.594	1.698
JSWNP-RMNP-PWS	BC3	0.243	3.482	0.523	1.525	0.398	1.537	0.148	1.354	0.406	2.529	0.772	1.625
JWS-SWS	BC6	0.045	0.279	0.435	0.552	0.260	0.438	0.127	0.506	0.228	0.618	0.582	0.533
JSWNP-JDNP-WCNP	BC8	0.004	0.131	0.378	2.745	0.182	1.746	0.062	1.410	0.081	1.254	0.483	2.530
RMNP-JWS	BC5	0.536	4.378	0.152	0.253	0.510	1.123	0.046	0.242	0.361	1.282	0.731	0.878
PNP-BWS	BC7	0.010	0.028	0.534	0.310	0.315	0.243	0.087	0.159	0.157	0.194	0.642	0.269

Table contd.

Protected Area Network	Code	Sambar		Tiger		Wild pig		Yellow-throated marten		All species	
		Mean	%	Mean	%	Mean	%	Mean	%	Mean richness	% richness
Bumdeling Wildlife Sanctuary	BWS	0.212	1.988	0.141	3.437	0.434	3.465	0.258	3.517	3.442	3.188
Jigme Dorji National Park	JDNP	0.206	3.908	0.459	22.605	0.245	3.945	0.217	5.971	3.006	5.625
Jigme Khesar Strict Nature Reserve	JKSNR	0.171	0.782	0.114	1.348	0.364	1.412	0.212	1.407	2.867	1.291
Jigme Singye Wangchuck National Park	JSWNP	0.410	5.471	0.290	10.067	0.394	4.479	0.367	7.113	4.914	6.474
Phrumsengla National Park	PNP	0.299	2.117	0.108	1.995	0.511	3.081	0.314	3.230	4.087	2.859
Phipsoo Wildlife Sanctuary	PWS	0.605	1.252	0.186	1.002	0.588	1.034	0.230	0.691	6.924	1.413
Royal Manas National Park	RMNP	0.537	4.284	0.298	6.170	0.398	2.700	0.320	3.715	6.501	5.120
Sakteng Wildlife Sanctuary	SWS	0.211	1.219	0.135	2.029	0.250	1.234	0.206	1.737	2.594	1.482
Wangchuck Centennial National Park	WCNP	0.175	3.499	0.337	17.487	0.265	4.507	0.204	5.930	2.688	5.304
Jomotshangkha Wildlife Sanctuary	JWS	0.559	1.513	0.247	1.735	0.755	1.739	0.161	0.634	6.201	1.657
JDNP-JSWNP	BC2	0.457	0.971	0.079	0.434	0.666	1.202	0.282	0.870	4.368	0.915
JKSNR-JDNP	BC1	0.170	0.197	0.093	0.280	0.187	0.185	0.173	0.292	1.871	0.214
PNP-JSWNP-RMNP	BC4	0.366	1.434	0.152	1.542	0.479	1.595	0.430	2.445	4.445	1.717
JSWNP-RMNP-PWS	BC3	0.494	1.425	0.117	0.874	0.569	1.397	0.366	1.533	5.665	1.612
JWS-SWS	BC6	0.343	0.431	0.138	0.451	0.442	0.472	0.389	0.710	4.631	0.574
JSWNP-JDNP-WCNP	BC8	0.348	2.500	0.147	2.744	0.432	2.639	0.277	2.891	3.363	2.383
RMNP-JWS	BC5	0.659	1.084	0.116	0.494	0.788	1.103	0.097	0.233	5.590	0.907
PNP-BWS	BC7	0.406	0.234	0.030	0.045	0.574	0.280	0.379	0.317	4.248	0.241

Mean relative richness (Mean) = average of habitat suitability pixels of each species
*Percent habitat suitability (%) = sum of pixels with values < 0 in each PA or BC / total sum of suitable pixels across all PAs and BCs * 100*

3.4 Simulation of areas of high conservation importance

We present the simulated optimal protected area selection rasters for each species in the supplementary material (Figures S20). As exemplars, given space limitations, we present only two species here (Figure 5), in addition to the weighted multiple species selection raster (Figure 4).

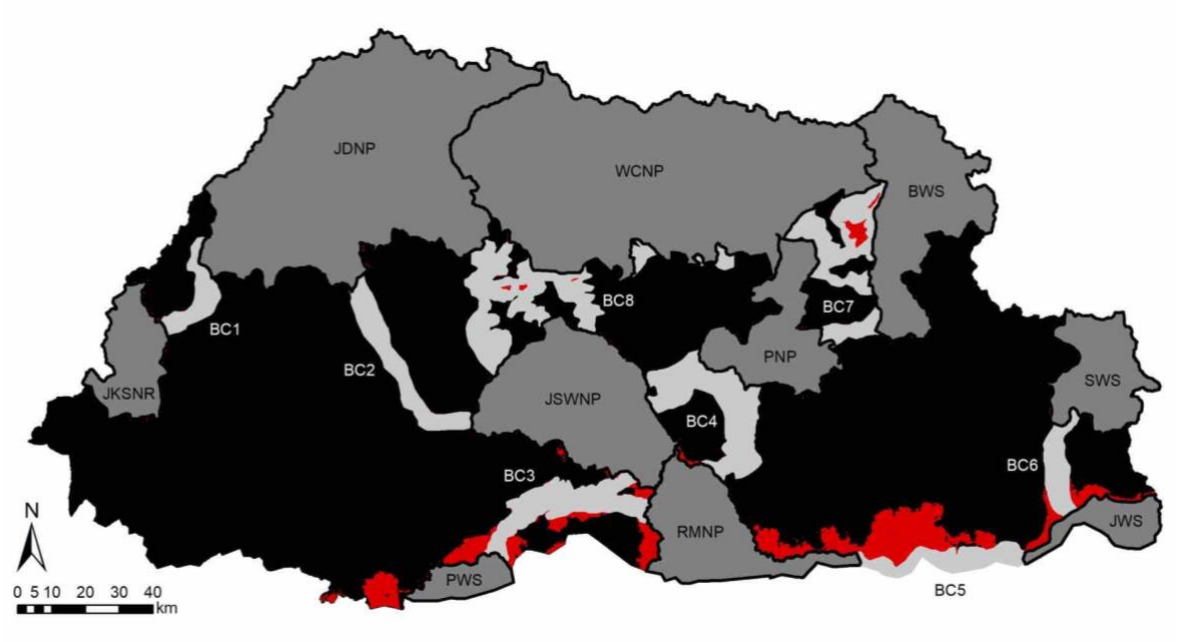


Figure 4. Recommended optimal additions to the protected area network. The red polygons are areas with high habitat suitability for all sixteen species. Dark grey and light grey polygons represent protected areas and biological corridors, respectively. JKSNR – Jigme Khesar Strict Nature Reserve, JDNP – Jigme Dorji National Park, WCNP – Wangchuck Centennial National Park, JSWNP - Jigme Singye Wangchuck National Park, PNP – Phrumsengla National Park, RMNP – Royal Manas National Park, PWS – Phipsoo Wildlife Sanctuary, JWS – Jomotshangkha Wildlife Sanctuary, SWS – Sakteng Wildlife Sanctuary, BWS – Bumdelling Wildlife Sanctuary, BC – Biological Corridor

3.5 Conservation areas for Dhole and Asian black bear

Dhole had a high proportion of potential additional optimal conservation areas adjoining the protected areas JKSNR, JSWNP, PNP and BWS, and biological corridors connecting JSWNP and JDNP, JSWNP and WCNP and PWS and RMNP (Figure 5A). Similarly, for Asian black bear, a large proportion of optimal additional conservation areas lie adjoining JKSNR, JSWNP, PNP and BWS and biological corridors connecting JSWNP and JDNP, RMNP and PNP and RMNP and JSWNP, JSWNP and WCNP and JWS and SWS (Figure 5B).

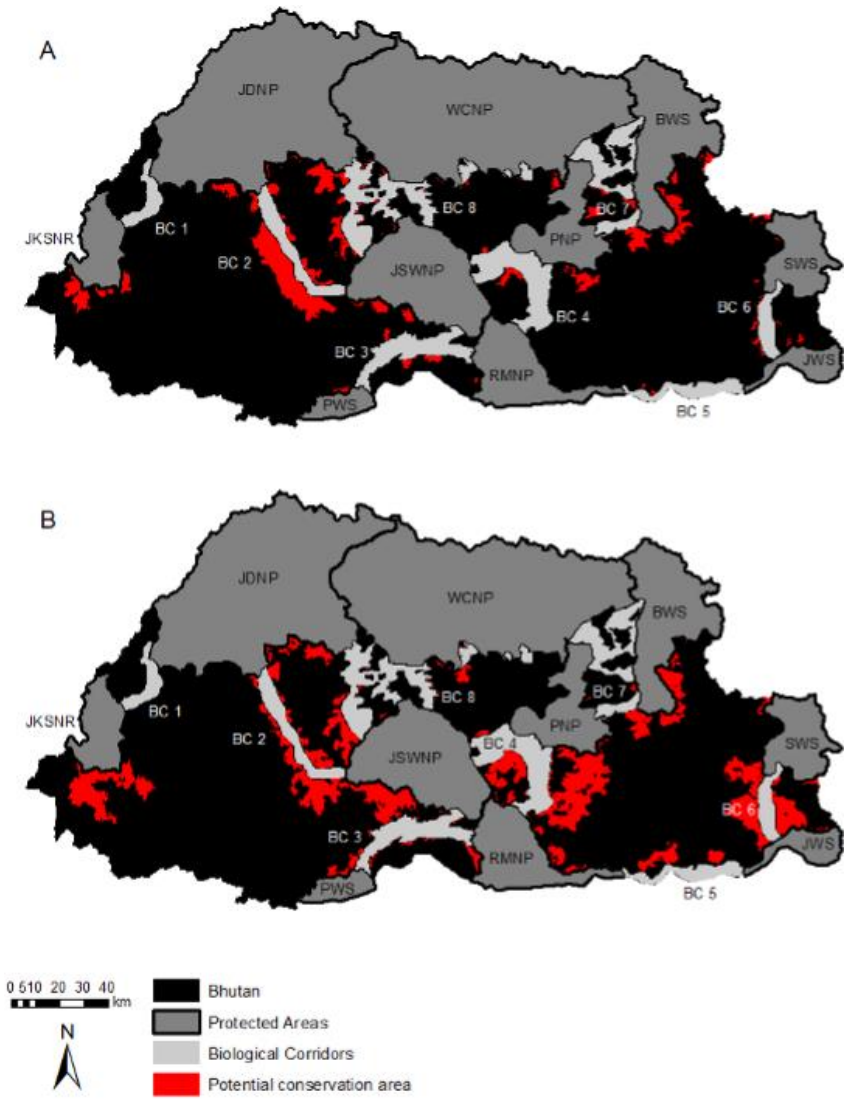


Figure 5. Optimization of priority conservation areas (red polygon) for dhole (A) and Asian black bear (B) identified through simulation based on habitat quality, proximity to existing protected area and connectivity across the population

3.6 Relative similarity and overlap of optimal cells between species

The full pair-wise correlation matrix (Figure 6a) shows that, for several species, their optimal additional protected areas intersect relatively poorly with those of most other species and for the multi-species scenarios (e.g., wild pig, masked palm civet). It also shows several that appear to be relatively strongly associated with optimal new conservation areas for multiple other species. For example, there is a high correlation between tiger-dhole, tiger-marbled cat, tiger-clouded leopard, leopard cat-gaur, common leopard-dhole, common leopard-marbled cat.

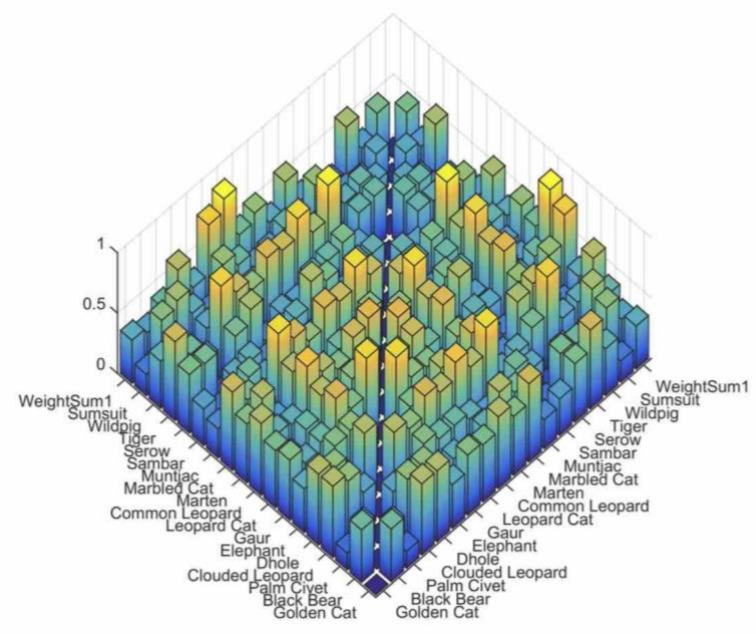


Figure 6a. Pixel-wise correlations between values in the output protected area selection raster (value 0-50) between each pair of species and the two multi-species scenarios. The height of the bar is proportional to the strength of the correlation. This shows the strength of the match between the predicted optimal protected areas between each pair of species. A high correlation means that a pair of species has high overlap between areas of high frequency of selection in the simulation of optimal new protected areas. A high correlation means that areas that are optimal for protection for one species are optimal for protection of the other as well

3.7 Efficacy of multi-species prioritization strategies in providing optimal protection for each species

There were large differences in the performance of the two multi-species selection scenarios in terms of their overall efficacy of providing optimal selection for each species, and across species (Figure 6b). The unweighted sum of habitat suitability scenario had generally low performance, as measured by the correlation between the optimally selected areas for protection and predicted suitability across species (Figure 7a). In particular, the unweighted analysis performed very poorly in protecting the species that had the largest overall umbrella performance (marbled cat, tiger, clouded leopard, common leopard, guar). It had a higher performance for civet, muntjac, black bear, which are notably among the weaker umbrella species and also relatively lower conservation priority.

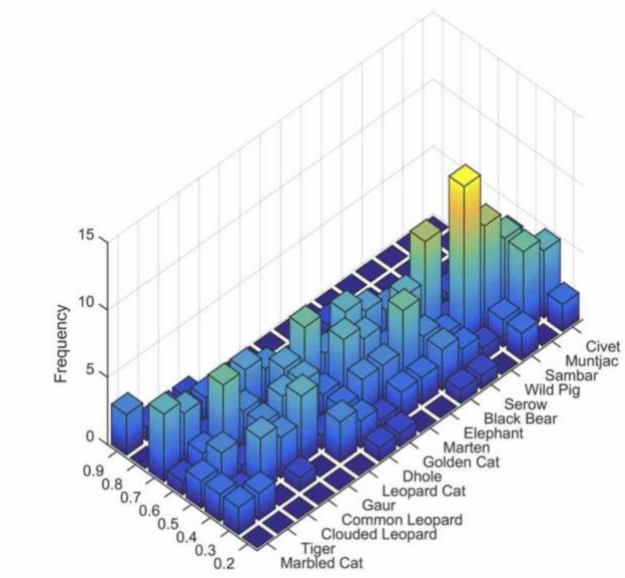


Figure 6b. Frequency of different strengths of pixel-wise correlation between the optimal protected area selection raster for each species with the 15 other species. This figure shows the results of Figure 6a as histograms, ranked from highest frequency of high correlation to lowest. A species with many high correlations of optimal additional protected area with other

species optimal protected areas means that protecting optimal areas for that species would also protect optimal areas for many other species

In contrast, the conservation-priority-weighted multi-species scenario performed much better overall, based on average correlation across individual species (0.53 vs 0.26), and performed particularly well relative to the most effective umbrella species (Figure 7b, marbled cat, tiger, clouded leopard, common leopard, and gaur) and the species with the highest conservation importance (Table S2).

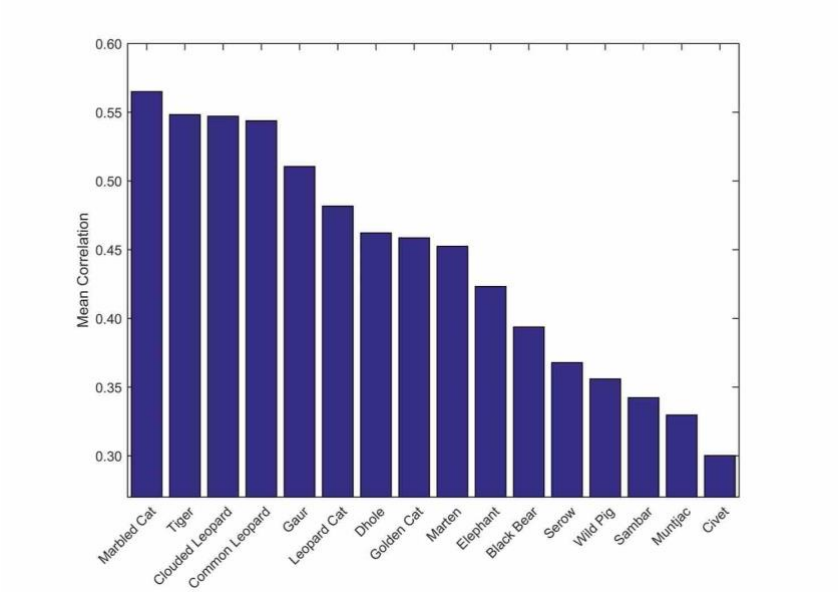


Figure 7a. Mean pixel-wise correlation between the optimal protected area rasters for each species and all 15 of the other species. This gives a single value of the relative effectiveness of protecting optimal additional areas for each species in terms of its ability to protect optimal areas for all other species simultaneously. A species with a high average correlation between the optimal protected area rasters of all other species is a good umbrella species whose protection provides effective protection of many other species as well

3.8 Umbrella species effectiveness

Most ungulate species emerged as effective umbrella species based on the mean percentage of total suitability (Figure 8a). Muntjac was the most effective umbrella followed by wild pig, serow and sambar. Amongst the carnivores, Asian golden cat was relatively strong umbrella species. On the contrary, gaur was the least effective umbrella species probably due to small and restricted geographic range which may not offer wider habitat protection like the more ubiquitous muntjac or wild pig. Indicator analysis based on cluster dendrogram yielded five distinct clusters (Figure 8b).

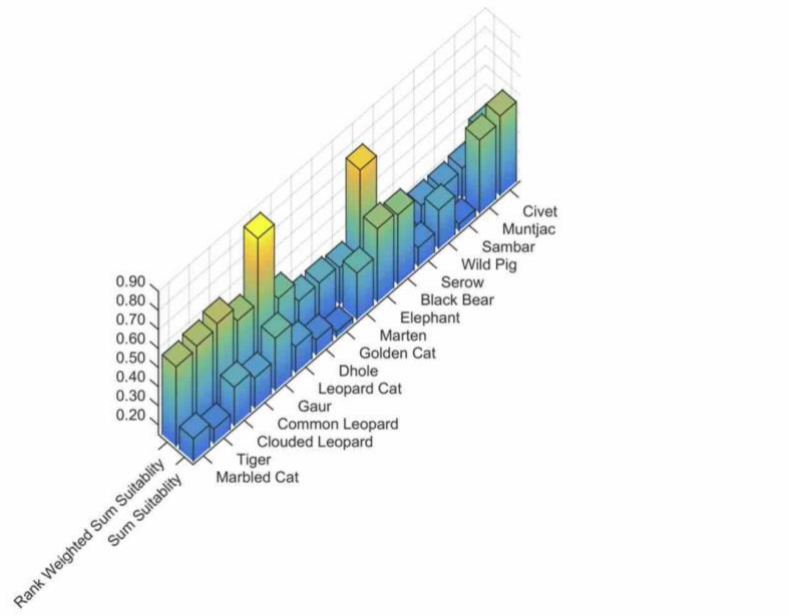


Figure 7b. Pixel-wise correlation between the value of the optimal protected area selection raster for each species and the two multi-species selection scenarios. This figure shows the effectiveness of the two multi-species conservation scenarios (weighted and unweighted) in terms of their ability to protect the optimal unprotected areas for each individual species

3.9 Indicator species effectiveness

The multivariate hierarchical cluster analysis identified five species groups based on similarity in their spatial patterns of habitat suitability (correlation of habitat suitability predictions, Figure 9). Cluster 1 consisted of three carnivores (marbled cat, clouded leopard

and yellow-throated marten) and one omnivore (Asian black bear). Cluster 2 had two large ungulates (Asian elephant and gaur) and one omnivore (Masked palm civet). Cluster 3 was the largest group with five species: three of which were ungulates (muntjac, wild pig and sambar) and the other two were felids (leopard and leopard cat). Tiger was the singleton species in cluster 4. Finally, cluster 5 consisted of two medium-sized carnivores (Asian golden cat and dhole) and one ungulate (Himalayan serow).

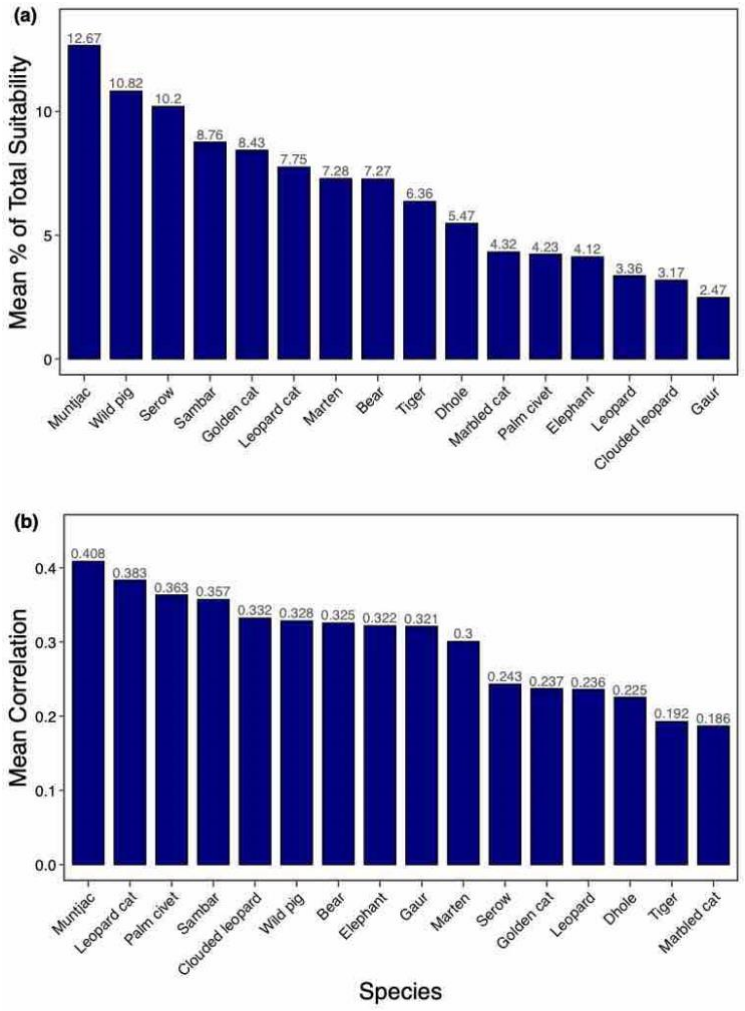


Figure 8. Mean percentage of total suitability and mean correlation between optimal protected areas to identify umbrella (a) and indicator (b) species

Asian black bear and yellow-throated marten in cluster 1 were paired more similarly together than marbled cat and clouded leopard and occur widely in Bhutan. Therefore, we would suggest one of these species (Asian black bear or yellow-throated marten) as a good choice of indicator for species in that cluster. In cluster 2, Asian elephant and gaur were clustered more closely than masked palm civet. The range of the former two is smaller than the latter but they represent better indicator species for lowland forest ecosystems and megafauna that depend on them. In cluster 3, besides common leopard, the four species (muntjac, wild pig, sambar and leopard cat) were closely clustered and are fairly ubiquitous. Thus, they represent a strong indicator of each other while common leopard has relatively weaker association with the full cluster. Therefore, we suggest common leopard as a focal species, but sambar as an indicator species for these lowland forest associated species. Tiger, in the fourth cluster, is the sole indicator species. In the fifth cluster, all three species join near each other and hence they are equally good indicator species. However, from a conservation point of view, dholes are a better indicator, given their conservation interest, ecosystem role as an apex predator, and their association with a wide range of habitat.

Muntjac had the highest mean habitat suitability correlation with all other species (0.408) serving as a top overall indicator species across all species groups. Leopard cat (0.383) and masked palm civet (0.363) also displayed high mean correlation thus serving as important carnivore and omnivore indicators, respectively.

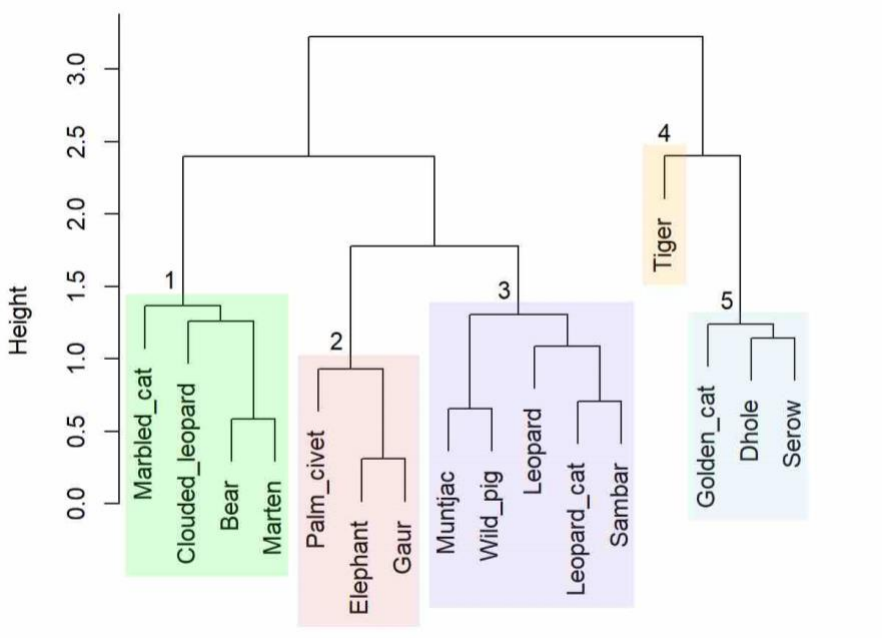


Figure 9. Cluster dendrogram used for identifying indicator species. The five clusters (numbered 1:5) are based on the predictions from the generalized linear model fitted to binary data of 16 terrestrial mammals in Bhutan

4 Discussion

Our analyses highlight the importance of multiscale assessment in identifying predictors influencing species distribution. In general, habitat suitability was positively influenced by environmental variables while anthropogenic variables had an overall negative influence. We assessed the effectiveness of the existing protected area network (PAN) and using simulations, identified potential conservation areas outside the existing PAN. Forests outside PAN across the south-central region have a high potential for terrestrial mammal conservation. Our indicator and umbrella species assessments suggest that multiple common and widely distributed species could offer broader protection than a single apex predator.

4.1 Species-habitat relationships

Multi-scale species-habitat modeling revealed that our study species, in general, were positively associated with protected areas and forest cover, and negatively related to anthropogenic variables. Most of these relationships were strongest at relatively broad spatial scales. The selection of variables at a broad scale suggests the importance of preserving large landscapes under legal protection. The broad-scale negative association with anthropogenic variables, conversely, indicates that human land uses can have effects that extend beyond the immediate footprint of these activities, up to 16km in our models. Our findings suggest that terrestrial wildlife species in Bhutan often require extensive habitat and are often sensitive to human disturbance at relatively broad scales (Karanth et al., 2017). In terms of management, this highlights the importance of protecting large extents of natural ecosystems with low human impacts for species that are sensitive to anthropogenic disturbance and which have large home range requirements.

Forest-related variables had a strong positive effect on 50% of the modelled species (n=8, Table 2), highlighting the importance of forest in providing habitat for native wildlife in Bhutan. A similar finding was reported in a more diverse composition of 45 mammals showing a strong positive affinity for forest cover (Penjor et al., 2020). Topographical complexity seems to be positively related to habitat use of the majority of species we studied in Bhutan, as observed through the positive association between habitat use and topographical variables represented by slope and terrain roughness. The generally rugged topography of Bhutan is inaccessible to human settlement and unsuitable for agriculture farming. However, many areas that are potentially of the highest inherent ecological stability for wildlife are also facing the greatest impact by humans. These rugged landscapes likely offer refugia from human disturbance for large mobile species such as tigers (Krishnamurthy

et al., 2016, Reddy et al., 2019) as well as smaller meso-carnivores like yellow-throated marten (Vergara et al., 2016).

Approximately 50% of the modelled species were negatively associated with agriculture, suggesting that a landscape perforated or fragmented by agriculture, in general, is less suitable for the occurrence of the wildlife species (Table 2). Although agriculture may offer herbivores such as muntjac and wild pig access to high-quality forage, it is often at the cost of lethal conflict (Woodroffe et al., 2005). This is often even more serious for carnivores, such as leopards, which face a severe risk of fatal conflict in agricultural-village mosaic lands (Rostro-Garcia et al. 2016). While fragmentation and intermediate extents of an agricultural mosaic can sometimes increase habitat diversity, leading to higher densities and diversity of wildlife species (Cushman and McGarigal, 2003), increasing fragmentation of natural ecosystems by agriculture often brings animals close to humans and thereby escalates conflict (Sukumar, 2003). Past studies demonstrated that increasing extent and heterogeneity of agricultural land either contributed to elevated conflict between large felids and human (Rostro-García et al., 2016) or decreased occupancy of large ungulates in Bhutan (Penjor et al., 2020).

Biodiversity conservation in agricultural landscapes is costly and has produced mixed results (Green et al., 2005), raising the appeal of land-sparing, where existing farmland is intensively managed and improved to ‘spare’ other wildlife habitats (Green et al., 2005, Feber et al., 2015b). However, this tradeoff is context-dependent, and in places where remnant habitat in highly productive agricultural landscapes is essential for biodiversity, and/or the protected area is small in size compared to the species home range, it may be necessary to adopt a combination of land-sparing and land-sharing approaches (Johansson et

al., 2016). Multi-species, quantitative prioritization of areas of highest biodiversity value, as presented here, provides an objective basis to evaluate the relative merits of land-sparing and land-sharing conservation strategies.

4.2 Effectiveness of the existing PAN in protecting species richness

Bhutan has the constitutional mandate of maintaining 60% of the total geographical land under forest and identifying and protecting key biodiversity areas outside the existing PAN. However, there is little scientific guidance currently available to guide the optimal selection of areas for designation as new protected or conservation areas. Our analyses show that the south-central region encompassing JSWNP and RMNP had high effectiveness in protecting mean and total relative species richness (Figure 3). PWS and JWS were effective in protecting mean richness per unit area but less effective in protecting the total proportion of species richness. JSWNP and RMNP, together with Manas Tiger Reserve in India, form one of the largest (~6500 km^2) contiguous protected landscape in Asia, and one of the important global tiger conservation landscapes (WWF, 2015). The ecosystems within this landscape range from tropical grassland to snow-capped mountain, supporting a wide spectrum of wildlife. Further, JSWNP and RMNP have been recently accredited as CA|TS sites (conservation assured tiger standards). CA|TS certifies and credits important tiger conservation sites with high standards in protecting tigers, their prey and habitat (Pasha et al., 2018). Thus, our findings provide evidence that these PAs are not only important for large species but also medium-sized and yet smaller terrestrial mammals (Dorji et al., 2019) and these additional conservation areas could bolster the protected landscape from anthropogenic pressure and perhaps also foster the maintenance of the ecological integrity of this important wildlife conservation landscape in the eastern Himalayas.

Biological corridors (BC) also displayed high variability in terms of mean relative species richness and proportion of total cumulative relative species richness. A similar finding was reported by Dorji et al. (2019), who found that mammal diversity in BCs and non-protected areas were lower than in protected areas, confirming that PAs are critical to large mammal conservation in Bhutan. But we believe that this does not necessarily mean that the current BCs do not serve their purpose. We found that several designated BCs provided important habitat for species and biodiversity overall.

4.3 Optimal protection of species-rich areas outside PAN

By implementing a newly developed model to optimize the selection of new protected areas to maximize protection of quality habitat that is functionally connected to existing protected areas, we found several areas of conservation importance abutting the existing protected areas and BCs. Based on the spatial optimization to identify areas for protection outside of the current PAN, we found that the conservation-priority weighted sum of habitat suitability scenario for multi-species presented an overall better picture of optimal protection than the unweighted sum of habitat suitability scenario. This indicates that prioritizing species weighting based on conservation status improves the solution for all species collectively, and not just for those of highest conservation risk. Such weighted prioritization of species is vital to provide a better picture of conservation in an increasingly changing landscape (Sætersdal and Gjerde, 2011). Several optimal areas adjoining the existing PAN were identified through simulation. For example, subtropical forests were identified abutting RMNP, PWS and JWS and BCs 3, 5 and 8. These areas are minimally inhabited or not at all in some case and could offer important refuge to a wide spectrum of species (indicated by the weighted sum of multispecies richness). The weighted multi-species scenario performed well for species which could be considered as conservation focal species or umbrella species, such as tiger,

common leopard, clouded leopard, gaur and elephant. These species are declining rapidly globally and are increasingly at risk of extinction even though a large portion of conservation funding is directed to securing their future. Our analysis further strengthens the evidence that conservation of the habitat of these species would help provide overall protection for a wide range of species under their umbrella. It is relatively easy for conservation managers to garner support for species which are inherently respected and popular in history, religion and culture (Macdonald et al., 2015, Macdonald et al., 2017). Tiger and elephant, for example, are widely represented in Buddhist and Hindu mythology and although these species come into conflict with humans, they are better tolerated than other species such as wild pig or Asian black bear (Sukumar, 2003, Kusi et al., 2020). This makes them more effective as ambassador (Macdonald et al., 2017) or flagship species for conservation.

Based on the hotspots of relative species richness, we identified several focal areas outside of the existing biological corridors (Figure 9 *blue-colored numbers*). These are (i) subtropical and cool broadleaved forest in Samtse (Figure 3 [1]) adjoining JKSNR, (ii) cool broadleaved and temperate forest in Zhemgang (Figure 3 [2]) contiguous to PNP and BC4 (connecting PNP, JSWNP and RMNP), (iii) subtropical broadleaved forest in Pemagatshel (Figure 3 [3]) adjoining BC5 which connects RMNP to JWS, (iv) subtropical and cool broadleaved forest in Chhukha (Figure 3 [4]) forming contiguous forest corridor with Buxa Tiger Reserve in India, (v) subtropical and cool broadleaved forest adjoining JWS (Figure 3 [5]) and (vi) cool broadleaved forest adjoining BWS (Figure 3 [6]) to the east. These focal areas could be high priority candidates for conservation outside PAN because of their high predicted species richness and could serve as habitat for species while also bolstering the current PAs against the growing anthropogenic impacts.

4.4 Identification of umbrella and indicator species

Muntjac, wild pig, Himalayan serow, sambar and Asian golden cat emerged as the most effective umbrella species for optimal protected area designation. It might be surprising that an ungulate was identified as the most effective umbrella species in a landscape containing powerful and charismatic predators like tiger and common leopard. However, our results, based on a simulation study, suggest that trophic level and body size alone are not necessarily the best indicators of umbrella species effectiveness (Cushman and Landguth, 2012). Common species may often serve as a better umbrella due to their adaptability and likelihood of surviving dynamic and hostile environments (Berger, 1997a). It would be sensible to design conservation programs to protect areas using more than one umbrella species. Our results suggest selection of four ungulates and one medium-sized carnivore as umbrella species, which have a broader habitat niche, more extensively occupied habitat and higher probability of long-term survival than the rare apex carnivores (Caro, 2003b). Lastly, for an organism at the higher trophic level to survive (example the apex predators), healthy prey populations are essential (Ripple et al., 2016). Designating ungulate species, which are generally much more widespread and abundant than apex predators, as umbrella species ensures that top carnivores like tiger, leopard and dhole are provided with sufficient prey populations, which enhances their reproductive potential and ultimately regulating food chain, providing check and balance to the ecological food web.

Our indicator analysis revealed findings that will benefit management as well as enhance our understanding of the choice of indicator species. The five clusters are the five groups of species that are most internally similar in terms of their patterns of habitat quality across Bhutan. Species in cluster 1, marbled cat, clouded leopard, Asiatic black bear and yellow-throated marten, are associated with highly forested upland habitats. One of these species

could be chosen as an indicator to monitor the condition of this group of species and other species associated with the same forested upland environment. Cluster 2, in contrast, consists of three species, including two herbivorous megafauna, elephant and gaur. Given the high conservation importance of elephant and guar, it is likely that future monitoring will be employed to track the populations and distributions of both species. Their close clustering, however, shows they inhabit very similar low land, flat forested habitats. The third cluster contains muntjac, wild pig, common leopard, leopard cat and sambar. This species group is associated with low elevation river valley ecosystems and lower slopes of foothill landscapes, often in mosaics of agricultural and forest lands. It is likely that common leopard will be individually the focus of conservation given its high charisma (Macdonald et al. 2017). Our results suggest that sambar would be a good choice as an additional indicator of the habitat condition of valley mosaic habitats and the species associated with them. Tiger is the sole species in cluster 4, suggesting that its habitat characteristics are most different from all of the other species. It, therefore, is a poor indicator of other species; but given its exceptional high conservation profile, it likely will be the focus of conservation planning in its own right. It is important, however, to note that based on our results conservation planning optimized for tiger is not likely to be optimal for most other species. This emphasizes the importance of optimizing multispecies conservation planning. The fifth cluster consists of golden cat, dhole and serow. These species are associated with upland ecosystems with relatively low human footprints and high forest cover.

Conservation planning based on indicator and umbrella species is controversial (Carignan and Villard, 2002). On the one hand, a focus on umbrella/indicator species can make conservation planning simpler, monitoring more tractable and communication with public stakeholders easier, which helps managers leverage better community support (Macdonald et

al., 2012). On the other hand, many of the species identified as the best indicators and umbrella species in our analysis are conflict-prone species such as tiger, Asiatic black bear, Asian elephant, which can reduce public support for conservation planning built around them.

Conservation should strive to a strike balance between species protection and human wellbeing. Bhutan has a largely agrarian population, subsisting on small-scale farming and livestock rearing. Crop and livestock depredation by wild animals results in significant loss of annual household income in Bhutan (Wang and Macdonald, 2006, Sangay and Vernes, 2008) leading to increasingly aversive sentiment towards wildlife (Woodroffe et al., 2005). Therefore, alternatives that promote coexistence should be integrated into conservation management plans. Community participation in conservation is an essential approach to wildlife conservation and management (Andrade and Rhodes, 2012). A joint management approach involving communities could be initiated in areas of high conservation importance outside protected areas, offering stewardship and regulating resource extraction by providing alternatives such as ecotourism.

4.5 Scope and limitations

Although the current PAN in Bhutan protects a wide array of ecosystems, it omits some areas of critical biodiversity value which are increasingly at risk due to expanding infrastructure, hydropower and other developments. While our study provides a comprehensive multi-species and multi-scale approach for identifying important habitat and conservation areas, future work should improve and enhance the robustness of the models by including human dimensions of conservation, such as the threat to wildlife arising from direct persecution, human-wildlife conflict and ancillary pressure on wildlife habitats from expanding human

settlement. In addition, our assessment of BCs is based on their habitat suitability and not their functional performance in facilitating movement. Future work could use telemetry (e.g. Cushman et al., 2016) or landscape genetics (e.g. Cushman et al., 2006) to demonstrate the effectiveness of the BC network for facilitating movement and gene flow (Zeller et al., 2018). We also acknowledge that the current habitat suitability analyses do not account for detection heterogeneity arising from the non-detection of species (MacKenzie et al., 2002). Non-detection does not imply absence, but it could mean that the species was not present during our survey or the survey effort was inadequate to detect it. It is difficult to distinguish the observation process from the latent ecological process when detection probability is unaccounted. Models which cannot distinguish between state process (or ecological process, e.g., site occupancy) and observation process (i.e., variability in sampling process) often confuse between the true state of the animal and its absence due to one-time survey of a site and hence results in an underestimation of occupancy. Confusion between these processes risks spurious results, especially when considering species that are both cryptic and of high conservation concern. Temporal replication, therefore to estimate detection probability, improves the estimates of species diversity for a site (Iknayan et al., 2014). Hence, we caution readers to interpret our habitat suitability only as a probability of relative use (apparent) and not strictly as true occupancy. Finally, the low AUC for some species (<0.75; Table 2) cautions us that for these species the prediction accuracy is only slightly better than by chance. However, AUC cannot be considered as a sole measure of a model's predictive power because it is in itself inappropriate for presence/absence data (Lobo et al., 2008).

5 Conclusions

We urge policymakers and conservation managers to broaden the scope of conservation by exploring and prioritizing alternative conservation areas based on multi-species optimization

that combines both habitat suitability and network connectivity, as we present here. This study highlights the need to protect optimally located species-rich areas outside the current PAN (Tyrrell et al., 2020) and to reduce direct human-wildlife conflict through intensive anti-poaching patrols and law enforcement and community participation. Taking proactive measures such as optimally identifying and expanding protection would not only help fulfil global biodiversity targets (e.g., Aichi Targets) but also set new standards for science-based conservation and replenish the motivation for conservation amid escalating wilderness loss to human pressure.

6 Authors' contributions

All authors contributed to the study conception and design. Material preparation and analyses were performed by Ugyen Penjor supported by Samuel Cushman. The first draft of the manuscript was prepared by Ugyen Penjor. All authors contributed to subsequent drafts and gave the final approval for publication.

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Chapter 3

Landscape potential for supporting multispecies population connectivity in a Himalayan biodiversity hotspot

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Abstract

Context: Successful conservation hinges on the reliable prediction of large-scale population core habitats and dispersal corridors. However, sole reliance on single species connectivity has produced mixed results and, in most cases, failed to protect other species under the appealing but often unfulfilled guise of umbrella protection.

Objectives: The main objectives of this study were: 1) to identify core habitats and dispersal corridors for population connectivity of 15 terrestrial mammal species across the nation of Bhutan, 2) to develop composite multispecies connectivity maps and identify gaps in the existing protected area network, 3) to evaluate the effectiveness of connectivity umbrella and indicator species, and 4) quantitatively to prioritise core areas and dispersal corridors for the focal species.

Methods: We used two spatially synoptic methods to identify core habitats and dispersal corridors for each species: resistant kernel density (KD) and factorial least-cost path (LCP). We summed and multiplied individual KD and LCP to produce multispecies core habitats and corridors. We used correlation and cluster analyses to identify focal umbrella and indicator species, respectively. Finally, we performed a quantitative ranking to prioritise core areas and corridors for the focal species.

Results: Asian elephant was identified as the most effective umbrella species for core habitat protection followed by leopard cat, muntjac and sambar deer. Ungulates were generally more effective than carnivores in core habitat protection. Muntjac was potentially the most effective umbrella species for corridor protection followed by mesocarnivores such as masked palm civet, leopard cat and yellow-throated marten. Based on multivariate cluster

analyses of KDs and LCPs, we identified six focal indicator species for core and corridor protection: tiger, dhole, clouded leopard, Asiatic black bear, Asian elephant, and sambar deer. Among the focal indicator species, dholes had the most fragmented core habitat while Asian elephant had the single largest unfragmented core. Most core areas and dispersal corridors outside the protected area network (PAN) were found in southern Bhutan.

Conclusions: Our results show that large parts of Bhutan offer suitable core areas and corridors for multispecies conservation. The existing PAN encompasses most predicted cores and corridors, but a substantial portion remains outside the protected network. Identifying connectivity patterns of multiple species, mapping distribution of core areas and corridors and potential barriers and fracture zones provides useful information needed to effectively manage wildlife in diverse, fragile, and dynamic landscapes.

Keywords: biodiversity hotspot, connectivity, core, kernel density, least-cost path, multi-species

1 Introduction

The long-term viability and sustainability of animal populations depend on the protection of critical habitats and a network of dispersal corridors that facilitates movement, gene flow and resource utilisation among them. However, growing human pressure on natural resources coupled with climate change is shrinking natural habitats throughout the world (Newbold et al., 2015a, Barlow et al., 2016). Habitat suitability and functional connectivity for many species decline with human modification leading to habitat fragmentation and loss, which may be the single largest threat to biodiversity (Noss, 1991). To counter this, identifying and

protecting core population habitats and linking them through a series of dispersal corridors is of paramount importance (Cushman et al., 2006). A well-connected landscape with large core habitats supporting populations will likely enable demographic dynamics which enable populations to fluctuate and for local extinctions to be recolonised without risking extinction in the regional metapopulation (Taylor et al., 1993). Further, large patches of habitats connected via corridors are vital to tracking climate shifts (Wasserman et al., 2012a) and allowing for range expansion (Chen et al., 2011).

Most corridor planning is based on a single, umbrella species which may or may not provide resource needs and protection to other species (Cushman and Landguth, 2012, Cushman et al., 2013a). Single focal species such as tigers are sometimes habitat generalists and thus cannot provide adequate umbrella protection (Simberloff, 1998). For example, Cushman et al. (2013) evaluated the ability of each of three focal species (swift fox [*Vulpes velox*], lesser prairie-chicken [*Tympanuchus pallidicinctus*], massasuaga [*Sistrurus catenatus*]) to serve as connectivity umbrellas for the others across the American Great Plains and found none of them were good surrogates for the others. Using a large simulation experiment, Cushman et al. (2013) evaluated the abilities of 144 species to serve as connectivity umbrellas for the others across a range of ecological niche characteristics and dispersal abilities. They found that the most commonly used focal species, such as large carnivores, were poor indicators of overall connectivity for biodiversity generally, and that in particular the parts of the landscape most vulnerable to habitat loss and fragmentation were particularly poorly matching to connectivity for those species.

As a result of the recognised shortcomings of single-species approaches to connectivity conservation, the multi-species approach to identifying core population habitats and corridor

planning is gaining popularity (Cushman et al., 2013a, Brodie et al., 2015, Brennan et al., 2020). This is because protecting a patch of habitat or corridor utilised by more than one species entails less cost and encompasses wider protection for a range of wildlife. Several studies have shown that the conservation effectiveness of connectivity designs is greater when the conservation of core habitats and corridors is strategised to meet the simultaneous needs of multiple species (Cushman and Landguth, 2012, Cushman et al., 2013a, Hand et al., 2014, Khosravi et al., 2018, Ashrafzadeh et al., 2020, Haidir et al., 2021), often resulting in better overall biodiversity protection and landscape connectivity (Cushman et al., 2013b, Brodie et al., 2015).

Several approaches exist to identify core habitats and corridors, such as cumulative resistant kernels (Compton et al., 2007, Cushman et al., 2014), least-cost path (Adriaensen et al., 2003), factorial least-cost path (Cushman et al., 2009, Cushman et al., 2013a), and current flow models (Circuitscape)(McRae et al., 2008, Brodie and Newmark, 2019). These models utilise resistance surfaces developed from GPS telemetry, expert opinion, genetic data, or habitat suitability layers (Zeller et al., 2012). The outputs of connectivity models predict and visualise core areas of animal occupation and/or connectivity linkages and delineate barriers that may fragment populations. Spatial prediction and prioritisation of core areas, corridors and barriers facilitates conservation planners to identify the drivers of habitat loss and fragmentation and develop effective strategies (Cushman et al., 2016, Cushman et al., 2018, Kaszta et al., 2020, Zeller et al., 2020).

The predictions of spatially synoptic patterns of connectivity based on resistant kernels (KD) identify all-directional dispersal (Compton et al., 2007, Cushman et al., 2010) as opposed to pair-wise corridors between predefined sources (Beier et al., 2008). This offers

greater flexibility to predict dispersal across the landscape and provides a complete picture of connectivity across space allowing identification of core population habitats (Cushman and Landguth, 2012, Cushman et al., 2014, Kaszta et al., 2020). A factorial implementation of least-cost paths (LCP) allows integration of a vast number of least-cost paths to show synoptic connectivity across large and complex landscapes (Landguth et al., 2012, Cushman et al., 2011). It helps in identifying which species have the most fragmented populations and maps the most important corridor linkages among population core areas where conservation efforts can be focused (Cushman et al., 2011, Cushman et al., 2018). Together, KD and LCP enable us to predict habitat core areas, identify fracture zones and barriers, and locate keystone linkages that provide connectivity among core areas (Cushman and Lewis, 2010, Cushman et al., 2011, Cushman and Landguth, 2012).

We assessed the landscape connectivity and corridor efficacy of 15 terrestrial mammal species in Bhutan. Bhutan lies at the intersection of two biogeographic realms: the Indo-Malayan and the Palearctic with rich biodiversity (Olson et al., 2001). Yet the fragility of the landscape makes species in this region particularly susceptible to environmental change (Penjor et al., 2020). Further, developing countries in Asia have some of the highest rates of forest conversion and degradation globally (Sodhi et al., 2004, Miettinen et al., 2011). Although Bhutan has a well-developed PAN, the structural and functional connectivity of the existing protected areas (PA) and biological corridor (BC) network (together PAN) have not been assessed yet. Rapid infrastructure development and climate change threaten to fragment wildlife habitats and drive shifts in species ranges. Thus, assessment of the efficacy of PAs and BCs is not only important for species population connectivity but also to provide crucial information to conservation managers to develop adaptive management plans in the face of growing human impacts and climatic change.

Using the habitat suitability models developed in Penjor et al., (2021), we built resistance surfaces for 15 terrestrial mammal species. We used a spatially synoptic approach (e.g., Cushman et al., 2014) and two complementary methods to assess landscape connectivity for these species. First, to define and quantify core areas of high-density movement for each species we applied cumulative resistant kernels (Compton et al., 2007). Second, to map and quantify dispersal corridors (narrow linkages) between the core area we used the factorial least-cost paths analysis (Cushman et al., 2013a). Using multivariate cluster analysis, we then identified focal species across carnivores and herbivores based on how well their predicted connectivity intersected with the connectivity of the other species. Finally, we used focal species to rank and prioritise core areas and corridor importance. Although the fact that no two species use habitat in identical ways imposes trade-offs on multi-species connectivity planning, this approach, however, may be more efficient than the single-species approach in protecting biodiversity and species communities per se (Early and Thomas, 2007, Carroll et al., 2010). Broadly, we aim to identify core population areas, linkages and barriers for each species individually and multiple species collectively across Bhutan, and to assess the functional connectivity of the current PA and BC network to guide conservation planning.

2 Materials and Methods

2.1 Resistance surfaces

We built resistance surfaces from the multi-scale habitat suitability models developed in Penjor et al. (2021). The details of the multi-scale habitat suitability modelling approach are presented elsewhere (e.g., Macdonald et al., 2018a, Macdonald et al., 2019b). Briefly, the analysis used a presence/absence design based on an extensive nationwide camera trapping

dataset coupled with multi-scale optimisation using logistic regression to predict habitat suitability across the full extent of Bhutan for each species.

Ideally, resistance surfaces should be developed using species movement or landscape genetic data, given that such data directly provide information on species movement in relation to landscape features (Zeller et al., 2016, Zeller et al., 2018). However, given that movement and genetic data are often lacking for many species in many parts of the world, habitat suitability layers are often used as surrogates (Mateo-Sánchez et al., 2015, Keeley et al., 2016). Studies show that habitat suitability often is an inferior predictor of landscape resistance in comparison to models built with genetic or movement data (Wasserman et al., 2010). However, when such data are not available habitat suitability may be the best proxy for estimating landscape resistance.

Several studies have suggested that the relationship between habitat suitability and resistance is non-linear (Mateo-Sánchez et al., 2015, Keeley et al., 2016). To transform the habitat suitability layer to the resistance surface, we used a negative exponential function (Mateo-Sánchez et al., 2015, Keeley et al., 2016, Kaszta et al., 2020, Haidir et al., 2021). We transformed habitat suitability to resistance using the formula,

$$R = (\exp(-1 * H/C) * 100) + Y$$

Where *R* is a resistance layer, *H* is the habitat suitability layer, *C* is the factor to determine the negative exponential relationship, and *Y* is the value used to convert minimum resistance to 1 (Figure S1).

The final resistance surface had continuous values ranging from 1 (indicating low resistance to movement) to 100 (high resistance) (Figure S2). Since the habitat suitability models did not include features impermeable to species movements such as highways, large river networks and high-density settlements, we incorporated them into the resistance surface with the resistance value of nearest neighbours. We also masked out elevation above 4500m, which was the boundary for the highest camera trapping point.

2.2 Source point locations

Accurate prediction of habitat connectivity requires animal source locations that reflect the distribution and density of the species (Cushman et al., 2013a, Cushman et al., 2018). We probabilistically distributed these source points across the habitat suitability layer such that source points were selected with a probability proportional to predicted habitat suitability (Kaszta et al., 2020). To do this, we first created a random raster with values distributed uniformly between 0 and 1. Second, we subtracted this random raster from the habitat suitability raster and reclassed pixels with positive values to reflect potential species occurrences. Finally, we randomly selected 2000 occurrence points from these potential source points that served as source locations for analysis to provide a consistent number between analysed species, which is necessary for accurate relative comparisons between species.

2.3 Connectivity modelling

To identify core areas, we used the cumulative resistance kernel method (Compton et al., 2007) and to identify linkages between them as dispersal corridors we applied factorial LCP analysis (Cushman et al., 2009). The cumulative resistance kernels predict the spatially explicit frequency of movement and the extent of the area that facilitates movement across

the landscape from a source location in suitable habitat (Compton et al., 2007, Cushman et al., 2013a). Factorial least-cost paths, on the other hand, identify paths between the points with the lowest resistance and movement cost (Cushman et al., 2013a). These two methods are complementary. LCP analysis identifies narrow movement linkages between the designated source location pairs, which is useful in the identification of dispersal corridors (areas too narrow to be inhabited by a species but can be potentially used for species dispersal) (Cushman and Landguth, 2012, Cushman et al., 2013a, Kaszta et al., 2020). Resistant kernels quantify movement across the entire landscape from designated source locations, yielding in a continuous surface quantifying the movement incidence function for every location in the landscape (not just between the source locations) (Cushman and Landguth, 2012, Cushman et al., 2013a). Therefore, only the resistant kernel analyses can be used to identify and quantify core population areas (Kaszta et al., 2020).

The resistant kernel and LCP approaches can incorporate biologically relevant information on species dispersal distance to accurately predict connectivity patterns (Cushman et al., 2013a, Cushman et al., 2013b). Due to the lack of movement data for the study species, we estimated dispersal distances using published relationships between species home range size and dispersal distances (Bowman et al., 2002). We gathered home range data through an extensive literature review for all study species across the distribution range (Table S1). For kernels, we used a direct movement threshold based on average home range size (Kaszta et al., 2020). For LCPs, we applied a threshold 4x higher than the dispersal threshold for kernels to reflect long-distance dispersal outside the established home range (Cushman et al., 2018, Kaszta et al., 2020). The resistance kernel and factorial LCP modelling were performed using UNICOR software (Landguth et al., 2012).

2.4 Indicator and umbrella species

We used hierarchical cluster analysis and mean pixel-wise correlation of resistant kernel and LCP to identify indicator and umbrella species. Using the predicted resistant kernel and LCP surfaces, we applied cluster analysis to identify and group species with similar spatial patterns of core areas and corridor networks. This identifies indicator species based on the similarity in predicted core areas and dispersal corridors. The pair-wise pixel correlation between predicted kernel/LCP surfaces resulted in the identification of species with the highest average correlation with all other species that offers umbrella protection (Cushman et al., 2010). The umbrella species quantifies how well the optimal protected core area or dispersal corridor for one species would encompass the core habitat and corridor for the other species.

2.5 Core areas and corridors prioritisation

We identified potential core habitats based on cumulative resistant kernel surfaces and identified dispersal corridors based on LCPs using the general approach first applied in Cushman et al. (2018) as improved by Kaszta et al. (2020). All the values of cumulative resistant kernel density surface equal to and greater than 80th percentile were considered as core area and this threshold likely indicates moderate to high predicted movement rate of species across the landscape. To identify dispersal corridors, eliminating at the same time weak and disconnected linkages, for the LCPs we defined a threshold at the 25th percentile. We then, for the indicator species identified by the cluster analysis, ranked the core areas and corridors by their importance. Core area ranking was based on the size and strength of the predicted kernel values whereas, corridor ranking was based on the sum of LCP and average sum of kernel values of core areas they link (Cushman et al., 2018, Kaszta et al., 2020). To produce composite core area and corridors maps across all 15 species we summed the binary

core and corridor rasters. For this, we used kernel and LCP surfaces assigning values one to all pixels above the threshold and zero to pixels below the threshold.

2.6 Multispecies connectivity

To generate alternative multi-species landscape connectivity layers, we summed and multiplied the continuous cumulative resistant kernel surface and LCP surfaces of all 15 species, respectively. Summation indicates areas of high-density movement across 15 species, whereas multiplication identifies areas important for composite multispecies predictions connectivity for all the 15 species together. We did this according to two assumptions: (1) by treating all species as equal from a conservation point of view; (2) by ranking species (assigning them weights) based on their national and global conservation importance (Table S2). For example, tiger was assigned the highest value due to its national and global significance while wild pig was assigned the lowest value. Finally, we evaluated the overlap of our multi-species core habitats and corridor surfaces with the current PAN to identify gaps in the current system and propose new effective core dispersal and corridor areas for future protection. Finally, we ranked the PAN and NPA based on the sum of multispecies kernel values and LCPs predicted within them.

3 Results

3.1 Umbrella species

We found a much higher average correlation between species core habitats than dispersal corridors (Figure 1). The correlation analyses identified Asian elephant *Elephas maximus* as the most effective umbrella species for the protection of core habitat closely followed by leopard cat *Prionailurus bengalensis* (Figure 1a). Ungulate species were more effective in providing umbrella protection of core habitats of other species compared with carnivores.

However, Asiatic black bear *Ursus thibetanus* was a better connectivity umbrella than other smaller carnivores such as Mustelids. Dhole *Cuon alpinus*, was the least effective umbrella species for the protection of core areas, perhaps due to its sporadic distribution. In terms of dispersal corridors protection (based on LCPs), muntjac *Muntiacus muntjak* was the most effective umbrella species (Figure 1b). Mesocarnivores (masked palm civet *Paguma larvata*, yellow-throated marten *Martes falvigula*) were the next most effective umbrella species. Amongst felids, leopard cat and marbled cat *Pardofelis marmorata* were better as umbrella species than tiger *Panthera tigris* or leopard *Panthera pardus*. The apex carnivore, tiger, was the least effective umbrella species for habitat connectivity.

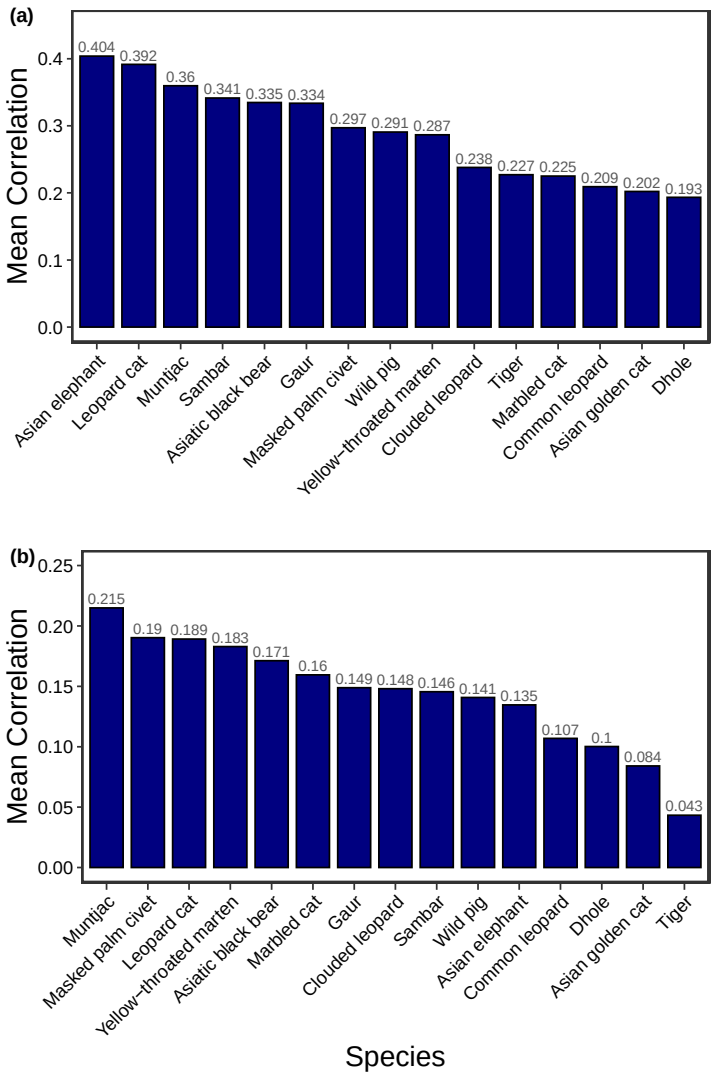


Figure 1 Mean correlation of resistant kernel (a) and factorial LCP (b) of 15 terrestrial mammals across PAN and non-protected area in Bhutan

3.2 Indicator species

Based on the clustering of resistant kernel values across 15 studied species, we identified five distinct clusters (Figure 2). The first cluster consists of four species: Asiatic black bear, yellow-throated marten, clouded leopard *Neofelis nebulosa* and marbled cat with possible groupings of Asiatic black bear/yellow-throated marten and clouded leopard/marbled cat. We propose two indicator species for core habitat protection in this group (Asiatic black bear and clouded leopard) due to their conservation importance at a local and global level. Further, the proposed species occupy a wide range of habitat and have overlapping core areas with yellow-throated marten and marbled cat but requires a larger area and hence their protection would encompass the habitats of the latter. The second cluster consists of muntjac, masked palm civet and wild boar *Sus scrofa* and we propose wild boar as an indicator due to their importance as prime prey for large carnivores. Dhole and Asian golden cat *Catopuma timminckii* formed the third cluster. Dholes are one of the apex predators critical in maintaining ecosystem stability by regulating the ungulate population (Singh et al., 2020). Due to their global conservation importance and tendency to utilise large habitats at varying altitudinal gradients, protecting them would ensure the protection of important core areas for other sympatric carnivores and prey species. The fourth cluster consisted of a mix of felids and large ungulates, i.e., leopard cat, common leopard, sambar deer *Rusa unicolor,* Asian elephant, and gaur *Bos gaurus*. We propose two representative species as indicators for core habitat protection in this group: Asian elephant representing habitat specialists and sambar deer representing important prey for carnivores. The final cluster had a singleton species, tiger.

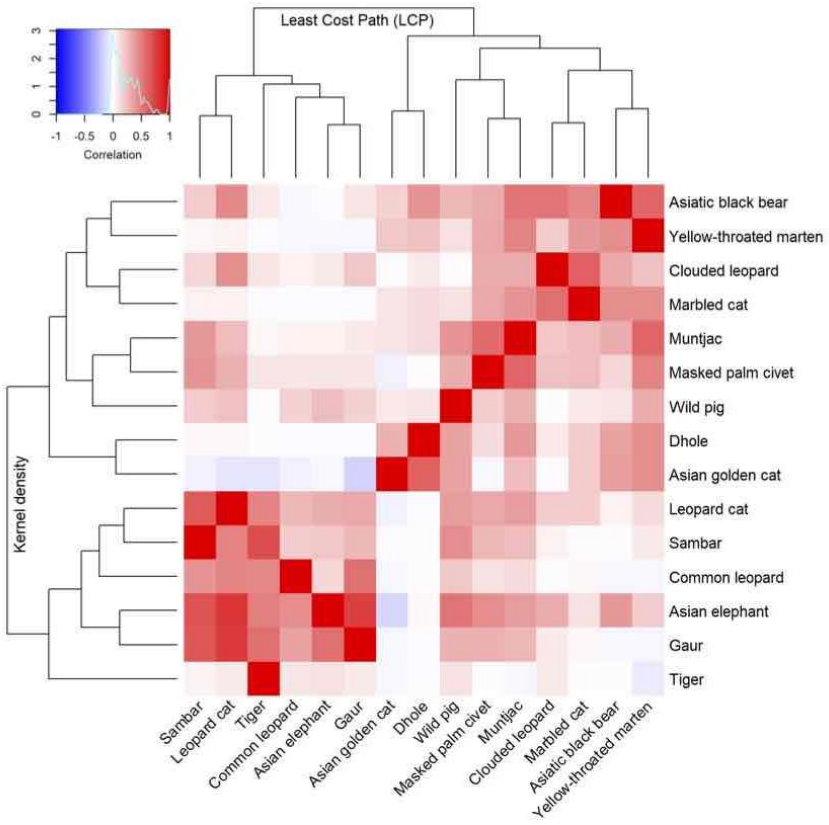


Figure 2 Bivariate hierarchical cluster dendrogram of the resistant kernel and factorial least-cost path of 15 terrestrial mammals used to identify focal species for core area and corridor conservation in Bhutan

The LCP cluster analysis identified four main clusters which were relatively consistent with the resistant kernel clusters (Figure 2). The first cluster, besides leopard cat, contained megafauna, namely sambar deer, tiger, common leopard, Asian elephant, and gaur. These species are clustered based on the similarity in location and strength of the factorial LCP network. Hence, we assign two focal species (tiger and sambar deer) considering the large home range size and greater dispersal ability as connectivity indicators for others in this cluster. The second cluster contained Asian golden cat and dhole and, given the importance of dhole as pack-living animals that require a large area and connectivity, we assign this species as an indicator. The third cluster contained wild boar, masked palm civet and muntjac. Although muntjac was the most effective umbrella species in terms of connectivity,

due to small home range and small dispersal distance, we instead pick wild boar as an indicator in this group. Wild boar is an important prey species for apex carnivores like tiger and dholes and hence protecting their connectivity corridors may also offer additional protection of movement corridors for these carnivores. The final cluster was composed of clouded leopard, marbled cat, Asiatic black bear and yellow-throated marten. This cluster is formed of two subclusters that are slightly different from each other: clouded leopard/marbled cat and Asiatic black bear/yellow-throated marten. One each of these groups can be considered for connectivity indicators, with clouded leopard and Asiatic black bear due to their charisma (Macdonald et al., 2017), public interest and extensive research that enables rigorous assessment and monitoring.

3.3 Core areas ranking for indicator species

Out of the six indicator species, dhole had the highest number (n=25) of core areas across Bhutan (Figure 3). About 41% (7433km^2) of the core area for dhole were protected in Bhutan and the neighbouring Indian states of Arunachal Pradesh, Assam, Sikkim, and West Bengal of which 6782km^2 are protected in Bhutan. The most important core area was predicted in Jigme Singye Wangchuck National Park (JSWNP) and Dagana division. The next important core area was identified in the west partially encompassing Jigme Khesar Strict Nature Reserve (JKSNR), Samtse and Gedu divisions (Figure 5g & h).

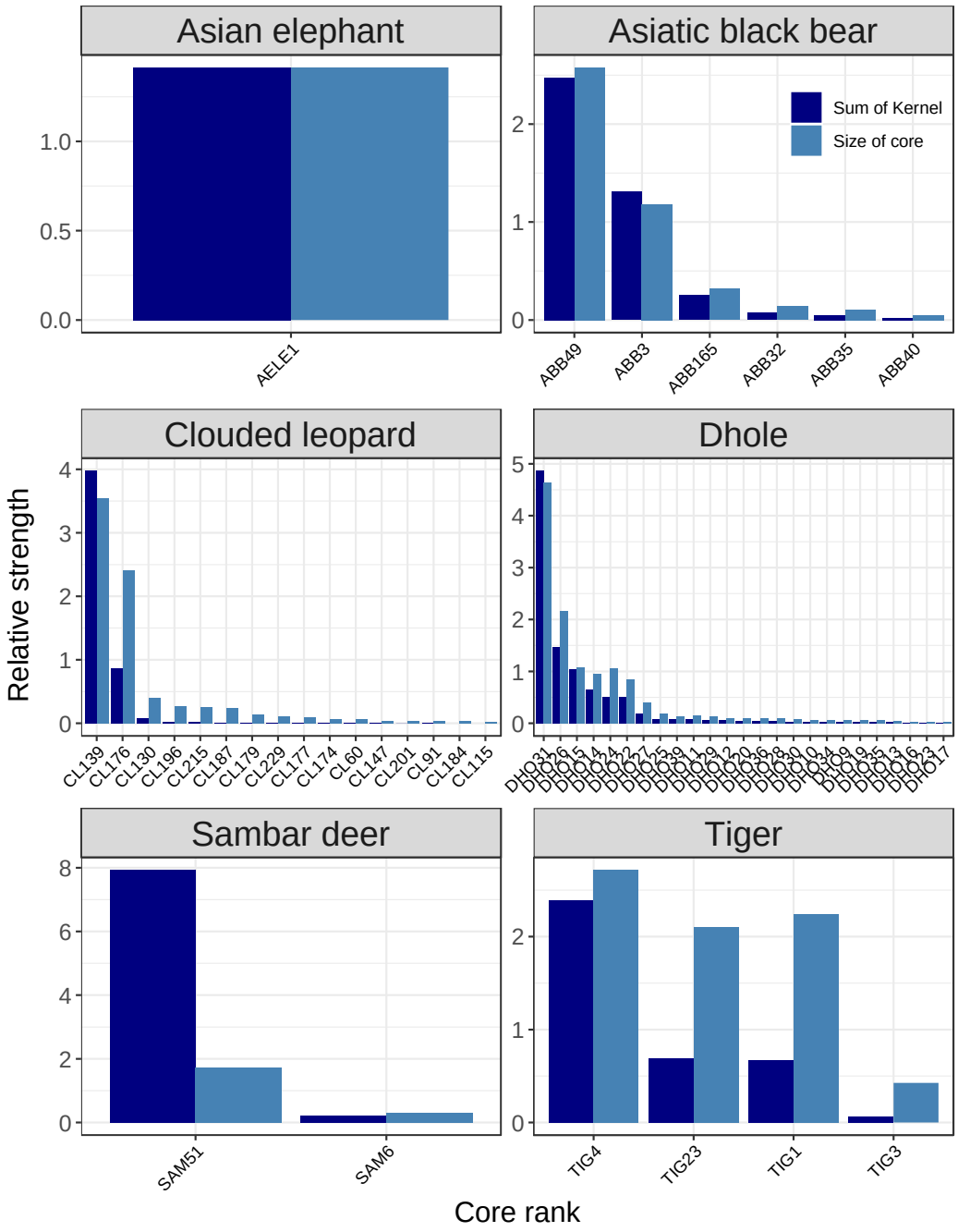


Figure 3 Rank of core areas for six focal species (Asian elephant, Asiatic black bear, clouded leopard, dhole, sambar deer, tiger). Core area ranking was based on the size and strength of the predicted resistant kernel values. The x-axes show core areas of each species in the ranking order from most important to least important

Sixteen core areas were identified for clouded leopard. About 60% (10344km^2) of the total core area were inside Bhutan and 31% (5351km^2) were protected by existing PAN. The

most important and contiguous core for clouded leopard was identified in JSWNP, Royal Manas National Park (RMNP), Phipsoo Wildlife Sanctuary (PWS), BC 3 and BC 4 (Figure 5e & f).

Asiatic black bear had six distinct core areas (total area 18019km^2) with the highest rank core in JSWNP, RMNP, BC 3, BC 4, Zhemgang, Tsirang, Gedu and Samtse divisions. Only ~ 39% (7015km^2) of black bear predicted core areas were under protection in both Bhutan and India (Figure 5c & d).

Tiger had four distinct cores with the highest-ranking core habitat in the southern parts of Bhutan, partially encompassing RMNP and PWS but extending to Indian states of West Bengal and Assam (also within PA and protected forests) (Figure 5k & l). Approximately 46% (8290km^2) of the overall predicted core habitats for tiger were inside Bhutan.

Two large cores were identified for sambar deer with a total area of ~18028km^2 (Figure 5i & j). Fifty per cent of the sambar core lie inside Bhutan and ~15% were under existing protection and the most important one in the south. In Bhutan and India, ~26% were under the PAN.

Asian elephant had a single large core area contiguous across southern Bhutan and three Indian states of West Bengal, Assam, and Arunachal Pradesh (Figure 5a & b). About ~40% (7123km^2) of the core habitats were inside Bhutan, of which ~38% (2696km^2) were inside the existing PAN. Bhutan's RMNP, Jomotshangkha Wildlife Sanctuary (JWS), PWS,

Zhemgang, Pemagatshel and Samdrupjongkhar divisions and India's Manas National Park (MNP) and southern Arunachal Pradesh harboured these core habitats.

3.4 Corridors ranking of indicator species

Of 15 corridors identified for clouded leopard, ~79% were inside Bhutan and, together with India, ~15% were under protection. The important corridor network for clouded leopard was identified in southern Bhutan adjoining PWS and in the eastern part of the country, connecting BWS and PNP (Figure 4; Figure 5e & f).

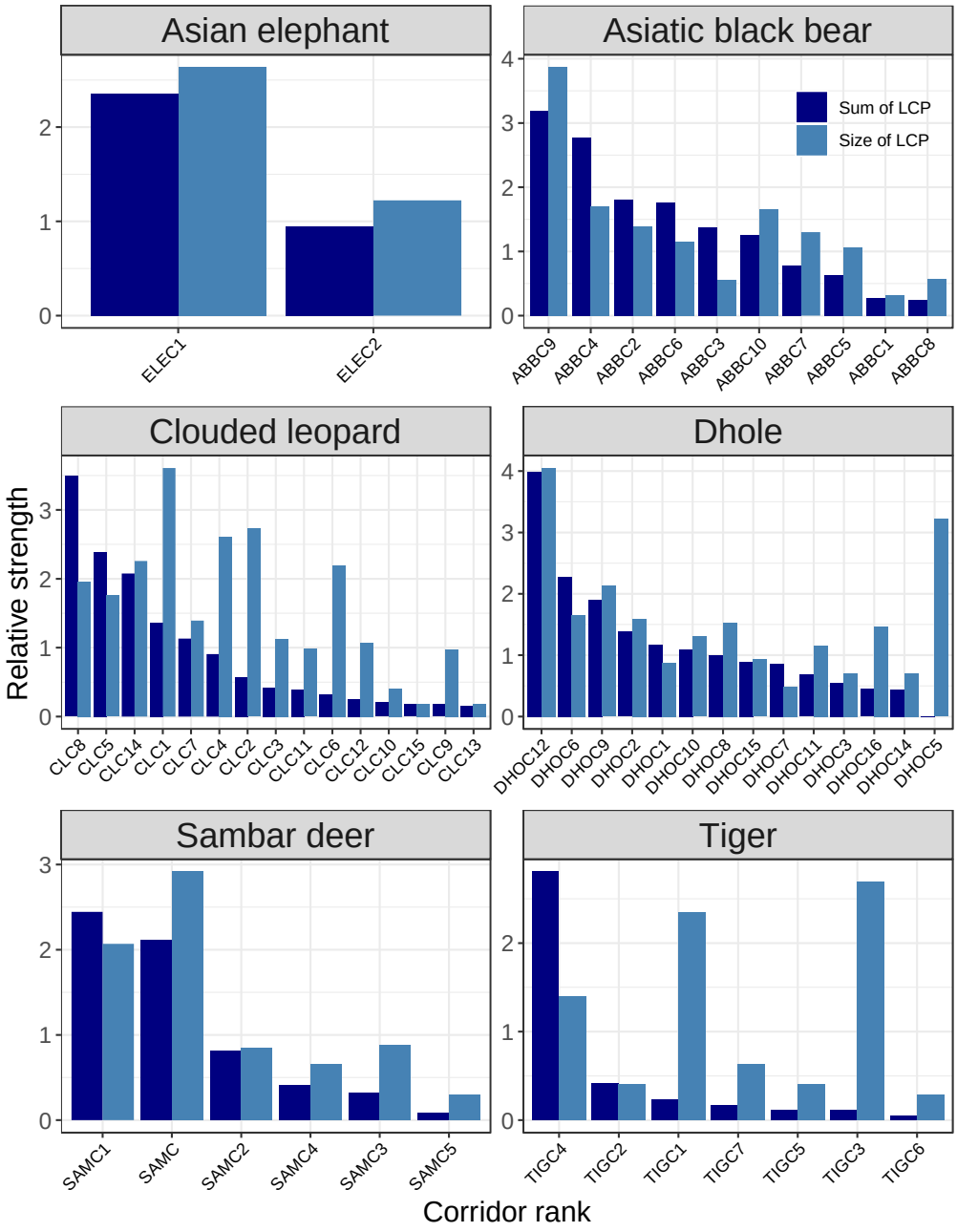


Figure 4 Rank of corridors for six focal species (Asian elephant, Asiatic black bear, clouded leopard, dhole, sambar deer, tiger). The corridor ranking was based on the sum of LCP and the average sum of kernel values of core areas they link. The x-axes show core areas of each species in the ranking order from most important to least important

Dhole had 75% of its corridors in Bhutan, with ~24% inside the existing PAN while ~30% (4634km^2) were jointly protected in Bhutan and India. The highest-ranking corridors for dhole connected JSWNP to JDNP and additional predicted cores outside the PA (Figure 5g & h).

Approximately 73% of the Asiatic black bear corridor area lie in Bhutan, with the main corridor identified in Tsirang division that had the highest sum of LCPs (Figure 5c & d). Bhutan alone protected only ~9% of black bear corridor, while Bhutan and India together protected ~15%.

There were seven corridors for tiger in Bhutan and neighbouring Indian states (Figure 5k & l). Bhutan included 98% of them. The combined protection in Bhutan and India encompassed ~34% of tiger corridor value, and Bhutan alone protected 34%. The most important tiger corridor was identified in the western part of Bhutan, partially overlapping JKSNR, BC 1, Jigme Dorji National Park (JDNP) and Paro division.

We identified six corridors for sambar deer across Bhutan and in four neighbouring states of India with the highest strength identified outside PA across Gedu and Thimphu divisions (Figure 5i & j). Bhutan contained ~91% of the total value of sambar corridors, but only 17% were protected.

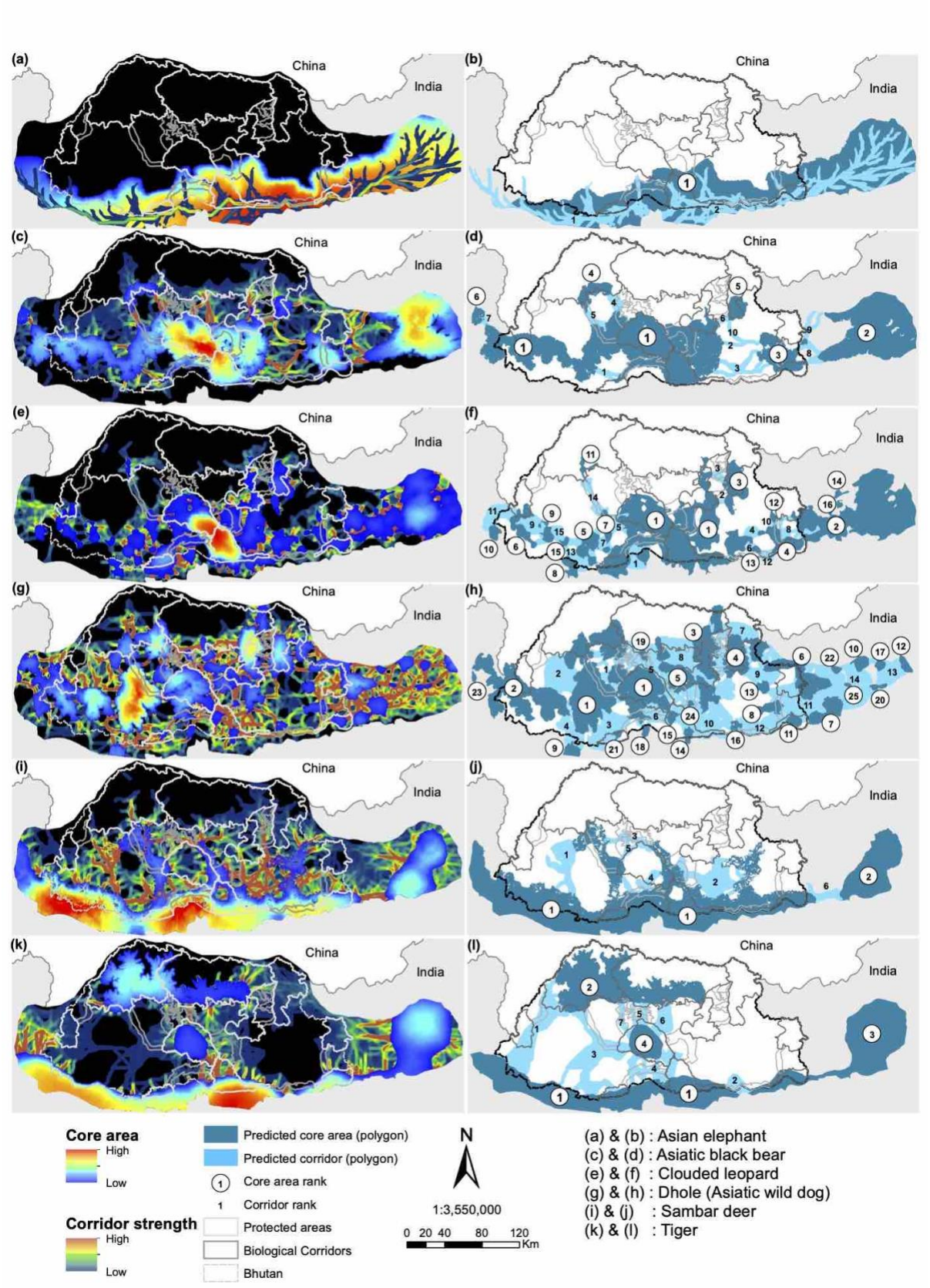


Figure 5 Predicted resistant kernel and least-cost paths for the focal species (left panel) with their ranking of importance (right panel)

Asian elephant had two important corridors entirely inside the predicted core (Figure 5a & b). Twenty-six per cent (2024km^2) of the predicted dispersal corridors were inside Bhutan and more than 52% (1062km^2) were protected. The important corridors were identified along the Bhutan-India border encompassing RMNP, PWS, JWS and India's MNP. Several critical linkages were also identified in Gedu and Zhemgang divisions in Bhutan and southern Arunachal Pradesh in India.

3.5 Multispecies core habitat and corridors

Based on the sum of kernel density, the overall area represented by multi-species core habitats across the study area was ~48,790km^2. The study area includes Bhutan and the four adjoining Indian states (Figure 7a). Effectively, ~38% (~18,554km^2) of the core area was under some form of protection. Approximately 67% (~32,743km^2) of the total core area lies inside Bhutan, of which ~40% (12,954km^2) was inside PAs and another ~8% (~2458km^2) inside BCs. Similarly, the total area of the predicted dispersal corridor under protection in Bhutan and the neighbouring Indian states was 13,362km^2 (31%) out of 42,460km^2 predicted. Bhutan alone had about 24% (10,268km^2) of the predicted corridors under protection.

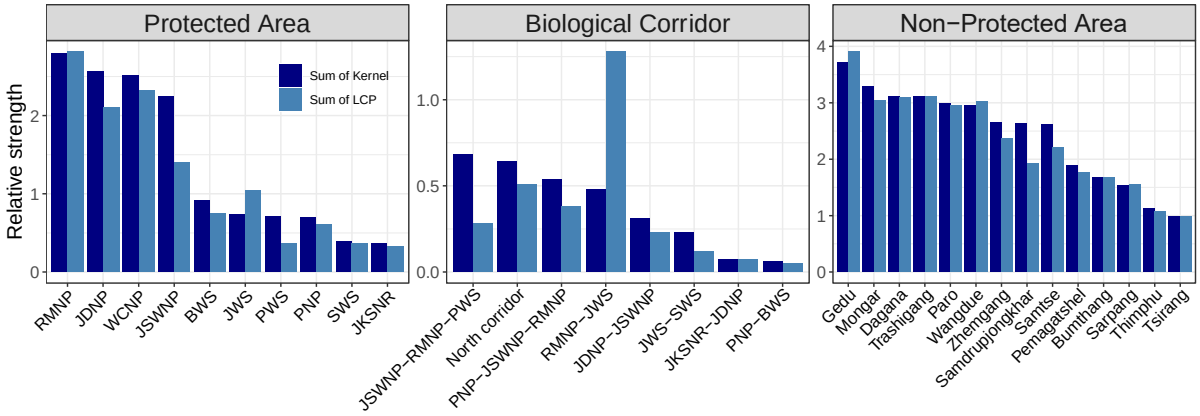


Figure 6 Sum of core areas kernel values and corridors (LCP) values inside each PA, BC, and NPA. The ranking was performed by calculating the relative sum and size of the kernel and LCP for each patch. The x-axes show core areas of each species in the order of the highest kernel value

The combined sum of kernel density and least-cost paths for all species shows that RMNP had the largest predicted multispecies core habitat and corridors, followed by JDNP and Wangchuck Centennial National Park (WCNP), while JKSNR had the smallest (Figure 6). The existing BCs also included substantial predicted core habitats; BC 3 which connects RMNP and JSWNP to PWS ranked top in protecting multispecies core habitat, followed by North corridor (BC 8), and BC 4 (connecting RMNP to JSWNP and Phrumsengla National Park (PNP)), while BC 7, connecting PNP and Bumdelling Wildlife Sanctuary (BWS), offered minimal protection. BC 5 which connects RMNP to JWS had the highest sum of least-cost paths, followed by BC 8 and BC 4, while BC 7 again had the lowest (Figure 6 & 7).

Among the NPA, Gedu Division had the highest strength of kernel values as well as the sum of LCPs while Tsirang had the lowest. Mongar, Dagana, Trashigang, Paro and Wangdue divisions were the next important NPAs for core habitat and corridor protection (Figure 6 & 7).

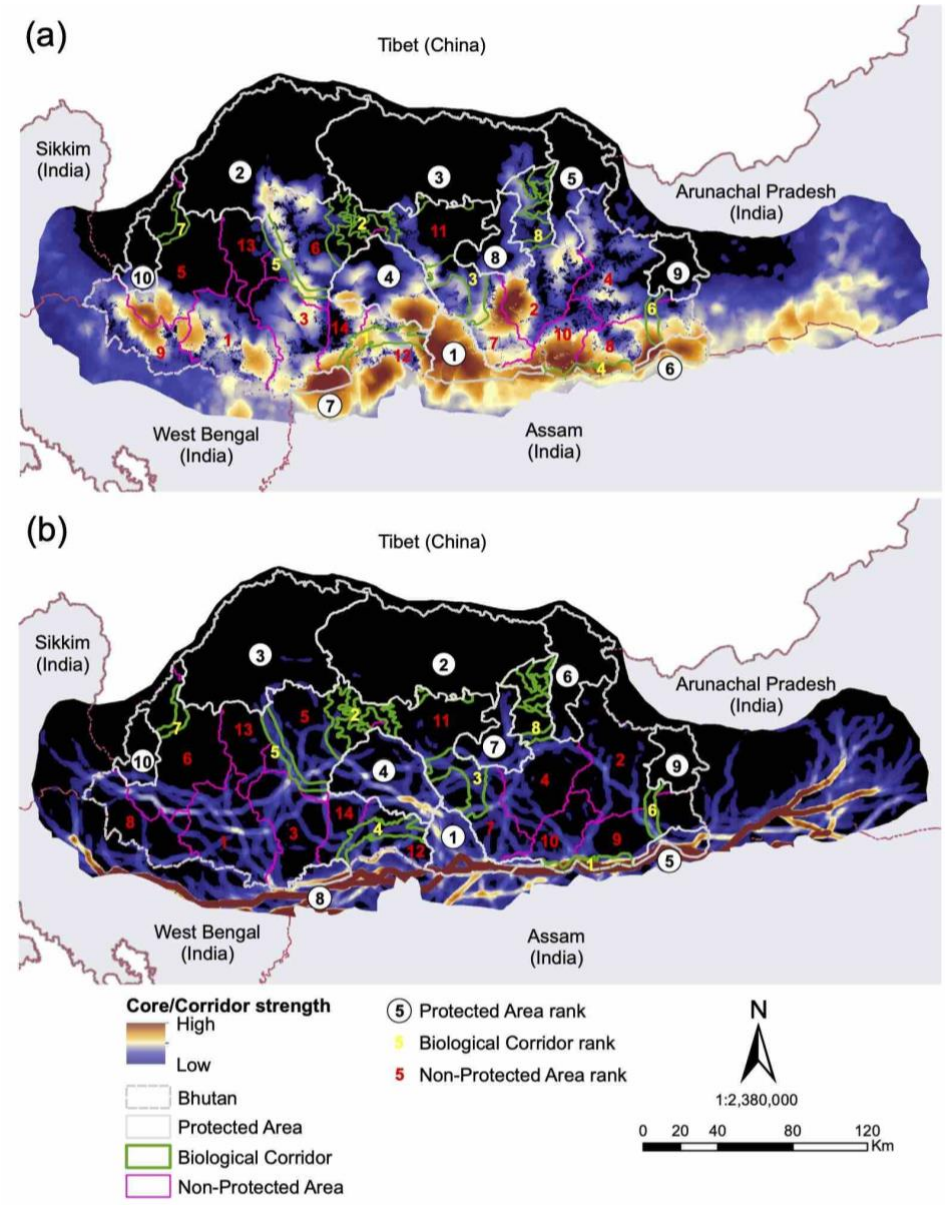


Figure 7 Predicted resistant kernel (a) and LCPs (b) for all species combined with their ranking of importance

4 Discussion

In this study, we present the first comprehensive and empirical evaluation of population connectivity for multiple wildlife species across Bhutan and India. Our analysis focused on identifying core habitats and dispersal corridors for 15 terrestrial mammals. Based on overlap

and similarity between landscape connectivity surfaces, we selected umbrella and indicator species. We assessed the proportion of predicted core areas and corridors under the existing PAN for these species and multispecies core areas and corridors. Asian elephant and muntjac were identified as the best umbrella species for core area and dispersal corridor protection, respectively. Asian elephant, Asiatic black bear, clouded leopard, dhole, sambar deer and tiger were identified as effective focal indicator species for core areas and corridor protection. Our study finds that overall, 40% of multispecies core areas in Bhutan lie within the current PAN. Core areas for most species overlap, but only partially, and the overlap of core areas of all 15 species together constitute a very small proportion of Bhutan, indicating spatial differences in core area use by mammal species across Bhutan. Likewise, ~24% of the multispecies predicted dispersal corridors were inside Bhutan under the existing PAN. Most species tend to utilise dispersal corridors suited to their needs suggesting the importance of multi-species consideration in designating or demarcating a wildlife corridor rather than a single species umbrella approach.

4.1 Umbrella and indicator species for core habitat and corridor protection

Our findings show that Asian elephant was the most effective umbrella species for core habitat protection followed by leopard cat, muntjac and sambar deer. Muntjac was the most effective umbrella species for corridor protection. Mesocarnivores (e.g., masked palm civet, leopard cat, and yellow-throated marten) were as effective as muntjac for habitat protection, though less so than muntjac for corridor protection. The umbrella species identified here best capture core habitat and connectivity for all the other species we considered. Asian elephants live in groups and have large home ranges offering umbrella protection to the biodiversity of the entire landscape they inhabit (Sukumar, 1989, Baskaran et al., 2013). Large-sized species tend to have large home ranges, hence, for them to maintain viable populations requires

protection of large tracts of habitat (Roberge and Angelstam, 2004). Therefore, irrespective of the feeding guild, large ungulate mammals are also regarded as prospective umbrella species (De Vires, 1995, Berger, 1997b). Muntjacs are commonly found across Bhutan and inhabit a wide range of habitats. Recent studies in southeast Asia found that muntjac was the primary prey of Asian golden cat and dhole (Kamler et al., 2020a, Kamler et al., 2020b) suggesting that conservation of muntjac would ensure continued supply of food for many carnivores at a higher trophic level. Common species serve as better umbrella species because of the higher probability of long-term persistence (Berger, 1997a). Although, large, threatened, and rare species are desirable, often their low reproductive rate, low density and large area requirement make them prone to extinction and ineffective as umbrellas in the long-term (Fleishman et al., 2000). A meta-analysis of umbrella species found that species richness of co-occurring species was higher in areas without carnivorous species as umbrellas, thus suggesting that species at lower trophic levels can serve as an effective umbrella (Branton and Richardson, 2011). Traditionally, species that are at risk of extinction are recognised as flagship or umbrella but species that are not threatened may still be suitable. Species that are common and infrequently involved in the conflict may make them effective ambassadors for conservation (Bowen-Jones and Entwistle, 2002, Macdonald et al., 2017).

The use of large ungulates (e.g., buffalo (*Syncerus caffer*), black rhinoceros (*Diceros bicornis*), wildebeest (*Connochaetes spp.*)) as umbrella species is not a new practice and has been found effective in African protected reserves (Caro and O'Doherty, 1999, Caro, 2001, Caro, 2003a). However, solely relying on a single umbrella species has generally proven inadequate (Roberge and Angelstam, 2004, Seddon and Leech, 2008, Kramer et al., 2019) because, if the umbrella population is endangered or under high pressure from poaching and

habitat loss, their population might dwindle rendering them ineffective, hence designating several umbrella species is advocated (Lambeck, 1997, Fleishman et al., 2001) provided they have a viable population with a low probability of extinction (Caro, 2003a). The proposal to use ungulates and mesocarnivores as umbrella species in this study contrasts with the use of traditionally charismatic species such as tigers, clouded leopards, and leopards (Wikramanayake et al., 2004, Macdonald et al., 2012, Kittle et al., 2018). Tigers and leopards occur in low density and are often sensitive to habitat disturbance. Further, people hold mixed views and often express fear and aversion to them due to conflict and predation of livestock (Sangay and Vernes, 2008). This suggests that while large cats elicit international funding and attention, the ungulates and smaller carnivores may offer better umbrella protection by garnering the support of local people (Bowen-Jones and Entwistle, 2002).

We identified both carnivores and ungulates as effective indicator species (focal) for core habitat and dispersal corridor protection. The effective indicator carnivore species were tiger, dhole, clouded leopard and Asiatic black bear whereas, effective ungulate indicators were Asian elephant and sambar deer. Tigers, dholes and clouded leopards are globally threatened carnivores and inhabit a wide range of habitats from grassland to subalpine forest. They are best suited as indicator species for core habitat and corridor protection because the home ranges of these species would encompass a wide range of habitats for other smaller carnivores and hence effectively include habitats indicative of landscape heterogeneity. Tigers and dholes are apex predators and mostly prefer prey rich areas (Karanth and Sunquist, 2000), hence are also indicative of the richness of a large ungulate prey population. Further, a healthy population of apex predators represents healthy ecosystems because they regulate the trophic level and provide crucial ecosystem services (Ripple et al., 2014, Bogoni et al., 2020). Clouded leopards are also arboreal and consume a wide range of small and

medium-sized prey species (Nowell and Jackson, 1996). The conservation of clouded leopard would also ensure the protection of forest structure and arboreal prey (Macdonald et al., 2012, Lam et al., 2014). Asiatic black bears are globally threatened species and inhabit montane forests (Sathyakumar, 2001), their presence indicates a healthy forest ecosystem and protection of heterogeneous habitat within core habitat and corridors. Asian elephants are found in the south inhabiting subtropical forests. Therefore, Asian elephants indicate the importance of protection of tropical and subtropical forests which are also home to a wide spectrum of tropical species. Sambar deer is ubiquitous and highly adaptive ungulate and feed on a variety of vegetation (McKay and Eisenberg, 1974, Geist, 1998). Sambar deer is one of the most preferred prey species of tiger and other large carnivores (Karanth and Sunquist, 1995, Wang and Macdonald, 2009, Thinley et al., 2011, Hayward et al., 2012). Therefore, they are indicative of a healthy carnivore population.

4.2 Landscape connectivity pattern of focal species

The landscape connectivity patterns were highly nuanced for the focal species. Dhole had the highest number of core habitats and about 32% of them were larger than the existing smallest PA (PWS, 269km^2) suggesting the fragmented nature of habitat at the landscape level (Rodrigues et al., 2021) but also indicates the potential that the protection of this species would ensure at least equivalent protection of habitat as the existing smallest PA. The top-ranked predicted core for dhole encompassed JSWNP, BC 2 (corridor connecting JSWNP to JDNP) and Dagana division. As a wide-ranging social carnivore, dholes require a large space, and the existing PA alone may not be sufficient for range expansion. Thus, we recommend merging predicted cores in Dagana with JSWNP and BC 2 to form a single large conservation area. Additionally, contiguous core habitats were also predicted in the west in Gedu and Samtse divisions and JKSNR further into the Indian state of Sikkim. Together the

western complex offers the immense potential of transboundary core habitat for this endangered species.

The top-ranked predicted core for clouded leopards encompassed JSWNP, RMNP, PNP and Zhemgang. More recently, Kaszta et al., 2020 identified Bhutan as one of the important countries for the protection of the global clouded leopard core habitat. Our results further support this by providing fine-scale spatial prediction of core habitats within Bhutan and beyond. Further, we predicted a high strength of core habitats in the Indian state of Arunachal Pradesh contiguous to JWS of Bhutan thus opening avenues for international collaboration for the conservation of threatened species. The highest-ranked core habitats of tiger were mostly predicted in the southern part of Bhutan including RMNP, PWS, JWS and NPA of Samtse, Gedu, Dagana and Zhemgang and adjoining PAs and reserve forests of India. The next best core habitats were predicted in JDNP, WCNP and JSWNP. This prediction corroborates with the macro conservation landscape proposed in the early 2000s called the Bhutan Biological Conservation Complex (B2C2) to harmonise conservation and socio-economic development and that defines the existing PAN. This also suggests that the existing PAs offer satisfactory protection to tiger, but the inclusion of additional areas could enhance ecosystem protection and bolster the existing PAs from the growing human pressure. The main core habitat of Asiatic black bear includes JSWNP, RMNP, BC 4, Zhemgang, Tsirang, Dagana, Gedu and Samtse divisions. These PA, BC and NPA form a large contiguous habitat which could be further connected to other PAs across Bhutan and neighbouring India forming a landscape-scale refuge. Asian elephant and sambar deer predicted core habitats encompassed four existing PAs and several NPAs. PWS, RMNP, JWS and JSWNP protected similar core habitats for both ungulates. Additionally, we identified NPAs that were crucial to the conservation of these species comprising of Gedu, Dagana,

Tsirang, Sarpang, Zhemgang, Pemagatshel and Samdrupjongkhar divisions. Further, the four Indian states also consist of a substantial amount of predicted core for both species. Asian elephant may be identified as an important transboundary species due to regular migration across the two countries here. While it is reassuring that habitats outside PAs could support ungulate diversity and abundance, it points to the potential human-wildlife conflict that could escalate due to flourished ungulate population. Thus, management should explore the balance between population recovery and mitigating conflict.

We found that RMNP had the highest number of predicted corridor networks based on the sum of LCPs within it. An intricate multispecies corridor network was identified connecting RMNP to JSWNP, MNP (India), Zhemgang, Sarpang and existing BCs indicating that RMNP has the potential to perform as core habitat as well as connectivity linkage. The existing BC also offered high connectivity suggesting that the existing BCs potentially offers structural connectivity. We found BC 5, which connects RMNP with JWS, had the highest predicted corridor strength. Other BCs did contain predicted corridors, but the strength and intensity were variable. For instance, BC 1 and BC 7 have the lowest predicted connectivity. However, we acknowledge that this study did not include alpine species such as snow leopard *Panthera uncia*, Bhutan takin *Budorcas taxicolor whitei* and bharal *Pseudois nayaur* and these high-altitude corridors probably facilitate the movement of high-altitude migrants (particularly Bhutan takin). Several corridors in NPAs were identified which could offer extended connectivity to existing BCs. The predicted corridors in Dagana, Gedu, Paro and Samtse ranked among the highest. Similarly, the predicted corridor network in Zhemgang could add to enhanced connectivity of RMNP, PNP and JWS. In a nutshell, the NPAs were equally important as PAs that could facilitate species movement due to high predicted corridor strength.

At the focal species level, clouded leopard had the highest predicted corridor network across Bhutan, but this was highly variable in strength. Important corridors were identified in the southwest and southeast Bhutan, mostly outside the existing PAN. Gedu, Samtse and Dagana form an important link between JSKNR, JSWNP and PWS that might facilitate the movement of this species. For Asiatic black bear, we identified a linkage in Tsirang that connects BC 3 and PWS to a predicted core habitat additionally to a corridor network in southeast Bhutan although weaker in strength but connects the predicted core habitat to the existing PAN. Dhole had the predicted corridors uniformly distributed across the country and overlapping with existing PAN. It is worth noting that the highest corridor strength was identified in Wangdue division contiguous to existing BC 2 that connects JSWNP and JDNP. Future expansion could potentially include this corridor to facilitate the movement of dholes between these two PAs. The predicted corridor for tiger corresponds to the existing PAN but additional corridors were identified in Dagana, Tsirang and Bumthang which may facilitate connectivity of the predicted core habitats with the existing PA. The predicted corridors for Asian elephant followed the international border of Bhutan and India suggesting that the two countries need to collaborate to protect the habitat and movement corridor of this charismatic yet controversial megaherbivore. On the other hand, sambar deer had predicted corridors outside of the existing PAN. Important corridors that need protection were predicted in Gedu, Thimphu, Zhemgang and Mongar.

4.3 Multispecies connectivity

Amongst the existing PA, RMNP ranked top in protecting predicted core habitats and corridors across all study species. RMNP adjoins India's UNESCO World Heritage site, MNP and together forms one of the important tiger conservation landscapes in Asia but also

protects a wide spectrum of wildlife including the endangered dhole, Asian elephant, wild water buffalo, one-horned rhinoceros, and critically endangered pygmy hog and their habitats. The predictions were made beyond the Bhutan boundary by extending the study area into the neighbouring Indian states of Assam, Arunachal Pradesh, Sikkim, and West Bengal (Figure 6). This was done to provide a better picture of the connectivity because species movement does not necessarily follow an administrative boundary. Our analysis shows that multispecies core habitats extend beyond the Bhutan boundary (Figure 7a) indicating the importance of transboundary collaboration to protect potential habitats on both sides of the border. Within Bhutan, JDNP, JSWNP and WCNP were the next best PAs harbouring a substantial number of predicted cores. These PAs are connected by a network of existing corridors forming one of the largest temperate and alpine PANs in the region.

Our findings also reveal the importance of existing BCs in protecting core habitat besides facilitating as movement conduits. This further shed light on the structural connectivity of the existing BCs. The corridor (BC 3) connecting PWS to RMNP and JSWNP ranked top in protecting predicted core habitats of all study species combined. Finally, we identified critical core habitats outside of the existing PAN that could serve as key biodiversity areas. We identified that Gedu has the highest strength of core habitat among NPAs. Contiguous with India's Buxa Tiger Reserve, Gedu offers potential landscape connectivity for the movement of megafauna like tiger and Asian elephants between tropical and temperate cloud forests. We also found that Mongar, Dagana Trashigang, Paro, Wangdue, Zhamgang, Samdrupjongkhar and Samtse divisions have the equal potential of multispecies core habitat protection outside PA within Bhutan. Both are contiguous to existing PAN and could serve as an important habitat for spillover species from PAs.

4.4 Management implications

Our research allowed us to compare the existing protected areas and biological corridors in Bhutan and identify potential gaps. Our findings show that about 38% of the core habitats and 31% of dispersal corridors across all study species are protected across Bhutan and in the neighbouring states of India. While a large portion of predicted cores and corridors are protected, there is still a substantial gap that warrants protection. Those in NPAs may be at risk of losing viability due to land conversion. Therefore, conservation managers and land planners should include these core habitats and corridors in future expansion and/or realignment of PAN or identification of important biodiversity areas.

Our results support Penjor et al., (2021) who identified suitable core habitats outside PAN for most megafauna species in Bhutan using habitat suitability models. However, the current study uses spatially synoptic connectivity approaches providing better predictions of core areas and connectivity linkages and allowing us to rank them based on the strength of movement and dispersal abilities of species (Cushman et al., 2014, Kaszta et al., 2020). Penjor et al., (2021) identified seven habitat patches and six putative corridors outside the PAN. We refined and extended those predictions in this study. Of the many important differences between Penjor et al., (2021) and this study, the most important one is that the former did not consider connectivity and based predictions only on habitat suitability, which is a relatively weak proxy for population size, movement patterns or connectivity (Cushman et al., 2009, Wasserman et al., 2010, Cushman et al., 2014, Shirk et al., 2015). We identified many of the same core areas as identified in Penjor et al., (2021) (e.g., Gedu, Samtse, Dagana, Zhemgang and Pemgatshel divisions) but additionally across all PAs and NPAs and in the neighbouring Indian states and this study bases core predictions on kernel values thus providing better spatial predictions of movement through each pixel (Kaszta et al., 2020).

Additionally, this study identified and mapped a spatially explicit corridor network optimised by factorial LCP algorithm (across PAN and NPA in Bhutan and neighbouring Indian states) and precisely predicted where they run (Figure 7b) across the landscape (Kaszta et al., 2020) which otherwise is not possible based solely on habitat suitability models. Together, the products developed in Penjor et al., (2021) and this study complement each other and can be utilised in land management to identify, mend, and strengthen the existing PAN in Bhutan.

We recommend that the existing PAN should be preserved and expanded with strategic inclusion of predicted core areas and corridors which we identified as of highest priority outside of the existing PAN, including, Gedu, Mongar, Dagana, Trashigang, Paro, Wangdue and Zhemgang divisions. Several studies in the past recommended the inclusion of biodiverse NPAs and/or expansion of existing PAs to encompass additional habitats (Dorji et al., 2019, Thinley et al., 2021, Penjor et al., 2021b). We propose the inclusion of additional areas to existing or perhaps as a new joint-protected landscape in addition to the current transboundary Manas conservation area (TraMCA) that encompasses RMNP, PWS, JWS in Bhutan and MNP in India.

We provide spatially prioritised predictive maps of core areas and corridors which are useful for prioritisation of areas for conservation. The predicted cores and corridors transcend international boundaries. This offers an opportunity to strengthen transboundary cooperation in addition to the existing Transboundary Manas Conservation Area (TraMCA) in the south and Kanchenjunga Landscape (Gurung et al., 2019) in the west. The transboundary cooperation could be extended in the east where SWS and JWS of Bhutan and Namdhapha conservation complex (Namdhapha Tiger Reserve, Mouling National Park, Pakke Wildlife

Sanctuary, Eagle Nest Wildlife Sanctuary, Dibang Wildlife Sanctuary) of India have the potential to form an important conservation network in the eastern Himalayas.

5 Conclusions

Our findings provide a means to prioritise and optimise the expansion of the PA and BC network in Bhutan to effectively protect multispecies connectivity across the full extent of the nation. Our analysis provides an objective, nationwide, multi-species prioritisation of which areas should be prioritised for additional protection. We suggest that the protection of multispecies core areas and connectivity linkages is more effective than focusing landscape conservation management on single species. Simply put, our findings suggest that the effective way forward for long-term biodiversity conservation in a fragile, Himalayan landscape is to maintain the existing PAN, bolster them by protecting the important habitats that abut them (e.g., Gedu, Mongar, Dagana Trashigang, Paro and Wangdue divisions) and enhance connectivity by protecting high priority multi-species corridors outside of PAN. The mapping of spatially prioritised core areas and corridors allows conservation managers to identify and protect high priority areas and can be used to intersect with future development plans to mitigate any adverse impact of infrastructure development. A similar approach could be undertaken in other Himalayan countries, or to provide an initial step in multi-national, regional efforts to visualise and prioritise transboundary conservation networks to safeguard mammals across the Himalayan region.

6 Authors' contributions

All authors contributed to the study conception and design. Material preparation and analyses were performed by Ugyen Penjor supported by Żaneta Kaszta and Samuel Cushman. The

first draft of the manuscript was prepared by Ugyen Penjor. All authors contributed to subsequent drafts and gave the final approval for publication.

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Chapter 4

Effects of land-use and climate change on functional and phylogenetic diversity of terrestrial vertebrates in a Himalayan biodiversity hotspot

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Under review by Diversity and Distributions

Abstract

Aim: The synergy between human land use and climate change is accelerating the global decline of biodiversity. In the fragile Himalayas, this trend has a strong ecological impact on wildlife communities and a better understanding is needed to discern changes in the biodiversity loss. This study aims to understand the effects of land use and climate variables on the functional (FD) and phylogenetic diversity (PD) of mammal and bird communities across the land-use gradient in Bhutan.

Location: Eastern Himalayan biodiversity hotspot, Bhutan

Methods: Mammal data were gathered from a camera trap survey and bird data from point counts. We used morphological and ecological traits of 45 mammal species and 336 bird species to construct functional trait space. We quantified FD and PD using standardised effect size of functional richness, functional dispersion, mean pairwise distance and mean nearest taxon distance. We used linear regression to evaluate the relationship between FD and PD and land use/climate variables.

Results: The functional space of mammals was structured by body mass (small-large) and diet (herbivore-carnivore) as one major axis, and habitat breadth (generalist-specialist) as the other whereas bird functional space was structured by beak shape and size (large and long - small and short), body mass (small-large), foraging strata (canopy-ground), and diet (ectotherm-scavenge) along four axes. Land use (agriculture and road) negatively affected mammal FD whereas both land use (tree cover and built-up area) and climate (temperature and precipitation) affected PD, although the effects were highly variable. Climate

(temperature) had a pronounced negative effect on bird FD while land use (agriculture, built-up area, and settlement) on PD.

Main conclusions: The realised functional space of the vertebrate groups can be represented by different planes on which species are clumped around a small number of functional strategies. The loss of species at the edge of functional space is non-random and could result in the loss of irreplaceable traits impacting long-term ecological and evolutionary processes. Our study demonstrates the filtering effect of anthropogenic pressure and climate change on vertebrate FD and PD. However, the association with land use suggests the potential for ecosystem services (particularly by birds). Our findings reveal nuances of dimensions of biodiversity and provide novel insights into the structure and drivers of vertebrate assemblages in the eastern Himalayas.

Keywords: Anthropogenic land use, biodiversity hotspot, birds, climate, eastern Himalaya, functional diversity, mammals, phylogenetic diversity

1 Introduction

The global expansion of agriculture and human settlement increasingly threatens natural ecosystems (Sala et al., 2000, Corlett, 2015), accelerating the risk of species extinction and corresponding loss of vital ecosystem services (Flynn et al., 2009a). This imperilment is augmented by the rapid alteration of global climate caused largely by anthropogenic activities (Radchuk et al., 2019a, Turvey and Crees, 2019). Human modification of landscapes results in altered ecological community diversity and structure (Malhi et al., 2016, Cadotte and Tucker, 2017) and often leads to functional, and phylogenetic homogenisation (McKinney,

2006, Devictor et al., 2007, Ibáñez-Álamo et al., 2017) making an ecological community inefficient in ecosystem functioning (Clavel et al., 2011, Grab et al., 2019). The synergy between human land use and climate change increases the overall impact accelerating the global decline of biodiversity (Brodie, 2016). This is amplified in a geographically dynamic and geologically unstable montane landscape like the Himalayas and needs a better understanding to discern the changes in the mechanisms – an understanding that is a prerequisite to the effective management of ecosystems (Xu et al., 2009).

Species richness, or taxonomic diversity (TD), is a classical diversity metric that underpins the theoretical aspect of community ecology and biogeography (Colwell and Coddington, 1994). However, TD alone provides little information about the changes in phylogenetic relatedness of species and individuals within assemblages or changes in a functional trait that impacts overall ecosystem functioning (Swenson, 2013, Violle et al., 2014). For instance, several authors have reported that the overall TD remained stable despite losing functionally important species (Ernst et al., 2006, Spaak et al., 2017) indicating functional homogenisation and perhaps redundancy (Petchey et al., 2007, Aguirre-Gutiérrez et al., 2017). Biodiversity is a multidimensional concept that integrates phylogenetic, functional, and taxonomic diversities (Scheiner, 2012, de la Sancha et al., 2020). Phylogenetic diversity (PD) represents the evolutionary history and patterns of evolutionary relationships in a community (Faith, 1992), while functional diversity (FD), helps understand the functional uniqueness and patterns of functional trait distribution in communities (Cadotte et al., 2011, Flynn et al., 2011, Gossner et al., 2013). FD is linked with environmental conditions and biotic interactions and better predict ecosystem functioning and services than richness (Petchey et al., 2004, Flynn et al., 2009a, Swenson, 2013). PD may remain stable during community change if the newly arriving species replace the lost ones,

but this does not necessarily guarantee the maintenance of ecological functions (Sobral et al., 2016). Together FD and PD provide insights into the community assembly (or accumulation) process (Pavoine and Bonsall, 2011), ecosystem functioning (Petchey et al., 2004, Cadotte et al., 2009, Bässler et al., 2014), conservation value (Mace et al., 2003, Winter et al., 2013) and community resilience (Díaz et al., 2007, Cadotte et al., 2012, Mouillot et al., 2013). Thus, maximising both evolutionary value and ecosystem function (Bregman et al., 2016, Ribeiro et al., 2016) is essential to maintain community resilience to environmental perturbation (Socolar et al., 2016).

Many community studies have incorporated all three metrics of biodiversity, but very few have accounted for variation in detection probability while assessing them (Edwards et al., 2015, Jarzyna and Jetz, 2016, Jarzyna and Jetz, 2017, Si et al., 2018, Cannon et al., 2019, Palacio et al., 2020). It has been shown that ignoring detection probability can lead to an underestimation of these metrics (Jarzyna and Jetz, 2016, Si et al., 2018, Montaño-Centellas et al., 2021) or bias in their interpretation (Palacio et al., 2020). This happens because nuances in functional traits or phylogenetic characteristics of species lead to variation in detection (Garrard et al., 2013, Sólymos et al., 2018) which might influence predictions of functionally or phylogenetically distinct species across assemblages. This could dramatically affect FD or PD estimates if the missed species disproportionately contribute to overall FD or PD (Si et al., 2018).

Mammals and birds are well-known taxonomic groups with the easily available global trait and phylogeny data (Jetz et al., 2012, Wilman et al., 2014, Upham et al., 2019), are good indicators of wider biodiversity response to environmental change (Dirzo et al., 2014, Edwards et al., 2014), and play critical roles in ecosystem functioning (Sekercioglu, 2006,

Bogoni et al., 2020). Mammals and birds are an integral part of ecological networks. When we envision a complex ecological network of interacting species and the functional and phylogenetic integrity of this intricate system, it reminds us of the 'tangled bank' of Charles Darwin (Darwin, 1909). This complex system, however, is under increasing stress from human modification.

Here, we studied the effects of land use and climate variables on the FD and PD of mammal and bird communities across the land-use gradient in Bhutan, a global biodiversity hotspot in Eastern Himalaya (Myers et al., 2000). Specifically, we investigate the functional composition of the bird and mammal communities, the effects of land use and climate change on FD and PD and examine whether constraints imposed by anthropogenic land use and climate result in the filtering of specific traits and lineages. The influence of biodiversity on ecosystem processes is underpinned by underlying trait distributions. A decline in FD could indicate the loss of functionally distinct species that are not readily replaced by the remaining species. We hypothesise that anthropogenic disturbances may act as filters reducing FD and PD (Hanz et al., 2019). We also hypothesise that communities in human-dominated landscapes will be comprised of closely related species (clustering), those able to tolerate perturbations. If species sensitive to anthropogenic pressures and extreme climates were negatively impacted, this would affect the major gradient across the functional trait space and hence reduce the overall diversity (Flynn et al., 2009). This study thus enhances our understanding of the FD and PD of terrestrial vertebrates and provides new insights into the effects of anthropogenic land use and climate change in a Himalayan biodiversity hotspot.

2 Methods

2.1 Data

2.1.1 Species data

We used mammal data from the camera trapping survey conducted in 2014-15 and bird data from the point count survey in 2019-20. The camera trap survey comprised 1129 paired, unbaited, passive infra-red camera traps placed across the country each within a 5km x 5km grid at an average distance of 2.9km (1.2km SD). Trap placement followed existing animal trails, mineral licks, and water holes but in the context of terrain accessibility. Details of the camera trap survey are described elsewhere (Penjor et al., 2020). The bird point count transect surveys were conducted in three geographically representative regions across Bhutan between 150m and 1900m elevation. The transects were laid along the highway between October 2019 and March 2020. Point counts were laid along the transect at 300m-interval surveying 679-point counts in total. At each sample location, a 15-min early morning (0600 – 1000 hrs) observation was made to record all birds (seen only) within a 50m fixed radius of the sample location. For analysis, migrants and vagrants were excluded.

2.1.2 Environmental data

Based on *a priori* hypotheses, we selected variables that have been shown to influence mammals and birds at the community level in past studies (Penjor et al., 2020, Penjor et al., 2021a): agriculture, settlement, built-up area, road, forest cover, elevation, temperature and precipitation. We rasterised vector layers of agriculture, settlement, and built-up (obtained from the Department of Forests and Park Services, Bhutan). Agriculture, settlement, built-up area, and forest cover were quantified as the percentage of land (%) within a fixed radius (see below), and road as the distance to the nearest road. We derived tree cover from global forest change data (Hansen et al., 2013) corresponding with mammal (2015 data) and bird (2019 data) survey years (Boyle et al., 2014). We used Shuttle Radar Topography Mission's (SRTM) digital elevation model (DEM) (Jarvis, 2008) to extract the elevation data. We used

climate data from CHELSA (Karger et al., 2017) and extracted mean values of all the variables at each study site (within 500m radius for camera trap and 100m for point count location). Since the bioclimatic variables were highly correlated, we used Principal Component Analysis (PCA) to avoid multicollinearity and to reduce the number of predictor variables. We retained the first two PCA axes which accounted for more than 80% of the variance (87.8% for mammals and 92.6% for birds; supplementary material). Axis 1 of mammals mostly captured an increase in temperature seasonality and temperature annual range (hereafter temperature) and axis 2 mainly captured precipitation of coldest quarter and driest month (hereafter precipitation). Likewise, PCA axis 1 for birds captured increase in temperature seasonality and isothermality and axis 2 mostly captured temperature-related variables (maximum temperature of the warmest month and mean temperature of the wettest quarter; hereafter temperature) (see supplementary material).

2.1.3 Trait data

We compiled trait data that describe functional trait space and ecological strategies of mammals and birds (Cooke et al., 2019). For mammals, we used seven functional traits: body mass, litter size, habitat breadth (number of IUCN habitats listed as suitable), generation length, snout-vent length, diet (plant and animal; see below). For birds, we used 11 traits: body mass, beak length at culmen, beak depth, hand-wing index (a measure of wind shape), foraging strata (canopy, understorey, ground) and diet (ectotherm diet, invertebrates, nectar, scavenge). We gathered trait data from published sources (Cooke et al., 2019, Myhrvold et al., 2015, Sheard et al., 2020, Tobias et al., 2022, Wilman et al., 2014). To select diet (out of ten), foraging strata (out of seven) and beak (out of four) data, we performed principal component analyses (supplementary material). Axis 1 of mammal PCA captured diet gradient from herbivores (plant) to carnivores (a diet consisting of mammals and birds) and axis 2

captured general diet (supplementary material). The first four principal components explained ~60% of the total diet variance in birds. The first axis captured the invertebrate materials, the second axis captured mammal/bird materials, the third axis captured plant/seed and the fourth captured scavengers (supplementary material). For beak PCA, the first two axes explained ~100% of the variance with beak length at culmen and beak depth emerging as important traits. The first axis of foraging strata PCA captured canopy and ground strata and the second captured understorey. Trait data were transformed: $\log_{10}$ transformation of body mass and all other traits were scaled and centred to have 0 mean and unit variance (Cooke et al., 2019). Since trait data were available for all species, no trait imputation was required.

2.1.4 Phylogenetic data

We obtained global phylogenetic trees of mammals and birds from published sources. For birds, we averaged 100 trees based on the Hackett backbone (Hackett et al., 2008) downloaded from http://birdtree.org (Jetz et al., 2012). Similarly, for mammals, we downloaded 100 trees built based on the "backbone-and-patch" approach (Upham et al., 2019) from http://vertlife.org, averaged and pruned to our local list for further analyses.

2.2 Estimation of functional trait space, functional diversity, and phylogenetic diversity

We built trait space from transformed and standardised traits using PCA. Across this space, the ordination of species is represented in two- (mammals) or four-dimensions (birds) by integrating all final trait dimensions (Cooke et al., 2019). We estimated multivariate kernel density and calculated probability contours of trait space at different thresholds (0.50, 0.95 and 0.99) using unconstrained bandwidth selectors to smoothen the kernel (Cooke et al., 2019).

We implemented multispecies community occupancy models (MSOM) to estimate species richness and community parameters (Dorazio and Royle, 2005). MSOMs model the latent occurrence of species while accounting for detection probability. The sharing of information across species strengthens the precision and accuracy of parameter estimates. This is particularly useful because sharing information allows us to retain rarely detected species for richness summaries (Iknayan et al., 2014). Full details of the modelling framework are presented elsewhere (Penjor et al., 2021a) (Supplementary Chapter 2).

We used the detection-corrected occurrence matrix (averaged over 2700 matrices) to estimate FD and PD. The facets of diversity derived from this matrix fully account for imperfect detection (Jarzyna and Jetz, 2016). To estimate FD, we used detection-corrected site x species and species x trait matrices. We implemented Hill number (diversity expressed as an equivalent number of species) correction to FD estimates by assigning relative importance to species weights through a threshold on functional distances to identify the functionally distinct set of species (Chao et al., 2019). We estimated distance-based functional richness (FRic) and dispersion (FDis) (Villéger et al., 2008, Laliberté and Legendre, 2010). FRic measures the volume of minimum convex hull enclosing all taxa and represents the maximum range of traits in a community but this metric is sensitive to outliers (Legras et al., 2018). FDis is the average distance of each species to the centroid of trait space and describes the spread of species in functional space (Villéger et al., 2008, Laliberté and Legendre, 2010). The PD and its associated metrics were calculated using the phylogenetic tree obtained from open sources as described in the 'Data' section. PD was calculated as the sum of branch lengths of the phylogenetic tree linking the species in a community at each site and represents the sum of the evolutionary history of the sampled community (Faith, 1992). FD and PD metrics are shown to correlate with species richness (Swenson, 2013, Cadotte et

al., 2019). We accounted for the influence of species richness on these metrics by employing the 'tip-shuffling' null model approach by comparing the observed community with 1000 null communities generated from the pool containing all species in the study. We then calculated abundance-weighted standardised effect sizes (ses) as, $ses = \frac{\mu_{observed} - \mu_{expected}}{\sigma_{expected}}$ using an independent swap algorithm (Gotelli, 2000). We computed (i) deviance of FRic and FDis as the proportionate difference between observed and null expectation (sesFRic and sesFDis), positive values suggesting overdispersion and clustering for negative, (ii) mean pairwise distance (MPD) as the average pairwise distance between species in a community (Webb et al., 2002), and mean nearest taxon distance (MNTD) as the mean distance between a species and the closest relative for PD. Positive values of sesMPD indicate functional or phylogenetic overdispersion while negative values indicate clustering relative to null communities. Positive values of sesMNTD suggest that distantly related species co-occur in the community while negative values suggest the coexistence of close relatives. Analyses were performed in R (R Core Team, 2021) using packages FD (Laliberté et al., 2014a), vegan (Oksanen et al., 2007), ks (Duong, 2007), picante (Kembel et al., 2010) and mFD (Magneville et al., 2022).

We regressed the biodiversity facets (sesFRic, sesFDis, sesMPD, sesMNTD) against land use (forest cover, agriculture, built-up area, and settlement) and climate (see Environmental data section for a selection of climate variables) variables using a linear mixed effect model (Supplementary material). We checked for spatial autocorrelation for each diversity metric using Moran's I test. For models displaying spatial autocorrelation, we treated sampling locations as random effects (e.g., birds). We performed the regression in the Bayesian framework to derive posterior central tendency and spread (credible intervals to measure uncertainty) of the parameters using JAGS (Plummer, 2003) in R using package jagsUI

(Kellner, 2019). For all measures, we assessed the significances of the regression coefficient estimates with 95% Bayesian credible intervals and model fit using Bayesian R^2 (Gelman et al., 2019).

3 Results

3.1 Functional trait space

The first two principal components (PC) explained about 71% of the total trait variation for mammals (Figure 1a). The primary axis of differentiation, PC1, integrates body mass (loading=0.45), snout-to-tail length (0.40) and generation length (0.40) and trade-off between herbivores (plant diet, loading =0.43), carnivores (diet consisting of mammals and birds, loading=-0.36), and litter size (-0.39). Species with high PC1 values are generally characterised by large body mass, longer body length (snout to tail length) and slow life-history (long generation length) but have small litter size and are generally represented by herbivores like elephant (*Elephas maximus*), gaur (*Bos gaurus*), water buffalo (*Bubalus arnee*), sambar deer (*Rusa unicolor*), serow (*Capricornis thar*). On the other hand, species with low PC1 values are represented by small body mass, shorter body length and faster life history and with carnivorous diet (e.g., spotted linsang (*Prionodon pardicolor*), Chinese ferret badger (*Melogale moshata*), pangolin (*Manis spp.*), weasel (*Mustela spp*.), dhole (*Cuon alpinus*), red fox (*Vulpes vulpes*), and jackal (*Canis aureus*)). PC2 characterises habitat generalists (habitat breadth loading =0.57), e.g., tiger (*Panthera tigris*), leopard (*P. pardus*), and wild pig (*Sus scrofa*) at high PC2 values, habitat specialists at low PC2 values, e.g., golden langur (*Trachypithecus geei*), Asiatic brush-tailed porcupine (*Atherurus macrourus*), Indian hare (*Lepus nigricollis*), and musk deer (*Moschus spp*.).

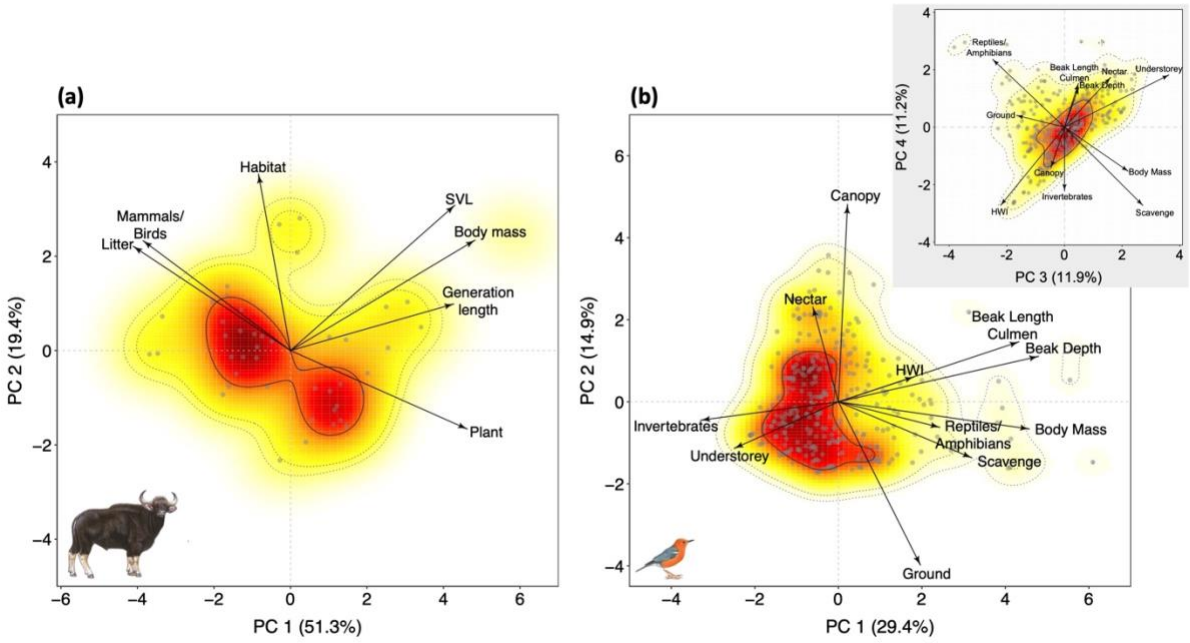


Figure 1. Principal component dimensions (PC) and trait loadings are based on all 9 traits for mammals (a) and 11 traits for birds (b). Colours indicate the density of species (increasing from yellow to red) on each 2-dimensional plane (mammal=45 species and bird=336 species)

In the case of birds, 67% of the variation in traits is captured by four PCs (Figure 1b). Trait variation was centred on a dense core with species having extreme morphologies scattered at the periphery (e.g., hornbills and vultures). The first axis (PC1; 29% of trait variance) describes beak shape (length at culmen and depth; loadings=0.47) and body mass (e.g., hornbills; loadings=0.45), primarily frugivores, while PC2 (15% of trait variance) separates canopy feeders (e.g., leafbirds, flowerpeckers and orioles; loadings=0.67) from ground feeders (e.g., pheasants, thrushes, doves; loadings=-0.55) along with trophic niche. PC3 (12% of trait variance) describes understorey (babblers and laughingthrushes; loadings=0.56) feeders and diet composed of reptiles and amphibians (ectotherms, e.g., shrikes, egrets and herons; loadings=-0.38) and the PC4 (11% of trait variance) describes scavengers (e.g., vultures; loadings=-0.43) and species with larger hand-wing index (HWI; loadings=-0.43) that are linked to migration and dispersal ability (e.g., cuckoos and swifts).

The hotspots (i.e., the smallest portion of functional space including 50% of the species (Díaz et al., 2016)) were different for mammals and birds. The mammals had a single hotspot with a bimodal distribution of species distinguishing carnivores with large litter sizes (dholes, foxes, jackals) from herbivores with small litter sizes (muntjac, goral, musk deer). In the case of birds, variation in traits is distributed such that the majority of species occupy dense core in the centre of trait space, with more extreme forms found towards the edges. Certain groups of species occupy distinct areas of trait space only apparent on PC axes that themselves account for low total variation, such as vultures on PC4.

3.2 Relationship between biodiversity facets and environmental variables

Richness-corrected FRic (sesFRic) of mammals was influenced by elevation, distance to road, precipitation, and temperature seasonality (R^2=0.21, Supplementary material) and sesFDis by elevation, distance to road, precipitation, and agriculture (R^2=0.012). Elevation had an opposite effect on FD (sesFRic decreased and sesFDis increased although both showed a non-linear relationship) whereas both increased farther away from the road and with increasing precipitation (Figure 2). FRic (sesFRic) decreased with temperature seasonality while sesFDis decreased with agriculture. Similarly, for birds, sesFRic and sesFDis were influenced by three variables: settlement density, temperature, and forest cover. sesFRic increased with settlement density but decreased with temperature and sesFDis decreased with forest cover (Figure 2f-h).

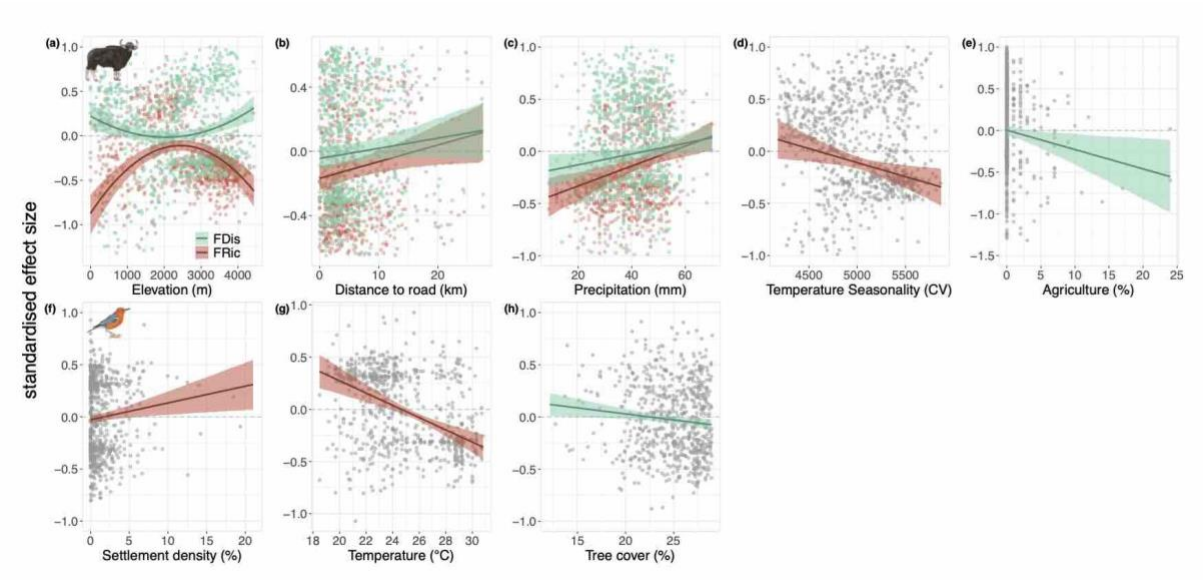


Figure 2. Relationship between FD (represented by FRic and FDis) and land use and climate variables for mammals (a-e) and birds (f-h). Predictions were made from the top model. Solid lines indicate mean, and polygons represent 95% credible intervals

Forest cover had opposing effects on mammals and birds: positive on both sesMPD and sesMNTD for mammals and negative for both sesMPD and sesMNTD for birds (Figure 3). Likewise, temperature-related variables had opposing effects: negative effect of temperature seasonality on mammals and positive effect of temperature of the warmest month on birds. Mammal sesMPD was positively associated with agriculture and negatively with precipitation (R^2=0.56; Supplementary material). sesMNTD of mammals was negatively associated with built-up area and precipitation but positively with the settlement (R^2=0.37). On the other hand, bird sesMPD was negatively associated with agriculture, built-up area, settlement, and precipitation (R^2=0.31). Bird sesMNTD was negatively associated with agriculture and settlement (R^2=0.28).

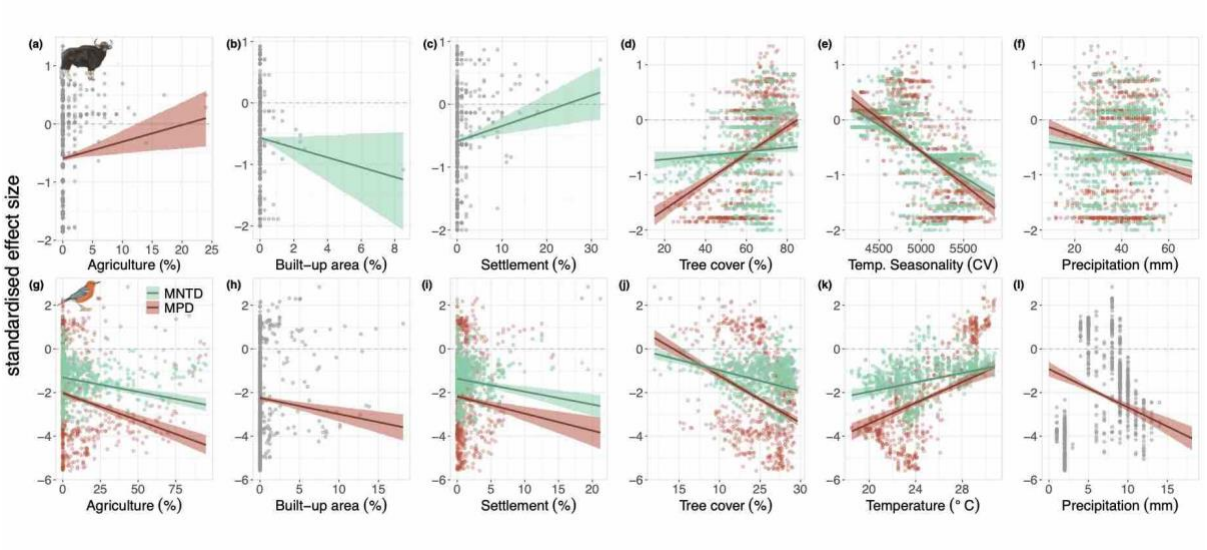


Figure 3. Relationship between PD (represented by MPD and MNTD) and land use and climate variables for mammals (a-f) and birds (g-l). Predictions were made from the top model. Solid lines indicate mean, and polygons represent 95% credible intervals

The overall FD and PD of both groups were lower than expected by chance indicating that communities were functionally and phylogenetically clustered (Figure 4). There were, however, subtle differences between the two groups: birds had higher richness but lower dispersion than mammals. Likewise, birds were more phylogenetically clustered (lower sesMPD and sesMNTD) than mammals, but mammals highly showed variable PD (bimodal distribution).

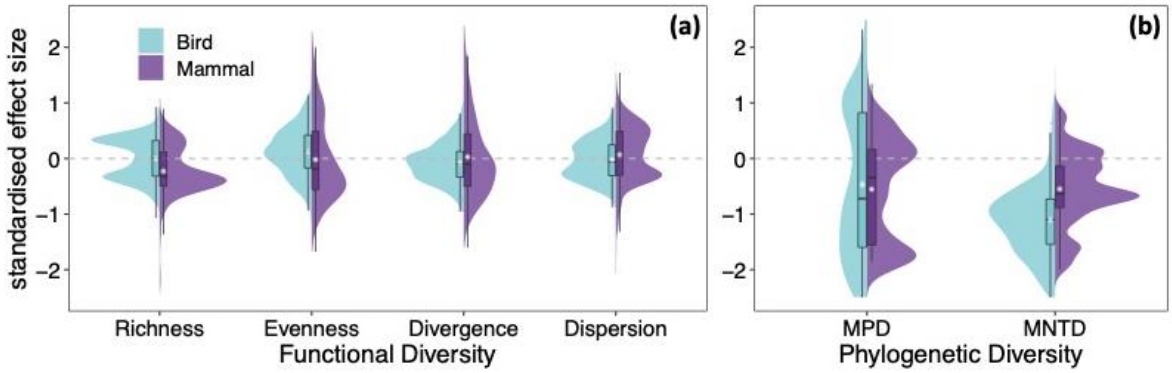


Figure 4. Overall FD and PD (corrected for species richness) of mammals and birds. Boxplots complement density plots with means indicated by white dots and medians by horizontal bars

4 Discussion

Using two groups of vertebrates, we show that realised functional trait spaces are constrained to a single plane in which species are clumped around a few strategies (Carmona et al., 2021). The diversity of mammal functional traits in the eastern Himalayas can be represented along a few axes of correlated trait variation representing body mass, diet, and habitat breadth whereas birds can be represented along four dimensions representing beak shape and size, foraging strata, diet and HWI. The nuances of FD and PD to land use and climate variables demonstrate the complex ways in which the synergy between anthropogenic disturbance and climate change can affect different dimensions of biodiversity.

Since the Pleistocene, many large animal species have gone extinct and the rate of extinction of larger species has been higher than that of smaller species (Fordham et al., 2020, Dirzo et al., 2014). This trend is likely continuing, exacerbated by the burgeoning human population and consumption patterns disadvantaging large longer generation length

species (Cardillo et al., 2005, Dirzo et al., 2014). However, smaller terrestrial (mammal) species are similarly imperilled because they tend to have low dispersal abilities making them vulnerable to extinction because of anthropogenic land-use and climate change (Carmona et al., 2021). Our findings show that species with large body mass, longer generation length, and long gestation period (those occupying the boundaries of functional space, e.g., elephants, water buffalo) are much more vulnerable than smaller species with shorter generation length and larger litter size (those occupying centre of functional space; high redundancy) to human disturbance (Carmona et al., 2021, Enquist et al., 2020). The loss of these vulnerable species (particularly the largest ones) could potentially create a lacuna in trait space due to the loss of unique ecological functions (Estes et al., 2011) and ecosystem services that are not readily replicated by smaller-bodied fauna (Enquist et al., 2020) and can impact ecosystem structure, function, and biogeochemical cycles (Cooke et al., 2019, Rule et al., 2012).

There were two (albeit indistinct) functional hotspots for mammals; the first aligned along with species with carnivorous diet and large litter size (e.g., fox, dhole, weasel) and the second along with herbivorous diet, small litter size and habitat specialist (golden langur, musk deer). The first PC of mammal trait space, in essence, reflects trophic interactions along body mass gradient which consequently affect nutrient cycling (Ripple et al., 2017). Multiple ecological functions, e.g., pollination, predation, herbivory, and seed dispersal, relate to body mass (Cooke et al., 2019). Axis 2 that solely explained variation in habitat breadth reflects responses of species and/or adaptability to change and/or modification of their surrounding environment (Cooke et al., 2019). A species with broad habitat breadth (generalist) has greater flexibility to environmental change and thus can shift its resource use or distribution with greater ability to cope and persist (e.g., wild boar and common leopard) than those with

narrow breadth (Cooke et al., 2019). Birds had a single hotspot that captured beak size, foraging strata, diet, and hand-wing index along four axes representing trait modalities related to food acquisition, functional feeding groups, foraging techniques, and dispersal ability. These hotspots captured most of the families, demonstrating a relatively high degree of convergence in ecological strategies (Cox et al., 2021). Some species, however, break the rule of conventional trait associations and therefore occupy remote corners of trait space with relatively fewer species than expected by chance (e.g., elephants and vultures). Elephants are the most distinct species representing large areas of trait, upholding critical functions, such as grassland regeneration, nutrient cycling, and habitat complexity. Likewise, the loss of species with a specific functional role (e.g., scavenging by vultures) could gravely impact ecosystem processes (e.g., carrion removal and control of the spread of disease).

The decrease of mammal FRic with elevation indicates that the volume enclosing all taxa decreases at higher elevations perhaps also decreasing the range of traits represented in a community (Legras et al., 2018) probably due to the filtering effect of cold temperature at high elevations allowing only closely related species that can tolerate extremes to cluster in trait space (Hughes et al., 2021, Voskamp et al., 2017). Large-bodied ungulates are rare at high elevation habitats (e.g., elephant, Asiatic water buffalo and gaur) and hence the services provided by them are absent or reduced. The negative relationship between FRic and temperature seasonality suggests that temperature significantly influences seasonal variation in FD and thus may be a limiting factor for forage or habitat availability for mammals (via an effect on primary production) and/or that seasonal temperature may be a direct or an indirect limiting variable for reproduction (i.e., via energetic constraints on thermoregulation) (McLean and Guralnick, 2021). On the other hand, precipitation of the coldest quarter positively influenced FRic and FDis. Given that precipitation drives primary productivity

(and influences habitat complexity) in most plant ecosystems, food availability is critical in maintaining positive energy balance to support mammal reproduction (Bronson and Perrigo, 1987), suggesting areas with higher precipitation support higher functional trait diversity. During the cold and dry season, it is likely that species in the Himalayas face greater stress due to water deficiency because the preponderance of rainfall occurs mainly during the monsoon (between July and September). In general, our findings concur with previous studies that energy and water (i.e., temperature seasonality and precipitation) play key roles in explaining the richness of species and functional traits (Ruggiero and Hawkins, 2008, Panda et al., 2017). Although the effects of precipitation and temperature on FD were nuanced, their synergy underpins the mechanism by which the contemporary climate affects the overall FD.

Similarly, the decrease in sesFRic with increasing maximum temperature of the warmest month suggests that during the warm season, temperature rise might impose additional stress to the energetics in endotherms. The increasing temperature and heatwaves likely affect the basal metabolic rates of birds reducing their overall efficiency in foraging, reproduction, and dispersal (Sekercioglu, 2012).

Interestingly, sesFDis decreased with forest cover suggesting potential trait homogeneity in bird assemblages due to change in forest cover (Cisneros et al., 2015). Forest interiors may harbour foraging and habitat specialists thus increasing functional redundancy due to similarity in functional traits (e.g., trait conservatism). On the other hand, forest edges may offer higher accessibility and visibility and favour assemblages (but mostly generalists) with divergent foraging traits thus increasing trait diversity (Penjor et al., 2021a). Further,

change in canopy structure could affect canopy specialists that occupy the boundary of functional trait space.

The Himalayas, in general, face greater pressure from anthropogenic disturbance. Mammal FRic and FDis increased further away from road whereas FDis decreased with agriculture suggesting possible niche packing with redundant traits in agricultural landscapes (Hughes et al., 2021). On the other hand, bird FRic increased at a higher settlement density. It suggests that mammals are intolerant of human disturbance whereas some level of human disturbance may be tolerated by birds supporting the intermediate disturbance hypothesis. Besides habitat loss and fragmentation, a decline in primary food sources (plants, insects and smaller organisms' abundance) as a result of land-use intensification and climate change may contribute to the decline of the bird and mammal population (Raven and Wagner, 2021). The risk of global climate change is more likely to be pronounced in local communities because functional redundancy is low in local communities with fewer species and extinction of a species (particularly those at the boundary of trait space) is likely to alter functioning with effects amplified across the trophic (Donohue et al., 2017).

The effect of agriculture, settlement, forest cover and temperature were nuanced for mammal and bird PD. Although the anthropogenic variables (e.g., agriculture, built-up area, and settlement) had negative effects on the PD of birds resulting in clustering and suggesting that species assemblages are non-random relative to land-use, and an altered landscape could potentially compromise the evolutionary uniqueness. Homogenisation of the physical environment across the Himalayan landscape may be creating filters allowing only some lineages to persist thus increasing phylogenetic homogenisation (decreasing MPD and MNTD in birds) (McKinney, 2006, Sol et al., 2017). This has implications on the health of

community structure because closely related lineages are vulnerable to pathogens and diseases which, in turn, increases the risk of disease emergence in human populations (Dharmarajan et al., 2021).

The positive relationship between mammal PD and human land use suggests that species attracted to agriculture and human settlement are distantly related (e.g., muntjac *Muntiacus muntjak* and wild boar) but not necessarily indicative of phylogenetic overdispersion. One possible explanation for higher PD may be due to the spillover of species from the nearby forest abutting settlement (i.e., edge effect). Another possibility is that the so-called 'winners' in anthropogenic environments may be disproportionately represented in a few distantly related clades (e.g., wild boar, the only member of the Suidae family found in this study) often lacking close relatives in the same community thus partially explaining phylogenetic overdispersion. Some species perceive human environments as ecological opportunities (Cox and Gaston, 2018), often dominating communities close to the settlement despite being rare in the surrounding natural environments (Møller et al., 2015) but still contributing to the regional PD. In our study, Assamese macaque (*Macaca assammensis*), Malayan porcupine (*Hystrix brachyura*) and muntjac, all distantly related, were positively associated with agriculture and settlement although infrequently detected at sites in deeper forests concurring with our field observations.

The increase in the phylogenetic distance between an individual and its neighbour (sesMNTD) of mammals indicate that habitats in forests are different from those in the human settlement in species composition and abundance (Matos et al., 2017), making communities more likely to have evolved from lineages at more terminal parts of the phylogenetic tree. On the other hand, decreasing sesMNTD for bird communities indicates

the existence of close relatives between sampled communities and those forest habitat specialists are clustered within the phylogeny (Sol et al., 2017). Overall, our findings provide evidence of the emergence of novel communities with different phylogenetic and functional properties due to ongoing land modification (Lurgi et al., 2012).

Mammals showed phylogenetic clustering with temperature and precipitation suggesting that extreme heat and precipitation may act as abiotic filters (Cunningham et al., 2021, Harrison et al., 2020). The increasing sesMPD and sesMNTD with temperature in birds indicates that only closely related species, probably those tolerant of a warmer climate, occur together. However, this contrasts with the FRic that showed a decreasing trend with temperature suggesting that a higher PD does not correlate with FD and that warmer climate may not necessarily foster diverse functional traits.

5 Conclusions

Our findings have broad implications for biodiversity conservation across human land-use gradients. We show that the projected loss of species on the edge of functional space due to anthropogenic pressures is non-random and could lead to the loss of irreplaceable functional traits and perhaps services associated with them. And could impact the long-term sustainability of ecological and evolutionary processes (Dirzo et al., 2014). Our study demonstrates that anthropogenic pressures act as habitat filters resulting in low levels of FD and PD (particularly mammal communities) suggesting possible loss of unique traits and distinct evolutionary lineages. Such losses are malign indicators of the decline of vital ecosystem services (Flynn et al., 2009a). On the other hand, a higher diversity of birds close to human settlement suggests the opportunity for ecosystem services but with caveats (e.g.,

human-wildlife conflict). Our work reveals novel insights into the structure and drivers of vertebrate assemblages in the eastern Himalayas.

6 Authors' contributions

UP conceptualised and designed analyses, SS designed bird survey and collected data, UP and SS curated data, UP analysed the data and interpreted the results, UP wrote the first draft. All authors contributed equally to revisions and gave final approval for submission.

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Chapter 5

Contrasting effects of human settlement on the interaction among sympatric apex carnivores

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Abstract

In the face of a growing human footprint, understanding interactions among threatened large carnivores is fundamental to effectively mitigating anthropogenic threats and managing species. Using data from a large-scale camera trap survey, we investigated the effects of environmental and anthropogenic variables on the interspecific interaction of a carnivore guild comprising tiger, leopard, and dhole in Bhutan. We demonstrate the complex effects of human settlement density on large carnivore interactions. Specifically, we demonstrate that leopard-dhole co-occupancy probability was higher in areas with higher human settlement density. The opposite was true for tiger-leopard co-occupancy probability, but it was positively affected by large prey (gaur) abundance. These findings suggest that multi-carnivore communities across land-use gradients are spatially structured and mediated also by human presence and/or the availability of natural prey. Our findings show that space-use patterns are driven by a combination of the behavioural mechanism of each species and its interactions with competing species. The duality of the effect of settlement density on species interactions suggests that the benefits of exploiting anthropogenic environments are a trade-off between ecological opportunity (food subsidies or easy prey) and the risk of escalating conflict with humans.

Keywords: eastern Himalaya, human settlement, interspecific interaction, large carnivores, multi-species occupancy model

1 Introduction

Interactions among species are the foundations of the structure and integrity of ecological communities (Polis et al., 1989). The carnivore guild is mainly shaped by competition and

intraguild predation (Caro and Stoner, 2003, Swanson et al., 2016, Polis and Holt, 1992). Large carnivores regulate trophic levels by controlling prey populations and by moderating mesocarnivore populations and their effects, thus indirectly affecting both herbivore and plant communities (Ritchie et al., 2009, Ford and Goheen, 2015). However, their ecological roles are compromised by anthropogenic-induced habitat loss and fragmentation, prey depletion, and mortality due to direct persecution (Ripple et al., 2014). Studies have shown that extirpation of apex predators from an ecosystem leads to an increase in ungulate populations, which in turn results in overgrazing and suppression of plant growth and ultimately degradation of habitat for a range of species (Atkins et al., 2019). Assessing the impact of anthropogenic and environmental changes on large carnivore communities is key to understanding broader community structure and resilience across the human land-use gradient. Yet, the most recent studies on the interaction among threatened large carnivores have been predominantly confined to small, protected reserves (a few hundred km^2) (Steinmetz et al., 2013, Karanth et al., 2017, Lahkar et al., 2021) but see also (Haidir et al., 2018). Making inferences about carnivore community interactions, beyond protected areas, at a landscape scale in order to better understand carnivore community structure and stability is surprisingly rare.

According to coexistence theory, competing species must segregate at least along one or more dimensions of their ecological niches in order to coexist (MacArthur and Levins, 1967, Schoener, 1974). When such niche differentiation is achieved, interspecific competition is reduced and a greater number of species can coexist (Loreau, 2010). Resource competition intensifies when two or more species occupy a similar ecological niche and hence vie to exclude each other (Hutchinson, 1957). According to intraguild predation theory, the distribution of dominant predators is influenced by food availability, whereas that of

subordinate species is determined by food availability and safety from predation (Polis and Holt, 1992). Hence, from this theory, it is apparent that resource productivity underpins large carnivore interactions. While coexistence stabilises ecosystem structure, lack of it leads to the population decline or extirpation of one of the interacting species, which can have rippling effects across the trophic level (Atkins et al., 2019). Antagonistic interactions among carnivores (i.e., competition and predation) change the species' spatial and temporal ecology (Hersteinsson and Macdonald, 1992, Palomares and Caro, 1999). One of the ways that large carnivores share prey and habitat is by spatial and temporal partitioning (Vanak et al., 2013). Food availability, it has been argued, is a principal driver of carnivore spatial organisation and thus guild structure (Macdonald, 1983). Where resources are rich and dispersed, sharing among carnivores is possible without additional cost to each species' fitness (Macdonald and Johnson, 2015).

One of the central tenets of community ecology is to understand interactions among species and their abiotic environments, as a way of predicting species' geographic distributions and abundances (Horn and MacArthur, 1972). Anthropogenic influences alter species interactions by benefiting some and disadvantaging others (Alberti et al., 2003). Studies have demonstrated that a decrease in large/apex carnivore presence benefits mesopredators (Wang et al., 2015) - a phenomenon known as mesocarnivore release - resulting in the decline of smaller-bodied prey populations (Crooks and Soulé, 1999) and the further intensification of competition among smaller carnivores. Although species sensitive to humans avoid encounters by altering their spatiotemporal behaviour or habitat use (Llaneza et al., 2018), human tolerant species can modify their behaviour to increase overlap with humans in order to reduce intraguild competition (Deuel et al., 2017). However, such behaviour comes at a heightened risk of conflict with humans (Ordeñana et al., 2010).

Furthermore, when human disturbances result in reduced carnivore diversity, it may lead to loss of ecological services if the prospering species are unable to perform the ecological functions of the extirpated ones (Flynn et al., 2009a), with detrimental consequences for ecosystem resilience (Mori et al., 2013).

The tigers (*Panthera tigris*), leopards (*Panthera pardus*), and dholes (*Cuon alpinus*) are syntopic across most of their range in the south and southeastern Asia and play an important role in regulating prey populations and balancing trophic levels. They are all categorised as "Threatened" on the International Union for Conservation of Nature (IUCN) Red List due to decreasing population trends and are therefore considered high-priority conservation species across their ranges (IUCN, 2021). They prefer prey of a similar size range and hence intraguild competition amongst them is likely high (Karanth and Sunquist, 1995). This study aims to assess the patterns of coexistence and evaluate factors mediating sympatry among the large carnivore guilds, beyond what has been already studied within protected areas. Our primary objectives were: 1) to investigate the effects of anthropogenic and environmental variables on the occurrence of large carnivores across human land-use gradient and 2) to examine the influence of human disturbance on spatial interaction of threatened large carnivores at site and landscape level. Given the previously reported sensitivity of many large carnivores to human disturbance (Penjor et al., 2019, Tempa et al., 2019, Thinley et al., 2018), we predicted that all three species will be negatively affected by human disturbance and that interaction between species pairs (tiger-leopard, tiger-dhole, and leopard-dhole) will be negatively affected by settlement density and disturbance at the site. We also tested the hypothesis that prey choice and prey abundance would be able to support multiple carnivores and facilitate sympatry (Lahkar et al., 2021). Our study is specifically

aimed at unravelling the spatial partitioning mechanism of large carnivores across human land-use gradient and its implications on the management of threatened large carnivores.

2 Materials and Methods

2.1 Study area

Our study area was Bhutan, a small country of 38,394 km^2 area, landlocked between the Tibetan Autonomous Region (China) to the north and India to the east, west and south (Appendix S1). About 70% of the country is covered by forests. The elevational gradient increases northwards from 100 m to 7000 m, mediating the vegetation composition: subtropical southern foothills are characterised by broadleaved forests, the temperate zone by cool-broadleaved and conifer mix forests, and the alpine and subalpine zones by Rhododendron-scrub mix forests and stunted shrubs. The topography is typically rugged terrain with deep gorges, narrow valleys, and steep slopes. The mean annual temperature ranges between 10 and 24°C and annual precipitation between 300mm and 6000mm. Human population density is low: 20 people km^{-2} (NSB, 2020). Bhutan is entirely within the eastern Himalayan biodiversity hotspot (Myers et al., 2000) and harbours a rich spectrum of wildlife including charismatic megafauna such as tigers, leopards, dholes, snow leopards (*Panthera uncia*), clouded leopards (*Neofelis nebulosa*), and Asian elephants (*Elephas maximas*) among others. More than half of the country's area is part of the national protected area network.

2.2 Camera trap survey

We conducted a camera trap survey following a regular square-grid design based on a putative female tiger home range of 25 km^2 to guide the placement of camera traps (Karanth and Nichols, 2002). We placed a pair of infrared motion-triggered camera traps in each grid cell along human or animal trails (except in absence of trails, when cameras were placed

randomly) at a height of ~45 cm above the ground with a 1 s reset time and burst image mode (for maximum captures). A total of 1129 unbaited camera stations were established. The camera models used were Bushnell, Cuddeback, HCO-Scoutguard, Reconyx, U-Way and Panthera. The mean distance between camera traps was 2.9 km (SD = 1.2 km) but this distance was highly variable depending on the terrain and site accessibility. We omitted grid cells that contained dense urban areas (more than 70% of the grid space), and those above 4500m altitude due to the low probability of capturing tigers, which was the primary objective of the survey. For logistical convenience, the country was divided into two blocks and camera traps were deployed during the dry season when most sites were easier to access. We deployed camera traps in the south block for 141 days (between March 2014 and June 2014) and in the north for 157 days (between October 2014 and March 2015). We monitored camera stations every 30th day to retrieve data, change batteries, replace memory cards, and clear the camera's field of view of vegetation.

2.3 Model covariates

We modelled variation in occupancy probability using covariates that addressed our hypotheses: human settlement density, forest cover, disturbance at the camera trap site, river density, slope, and prey abundance. We calculated settlement density using a point shapefile of all known households obtained from the Forest Department. After rasterising the number of households at 90m pixel resolution, we calculated the mean number of households among all pixels within a 4 km radius from each camera site in ArcGIS (ESRI, 2011). This variable reflects the density of houses per pixel (90 m) and when averaged across the 4 km radius characterises human-related influence at the landscape scale. Moreover, as this variable is highly correlated with other infrastructures such as farm roads and highways, it also serves as a proxy for built-up areas. We used global tree cover data (rescaled to 90 m resolution) and

averaged over a 4 km radius (Hansen et al., 2013) for each camera site. For river density, we rasterised the river shapefile (obtained from the forest department of Bhutan) at a pixel resolution of 90 m and calculated the per cent of river pixels within a 4 km radius of each camera station. The radius of 4 km was selected to represent the mean home range of the smallest species of the three carnivores (i.e., leopard's average home range size of ~50 km^2) (Snider et al., 2021). Studies have shown that large prey species were the most preferred prey of tigers, leopards, and dholes, accounting for a significant portion of the total prey biomass (Karanth and Sunquist, 1995, Wang and Macdonald, 2009, Kamler et al., 2012, Hayward et al., 2014). We used muntjac (*Muntiacus muntjak*), gaur (*Bos gaurus*) and serow (*Capricornis thar*) relative abundance as prey covariates in all large carnivore models. First, we used a hierarchical N-mixture model (Royle, 2004) to estimate the relative abundance of prey from camera trap data as a function of forest cover, elevation (extracted from digital elevation model) (Jarvis, 2008) and settlement density while accounting for imperfect detection probability using the "unmarked" package (Fiske and Chandler, 2011) in R (R Core Team, 2021). We then used site-level abundance as prey covariates in occupancy models of each species. The mean daily encounter rates (independent captures 30 min apart) of humans and livestock (dogs, cattle, and horses) were used as a covariate to represent the effect of disturbance (hereafter human disturbance) at the site level (camera trap site). The detection covariates were trail (coded as 1 for cameras placed on-trail and 0 otherwise), human disturbance and trap effort (number of days a camera trap was functional during the survey) to account for unequal sampling effort (83.3[1 – 156]). For details on the mean and variation of covariates, see Appendix S2. We controlled for the geographical variation of north and south blocks on occupancy by including blocks as a random effect in the marginal occupancy model.

2.4 Multispecies interaction model

We used the multispecies species occupancy model (Rota et al., 2016) to examine the interaction among large carnivores. This model extends the interaction model of (MacKenzie et al., 2004) but accommodates the effects of covariates and does not need a priori assumption of asymmetric interactions (i.e., need not consider one species dominant over the other). It models the interaction between two or more species using a multivariate Bernoulli (MVB) distribution, $Z_i \sim MVB(\psi_i)$ where, Z_i is a 3-dimensional vector of binary detection/non-detection data denoting latent occupancy state of all three study species and ψ_i is a 2^3-dimensional vector that denotes the probability of all possible states Z_i can take (Rota et al., 2016). For the three species, we modelled Z as,

$Z \sim \text{Categorical}(\psi_{000}, \psi_{100}, \psi_{010}, \psi_{001}, \psi_{110}, \psi_{011}, \psi_{101}, \psi_{111})$. Here, the latent occupancy state for all species present is represented as ψ_{111}, when all are absent as ψ_{000}, when either two are present as $\psi_{110}, \psi_{011}, \psi_{101}$ and only one is present as $\psi_{001}, \psi_{100}, \psi_{010}$. As in any occupancy model, ψ can be modelled as a function of covariates and it describes the probability a site is occupied by only one (first order), two (second order) or more (higher order) interacting species. The latent states for S species have 2^S-1 possible combinations described by natural parameters (f) (sensu Rota et al., 2016) which describe the log-odds a species occupies a site. For three species, the natural parameters are f_1, f_2, f_3, f_{12}, f_{13}, f_{23}, f_{123}. Fixingf_{12}, f_{13}, f_{23} and f_{123} to zero assumes independence in species occurrence. We modelled marginal occupancy (i.e., f_1, f_2, f_3 or no interaction) as a function of settlement density, forest cover, human disturbance, river density, slope, and prey abundance and conditional occupancy (i.e., f_{12}, f_{13}, f_{23} or pairwise interaction) as a function of settlement density, forest cover, disturbance, prey and interaction between prey and settlement density. We did not model higher-order interaction (i.e., f_{123} = 0) because we assumed the probability

that three species occurred together was purely a function of species-specific and pairwise interaction parameters.

We binned detection/non-detection data for each camera station into 15-day per sampling occasion replicates to increase temporal independence of detections and reduce overdispersion. We built a set of 19 candidate models to test our hypotheses regarding the effects of anthropogenic and environmental variables on the occupancy of each species and interspecific interactions (Table 1). We compared and ranked the models based on the Watanabe-Akaike information criterion (WAIC) (Hooten and Hobbs, 2015) and selected the model with the lowest WAIC value. We assessed model fit by comparing observed data to simulated data using Freeman-Tukey discrepancy and computed Bayesian *p*-value as a summary of posterior predictive check (Kéry and Royle, 2016). All covariates were z-standardised prior to analysis. We fitted models in JAGS (Plummer, 2003) called through R using the package jagsUI (Kellner, 2019). We used uniform priors on first order occupancy and detection intercepts and weakly informative normal priors on first and second order occupancy and detection slopes (see Data availability statement). We ran the models with three parallel chains of 100000 Markov Chain Monte Carlo (MCMC) iterations each, discarding 50000 iterations during adaptation and 30000 in burn-in phases and retaining every 50^{th} (thinning) posterior sample for inference. Model convergence was diagnosed using the Gelman-Rubin statistic ($\widehat{R}$) for all parameters and visual inspection of trace plots (Gelman et al., 2014). All parameters in our model achieved convergence ($\widehat{R} < 1.1$). The top-rank model adequately fitted our data (Bayesian *p*-value = 0.13, Appendix S4).

3 Results

Across the total survey effort of 73,259 sampling (trap) days at 849 stations (out of 1129, the rest were lost to animal vandalism, theft, and malfunction) in 2014 and 2015, we obtained 323, 497 and 421 detections of tigers, leopards, and dholes, respectively, at 151, 197 and 210 sites, respectively. The top model consisted of all pairwise interactions between species as a function of settlement density, human disturbance, and prey, and performed significantly better than models with constant (intercept only) pairwise interaction or independent occurrence (no interaction, Table 1). The marginal occupancy parameters in the top model were settlement density, human disturbance, forest cover, river density, slope, and prey (gaur, muntjac and serow) (Table 1).

Table 1. Model selection results

First order	Second order	Detection	WAIC	ΔWAIC
$\beta_0 + \beta_1$Settlement + β_2Disturbance + β_3Forest + β_4River + β_5Slope + $\sum_{x=0}^{X=3} \beta_x$Prey	$\gamma_0 + \gamma_1$Settlement + γ_2Disturbance + $\sum_{x=0}^{X=3} \gamma_x$Prey	α_0+α_1Trail + α_2Effort + α_3Disturbance	3585.2	0.0
$\beta_0 + \beta_1$Settlement + β_2Disturbance + β_3Forest + β_4River + β_5Slope + $\sum_{x=0}^{X=3} \beta_x$Prey	1	α_0+α_1Trail + α_2Effort + α_3Disturbance	3590.8	5.6
$\beta_0 + \beta_1$Settlement + β_2Disturbance + β_3Forest + β_4River + β_5Slope + $\sum_{x=0}^{X=3} \beta_x$Prey	0	α_0+α_1Trail + α_2Effort + α_3Disturbance	3592.6	7.4
$\beta_0 + \beta_1$Settlement + β_2Disturbance + β_3Forest + β_4River + β_5Slope + $\sum_{x=0}^{X=3} \beta_x$Prey	$\gamma_0 + \gamma_1$Settlement + γ_2Disturbance + $\sum_{x=0}^{X=3} \gamma_x$Prey + γ_iPrey × Settlement	α_0+α_1Trail + α_2Effort + α_3Disturbance	3596.2	11.0
$\beta_0 + \beta_1$Settlement + β_2Disturbance + β_3Forest + β_4River + β_5Slope + $\sum_{x=0}^{X=3} \beta_x$Prey + β_iPrey × Settlement	$\gamma_0 + \gamma_1$Settlement + γ_2Disturbance + $\sum_{x=0}^{X=3} \gamma_x$Prey + γ_iPrey × Settlement	α_0+α_1Trail + α_2Effort + α_3Disturbance	3617.8	32.6
$\beta_0 + \beta_1$Settlement + β_2Disturbance + β_3Forest + β_4River + β_5Slope + $\sum_{x=0}^{X=3} \beta_x$Prey	$\gamma_0 + \gamma_1$Settlement + γ_2Disturbance	α_0+α_1Trail + α_2Effort + α_3Disturbance	3621.9	36.7
$\beta_0 + \beta_1$Settlement + β_2Forest + $\sum_{x=0}^{X=3} \beta_x$Prey	$\gamma_0 + \gamma_1$Settlement	α_0+α_1Trail + α_2Disturbance	4221.1	635.9
$\beta_0 + \beta_1$Forest + $\sum_{x=0}^{X=3} \beta_x$Prey	$\gamma_0 + \gamma_1$Settlement	α_0+α_1Trail + α_2Disturbance	4226.6	641.4
$\beta_0 + \beta_1$Settlement + β_2Forest + $\sum_{x=0}^{X=3} \beta_x$Prey	1	α_0+α_1Trail + α_2Disturbance	4229.7	644.5
$\beta_0 + \beta_1$Settlement + $\sum_{x=0}^{X=3} \beta_x$Prey	$\gamma_0 + \gamma_1$Settlement	α_0+α_1Trail + α_2Disturbance	4237.7	652.5
$\beta_0 + \beta_1$Settlement + β_2Forest + $\sum_{x=0}^{X=3} \beta_x$Prey	0	α_0+α_1Trail + α_2Disturbance	4238.7	653.5

β_0 + β_1Forest + $\sum_{x=0}^{X=3} \beta_x$Prey	1	α_0+α_1Trail + α_2Disturbance	4240.8	655.6
β_0 + β_1Settlement + $\sum_{x=0}^{X=3} \beta_x$Prey	1	α_0+α_1Trail + α_2Disturbance	4245.2	660.0
β_0 + β_1Forest + $\sum_{x=0}^{X=3} \beta_x$Prey	0	α_0+α_1Trail + α_2Disturbance	4247.1	661.9
β_0 + β_1Settlement + $\sum_{x=0}^{X=3} \beta_x$Prey	0	α_0+α_1Trail + α_2Disturbance	4256.8	671.6
β_0 + β_1Settlement + β_2Forest	γ_0 + γ_1Settlement	α_0+α_1Trail + α_2Disturbance	4283.6	698.4
β_0 + β_1Settlement + β_2Forest	1	α_0+α_1Trail + α_2Disturbance	4294.2	709.0
β_0 + β_1Settlement + β_2Forest	0	α_0+α_1Trail + α_2Disturbance	4306.6	721.4
β_0	0	0	4344.8	759.6

β_0= marginal occupancy intercept; β_x= marginal occupancy slopes; γ_0= two-way interaction intercept; γ_x= two-way interaction slopes
0 = no interaction; 1 = constant two-way interaction (intercept only)
WAIC = Watanabe-Akaike information criterion
ΔWAIC = delta WAIC (difference between WAIC of the top and subsequent models)
Prey = gaur, muntjac, and serow

The detection probability of all species was positively associated with cameras placed on-trail than off-trail and trap effort. Human disturbance at the camera site had a strong negative effect on the detection probability of all three species (Appendices S11-13).

The density of river within 4 km buffer was strongly and positively associated with marginal occupancy probability of tiger (β[95% credible intervals] = 0.46[0.11 – 0.86]) and leopard occupancy (0.41[0.11 – 0.74]) but significantly negatively with that of dhole (-0.59[-1.08 – -0.15) (Figure 1). Slope had a strong positive effect on marginal occupancy of leopard (0.37[0.04 – 0.71]) and dhole (0.64[0.09 – 1.33]). Only tiger showed a strong positive association with forest cover (0.78[0.26 – 1.37]). Dhole and leopard were strongly and negatively associated with settlement density (-1.53[-2.83 – -0.46]) and serow abundance (-1.26[-2.54 – -0.10]), respectively (Appendices S5-7).

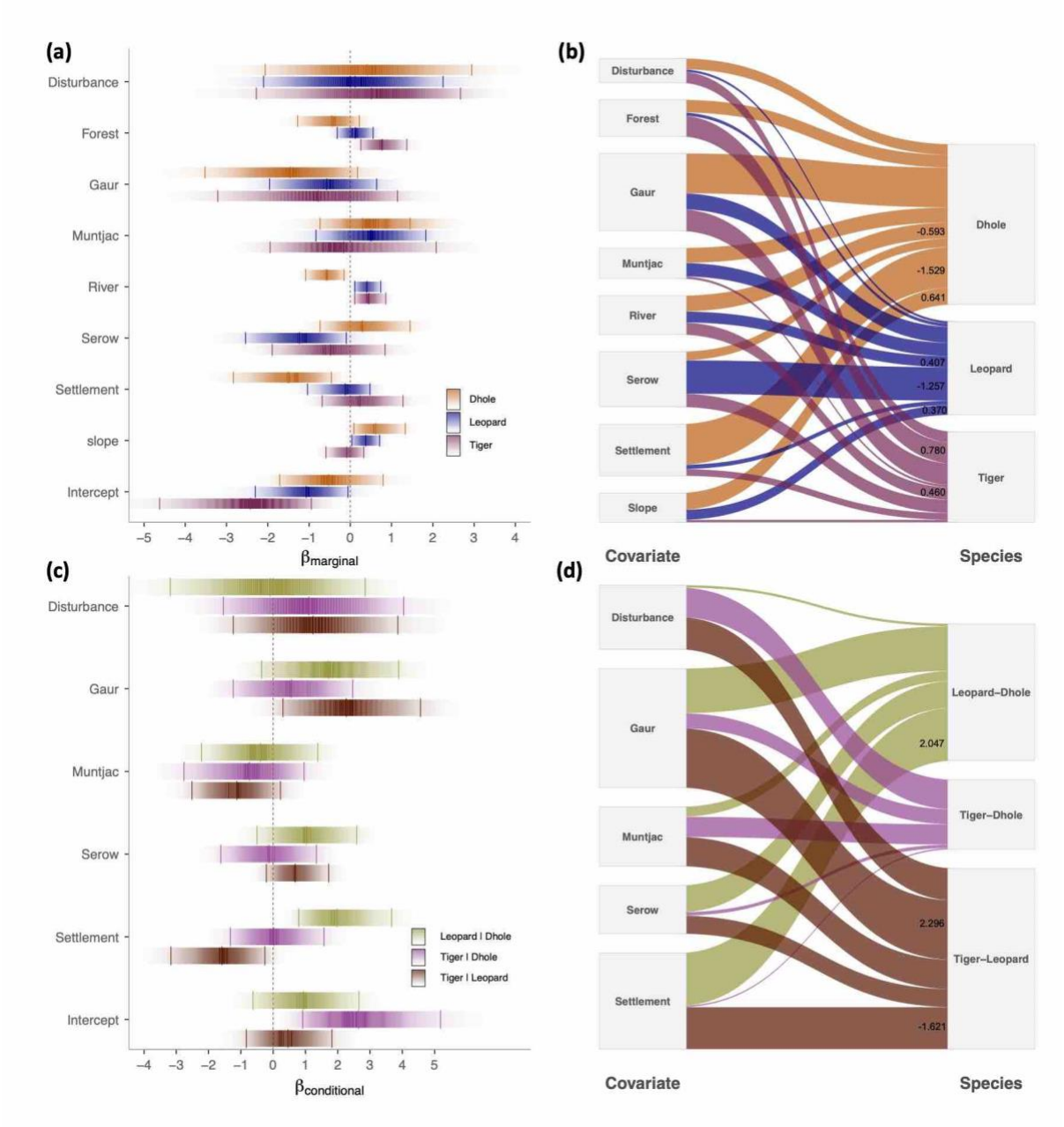


Figure 1. The effects of anthropogenic and environmental variables on individual species (a, b) and pairwise interactions (c, d). The posterior density plots (a, c) show $\hat{\beta}$-coefficients shaded in proportion to the posterior probability density (dark shade = high density). Effect sizes are on the logit scale and represent the effect of 1-SD change in covariate value. Lines indicate median and 95% credible intervals. Plots b and d show the relationship between covariates and species occupancy probability. Line width corresponds to the strength of the relationship. Significant relationships are illustrated with coefficient estimates

Evidence that the occupancy probability of one species varied in the presence and absence of another species was apparent for only one species pair: tiger and dhole indicated by the exclusion of zero from the credible intervals of intercept parameters in the linear models ($\gamma_0^{tig|dho}$ = 2.74[0.92 – 5.18]; Appendices S8-10). We found strong statistical support that the probability that two species occurred together varied as a function of the human settlement density within a 4 km radius of a camera station in two species pairs: tiger and leopard and leopard and dhole. The probability of occupancy of leopard as a function of settlement density varied markedly depending on whether tigers and dholes were present. At low levels of human settlement density, tigers were more likely to occupy sites if leopards were present ($\gamma_{Set}^{tig|leo}$ = -1.62[-3.16 – -0.26]) and occurred largely independent of dholes (Figure 2 panel 7). At a higher level of human settlement density, leopards were more likely to occupy sites where dholes were also present ($\gamma_{Set}^{leo|dho}$ = 2.05[0.79 – 3.76]) and occurred largely independent of tigers (Figure 2 panel 2). We found strong evidence that tigers and leopards were likely to occupy sites together when gaur was abundant ($\gamma_{Gaur}^{tig|leo}$ = 2.29[0.31 – 4.56]). However, there was no evidence that other prey species and human disturbance affected the interaction between species pairs (95% credible intervals straddled zero).

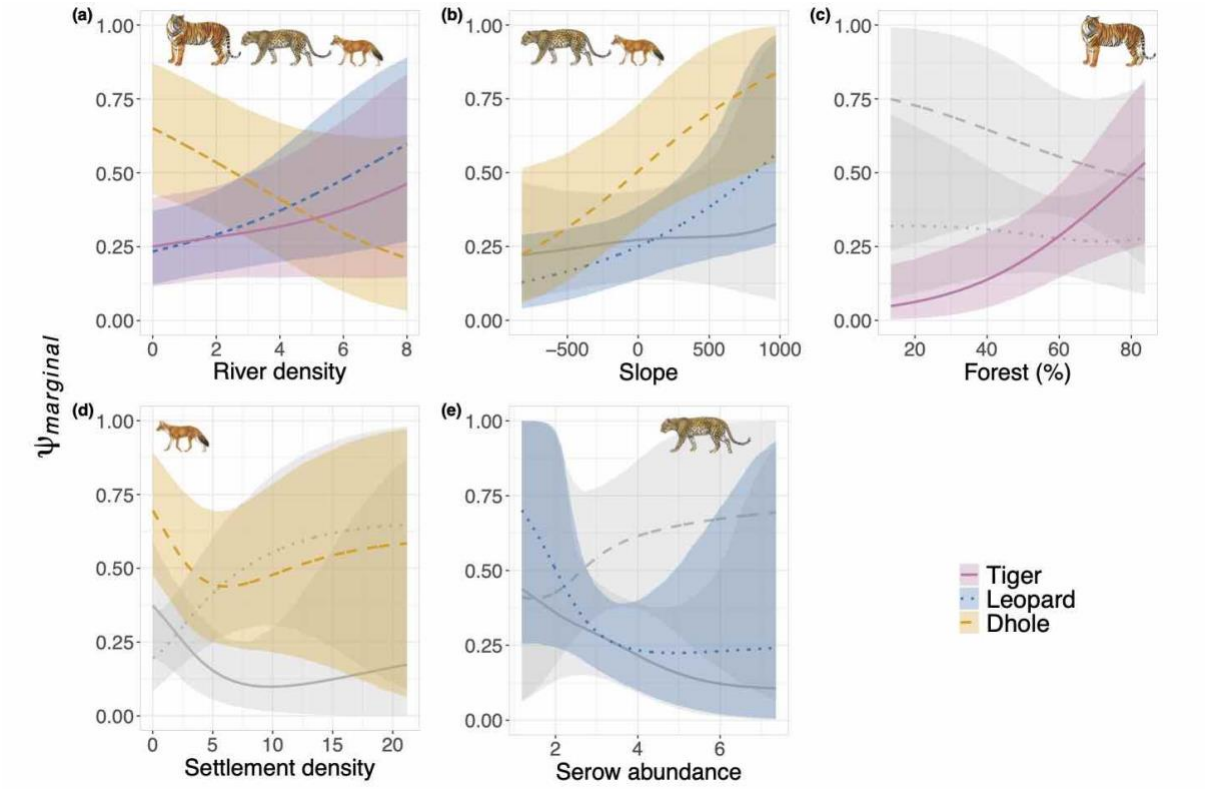


Figure 2. Marginal occupancy probability of the tiger (orchid), leopard (blue) and dhole (gold) as a function of river density, slope, forest cover, settlement density and prey (serow) abundance, Mean response and associated 95% credible interval are represented by lines and shaded ribbons, respectively. Light grey colour indicates a non-significant relationship (95% CRI straddles zero)

The probability of occupancy of dhole was highest (ψ_{dhole}=0.38[0.15 – 0.69]) followed by leopard ($\psi_{leopard}$=0.26[0.09 – 0.49]) and tiger (ψ_{tiger}=0.1[0.01 – 0.28]). Similarly, the probability of detecting a leopard was higher ($p_{leopard}$=0.08[0.05 – 0.12]) compared with tiger (p_{tiger}=0.04[0.02 – 0.07]) and dhole (p_{dhole}=0.04[0.02 – 0.06]).

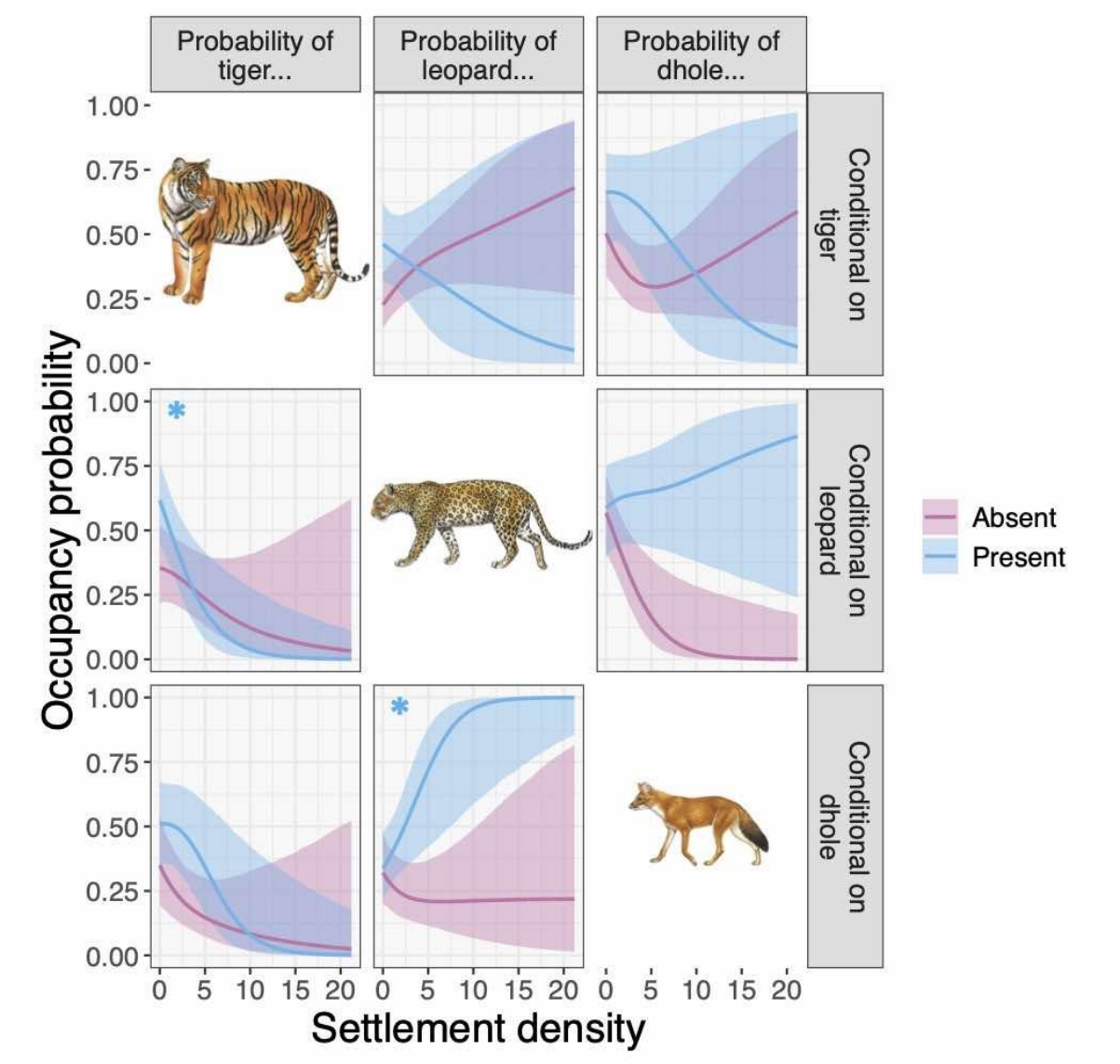


Figure 3. Occupancy probability of tiger, leopard and dhole conditional on the presence and absence of each of the other species along a human settlement density gradient around each camera trap. The probability of the species in each column is conditional on the presence and absence of the species in each row. The posterior means are represented by lines and 95% credible intervals by shaded ribbons. Asterisks indicate a significant relationship. Image courtesy (Francis, 2019)

4 Discussion

Our study revealed that patterns of sympatry among large carnivores in a heterogeneous landscape is mediated by settlement density and prey abundance. We provide evidence that human settlement modifies the direction and strength of interaction among carnivores. We show that the multi-carnivore system is negatively affected by human settlement density at the landscape level. Spatial overlap between tigers and leopards was lower in areas with high human settlement density, whereas it was higher between leopards and dholes in similar settings. Likewise, gaur abundance positively influenced tiger and leopard interaction. Our results improve our understanding of how human activity at the site level and human infrastructure at the landscape level affect large carnivore behaviour. The above findings demonstrate that space-use patterns are likely driven by a combination of the behavioural mechanism of each species (i.e., response to environmental factors such as habitat, prey, and disturbance) and interaction with competing species. This study examined interactions among globally threatened large carnivores in an understudied Himalayan landscape and provides important insights into the human-carnivore interface.

Human settlements are fragmenting natural habitats, increasingly forcing spatial interactions among large carnivores (Parsons et al., 2019). We demonstrate a clear difference in the effects of settlement density on these interactions. The strong positive interaction between the leopard-dhole pair in areas with high settlement density could be due to both species being attracted to anthropogenic resources (e.g., livestock, garbage), and that the benefits of accessing them are higher than any ensuing intraguild competition. Another plausible reason is that wild ungulates are attracted to crop fields – typically located near human settlements, which in turn attract carnivores (Thinley et al., 2018). However, large predators that share the same space and prey must, according to theory, segregate along the

temporal axis to coexist (Karanth et al., 2017). Such temporal segregation seems likely given that dholes are diurnal hunters whereas, leopards are nocturnal (Venkataraman et al., 1995).

On a cautionary note, increasing utilisation of areas with high human settlement density by leopards and dholes might be an ecological trap. Leopards and dholes are notorious livestock predators (Wang and Macdonald, 2006, Sangay and Vernes, 2008, Katel et al., 2014) and could perhaps face fatal retaliation from affected farmers. Poignant evidence to the effect of such persecution is that dholes in Bhutan were almost entirely extirpated in the early 1980s due to widespread poisoning of livestock carcasses in retaliation to predation (Wangchuk, 2004). Consequently, an explosion of wild pig (*Sus scrofa*) populations, in turn, increased damage to crops (Wangchuk, 2004). Such trophic cascade effects due to the removal of top predators from an ecosystem are widely recognised (Ripple et al., 2014). Perhaps a reminder of the toil suffered by dholes was partially reflected in our study by the negative response (marginal occupancy) to human settlement density. Lax livestock husbandry coupled with free-range grazing fuels the growing conflict between humans and large carnivores in Bhutan (Wang and Macdonald, 2006). Studies showed that livestock depredation by large carnivores mostly occurred in forests near the settlement where livestock was left unattended (Wang and Macdonald, 2006, Katel et al., 2014). Thus, our finding implies that the ubiquity of human presence may benefit carnivore interaction but must be traded off against the risk of escalating conflict with humans.

Settlement density, however, had a strong negative effect on tiger-leopard interaction. This suggests that tigers and leopards may compete more directly in resource-limited areas (Vanak et al., 2013) than leopards and dholes. This may result in spatial segregation (Karanth et al., 2017) and/or displacement of leopards to sub-optimal habitats (Odden et al., 2010).

Studies have documented that in the presence of tigers, leopards utilised habitats near human settlement, consequently increasing predation on domestic livestock and ultimately conflict (Wang and Macdonald, 2006, Harihar et al., 2011). In a multi-carnivore system, our findings demonstrate the negative effect of human settlement and its consequences on interaction and habitat use. Congruent with our hypothesis, gaur abundance positively mediated tiger-leopard interaction suggesting the possibility of co-occurrence in presence of abundant large prey. Although leopards may not directly hunt adult gaur, they are known to target calves and weaklings or scavenge on tiger kill carcasses (Hayward et al., 2006). Further, it is possible that in a prey-rich environment, tigers may prefer large-bodied prey sparing smaller prey species for leopards thus segregating along the diet niche (Andheria et al., 2007, Hayward et al., 2012). Our findings highlight that abundant large prey is critical for supporting large carnivore communities (Wolf and Ripple, 2016).

Although we did not find any concrete evidence of human disturbance (measured by the daily encounter rates of humans and livestock) on carnivore occupancy probability at a camera station level, growing evidence from other studies (both observational and experimental studies) suggests that large carnivores exhibit a strong fear response to humans (Kays et al., 2017, Nickel et al., 2020, Suraci et al., 2019). Our findings rather show that human disturbance at the camera station level was negatively associated with the detection probability of all three species. Studies elsewhere show mixed results, ranging from the negative effect on carnivore detections to neutral or positive effect on habitat use (Kays et al., 2017, Nickel et al., 2020, Reilly et al., 2017). These differences may partly be due to the spatial distribution of human presence on the landscape. For example, the human population density in western Bhutan is higher than in central, south, or eastern Bhutan where the spatial interaction between the two species was low (Appendix S16).

4.1 Limitations

Observational studies such as camera trap surveys are often inadequate to infer the true processes underpinning carnivore coexistence, and hence the causal effects. Future studies could undertake studies across multiple years to infer dynamics of interspecific interactions- a pattern worth exploring in changing landscapes (Fidino et al., 2019). We acknowledge that temporal segregation might facilitate syntopy (Karanth et al., 2017) but also allow coexistence with humans (Lamb et al., 2020). Moreover, study species abundance may induce heterogeneity in detection probability (Royle and Nichols, 2003, Cubaynes et al., 2010). Therefore, investigating the effect of abundance on interaction could help better understand the mechanistic underpinnings of co-occupancy. Direct observation of feeding behaviour and prey choice is impossible with a camera trap survey. Our results could be better interpreted if dietary information using the scat-analysis method was available (Klare et al., 2011). Furthermore, underlying correlates of human settlement such as poaching, roadkill and land expansion that affect carnivore co-occurrences warrant further research.

4.2 Management implications

The coexistence between humans and large carnivores is contentious (Lute and Carter, 2020) and in most instances, humans purportedly perceive carnivores as a threat to their lives and livelihoods resulting in conflictual responses. The polarity of human perceptions about coexisting with large carnivores has produced a mixed response and stymied conservation efforts. Management intervention aimed at protecting a single apex carnivore may need to consider the nature of interaction with other carnivores and its surrounding environments. For example, in India's Rajaji National Park, recovery of tiger population spatially displaced leopards to human-dominated habitats, the latter increased depredation on livestock and

consequently suffered a decline in their numbers due to conflict and retaliation (Harihar et al., 2011). Such imbalance may jeopardise conservation efforts and induce antagonism and aversion towards large carnivores.

Conservation of multi-carnivore system would benefit from limiting the conversion of forests to other land-use types and the protection of natural habitats (irrespective of topography, e.g., rugged terrain, river network) and prey. However, as the human footprint expands rapidly, human-carnivore interaction is inevitable. Land-sharing models (where humans and wildlife share the same landscape) may need to be adopted and tailored in the context of a working landscape mosaic. Our study suggests the importance of protecting habitats adjacent to human settlements and therefore highlights the potential for conservation prioritisation outside protected forest reserves. Further amending livestock husbandry practice to reduce spatial overlap between livestock and carnivores by employing guard dogs, corralling animals at night, securing overnight shelters, and supervising and guarding while grazing would be crucial to minimising conflict (Spencer et al., 2020). Protecting crop fields by employing strategies such as electric fencing, biophysical barriers and sound repellents may help deter wild ungulates and minimise crop raids. Hunting wild ungulates for meat or in retaliation to crop damage may severe the natural food supply for carnivores (Velho et al., 2012) and inadequate wild prey may drive carnivores to increase predation of livestock as an alternative (Puri et al., 2020). Therefore, implementing ‘collateral conservation’ measures (i.e., protecting habitat, removing snares) to protect a broad prey base may enhance carnivore conservation efforts (Wolf and Ripple, 2016).

5 Data availability statement

Data and code are available from github: https://github.com/ugyenpenjor1/Multispecies-Interaction-Model.

6 Authors' contributions

U. P.: conceptualisation, data curation, methodology, formal analysis, validation, visualisation, writing – original draft, writing – review and editing; C. A.: validation, writing – review and editing; S. A. C.: writing – review and editing; Ż. K.: writing – review and editing; D. W. M.: resources, supervision, funding acquisition, validation, project administration, writing – review and editing.

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Chapter 6

General Discussion

Main findings and contribution to the knowledge gap

Chapter 2

Using multi-scale models for multi-species terrestrial mammal communities, in Chapter 2, I show that protected areas and forest cover are the two most important variables associated with positive habitat use of most modelled species. Forest-related variables were positively associated with habitat suitability of carnivores such as Asiatic golden cat (*Catopuma timminckii*), clouded leopard (*Neofelis nebulosa*), tiger (*Panthera tigris*), dhole (*Cuon alpinus*) and yellow-throated marten (*Martes flavigula*), and herbivores such as muntjac (*Muntiacus muntjac*) and serow (*Capricornis thar*). Anthropogenic variables (e.g., agricultural land, built-up area, and road network), on the other hand, were generally negatively associated with habitat suitability of most species (e.g., tiger, dhole, Asiatic black bear (*Ursus thibetanus*), Asian elephant (*Elephas maximus*), marbled cat (*Pardofelis marmorata*) and serow), although a few species tend to tolerate human disturbance (e.g., wild pig [*Sus scrofa*] and sambar deer [*Rusa unicolor*]). Additionally, I found that topographic variables (terrain roughness, compound topographic index and slope position) contributed to habitat selection of most species suggesting that the remaining wildlife refuge may be areas unsuitable to human use. However, large-sized mammals (Asian elephant, gaur [*Bos gaurus*], sambar deer) showed a negative association with topographic roughness (or ill-suited to rugged terrain).

Using correlation analysis, I show that marbled cat was the most effective umbrella species closely followed by tiger, clouded leopard, and common leopard (*Panthera pardus*) among carnivores, and in particular felids. Likewise, gaur was the strong umbrella species of optimal protected area selection for other species. However, in the next chapter, I refine these

selection criteria based on the amount of core habitat and corridor each species protects (see Chapter 3). Using two conservation priority scenarios, I identified the nuances in the efficacy of optimal protection for each species. The unweighted sum of habitat suitability (scenario 1) of all species was weakly correlated with optimal protection for most species, particularly low for species with the highest umbrella performance (marbled cat, tiger, clouded leopard, common leopard, and gaur). On the contrary, the conservation priority-weighted scenario (scenario 2) performed better (based on average correlation across individuals) and particularly well for most umbrella species including Asian elephants. Similarly, there were differences in the effectiveness of the existing protected areas network based on the protection of the total proportion of species richness versus the per unit area species richness (mean). Existing large-sized protected areas that are relatively closer to other protected areas and dense forest covers better protected overall mean and total richness compared with smaller protected areas. In this chapter, I highlight the importance of managing lands outside protected areas for wildlife conservation using terrestrial mammal species.

Chapter 3

In this chapter, I show that using habitat suitability models developed in the preceding chapter and employing two spatially synoptic methods (resistant kernel density and factorial least cost path), ungulate species (Asian elephant, muntjac and sambar deer) were better (umbrella) at protecting overall core habitats than carnivore species. In terms of dispersal corridor, muntjac was the most effective umbrella species followed by small-sized carnivores (masked palm civet [*Paguma larvata*], leopard cat and yellow-throated marten). Using cluster analysis on kernel density and least cost path models, I identified six focal species (namely Asian elephant, Asiatic black bear, clouded leopard, dhole, sambar deer, and tiger) as indicator species for broad core habitat and corridor protection. I discovered that the dhole

had the highest number of fragmented core areas while the Asian elephant had the single largest core in southern Bhutan. The clouded leopard had the highest number of dispersal corridors identified and the Asian elephant had the single largest corridor embedded within the core habitat.

The sum of kernel density revealed that the overall area of multi-species core habitat was 48,790km^2 and of which about 38% was effectively under some form of protection. Similarly, about 31% of 42,460km^2 of predicted multispecies dispersal corridor (sum of least cost paths) was protected. A protected area in south-central Bhutan (Royal Manas National Park [RMNP]) had the largest predicted multispecies core habitat and corridors among the protected areas and biological corridor 3 (BC 3) which connects RMNP to Jigme Singye Wangchuck National Park and Phipsoo Wildlife Sanctuary had the highest predicted core habitat whereas, BC 5 which connects RMNP to Jomotshangkha Wildlife Sanctuary had the highest predicted dispersal corridors. Among the non-protected area, Gedu Forest Division (southern west Bhutan) had the highest predicted core habitat and corridor. Here, I show that dispersal is not just limited within a protected area and the long-term viability of wildlife populations would require protected habitats and corridors outside the existing protected area network.

Chapter 4

In this chapter, I show that the functional trait space of mammals was structured by body mass (small body mass to large body mass) and diet (herbivores to carnivores) as one major axis, and habitat breadth (from habitat generalist to habitat specialist) as the other. On the other hand, the functional trait space of birds was shaped by four axes: beak shape and size (from long and large bills to short and small bills), body mass (from small to large), foraging

strata (canopy feeders to ground feeders) and finally diet (diet composed of ectotherms [i.e., amphibians and reptiles] to scavenging). The functional hotspots (i.e., the smallest portion of functional space that includes 50% of the species) were different for mammals and birds. The mammals had a single hotspot with a bimodal distribution of species that distinguished carnivores from herbivores and those having large litter sizes (e.g., dholes, foxes, and jackals) from those with small litter sizes (e.g., muntjac, goral, musk deer). The functional hotspot of the birds was a single dense core in the centre of the trait space with more extreme forms dispersed towards the edge of the space.

The functional diversity of mammals was influenced by elevation, distance to road, precipitation and temperature seasonality, and agriculture. Elevation had the opposite effect (positive on sesFDis and negative on sesFRic) though the relationship was non-linear. Higher functional diversity of mammals was observed farther away from the road. The mammal sesFRic decreased with temperature seasonality while sesFDis with agriculture. In the case of birds, only three variables influenced functional diversity. The sesFRic increased with settlement density but decreased with temperature and sesFDis decreased with forest cover.

The mammal phylogenetic diversity (measured by mean pairwise distance [MPD] and nearest taxon distance [MNTD]) was positively associated with forest cover but the relationship was opposite for birds. Mammal sesMPD was positively associated with agriculture and negatively with precipitation. sesMNTD was negatively associated with built-up area and precipitation but positively with the human settlement density. On the other hand, sesMPD of birds was negatively associated with agriculture, built-up area, settlement density and precipitation. sesMNTD was negatively associated with agriculture and settlement density.

The overall FD and PD were lower than expected by chance for both groups indicating functional and phylogenetic clustering of communities.

Chapter 5

In Chapter 5, I used data from a large-scale camera trap survey and developed a multispecies occupancy model for carnivore guild comprising tiger, leopard, and dhole to investigate interspecific interaction and the effects of environmental and anthropogenic variables on spatial interaction.

The river density was significantly and positively associated with the marginal occupancy of tiger and leopard but significantly negatively with dhole. The slope had a strong positive effect on leopard and dhole marginal occupancy. Forest cover was only strongly positively associated with tiger marginal occupancy. The settlement density and abundance of serow was significantly negatively associated with the marginal occupancy probability of dhole and leopard, respectively.

There was evidence that the presence or absence of one species influenced the occupancy probability of the other in one species pair: tiger and dhole indicated by the exclusion of zero from the 95% credible intervals of the intercept parameter. However, I found strong evidence that the probability that interacting species were influenced by human settlement density within a 4 km radius of camera station in two species pairs: tiger-leopard pair and leopard-dhole pair. Tigers were more likely to occupy sites where leopards were present at low levels of human settlement density and high gaur abundance and largely independent of dholes. Leopards, on the other hand, were more likely to occupy sites with

dhole present at a higher level of human settlement density and occurred largely independent of tigers.

Relevance and implications for conservation across the Himalayas

As the world ventures into an increasingly human-dominated era, the so-called Anthropocene, so are the global conservation priorities. The remaining wilderness areas serve as green lungs to absorb greenhouse gas emissions and provide the much-needed ecosystem services that are vital to human recreation and survival. Bhutan offers promise to save a few remaining true wildernesses, partially aided by the landscape complexity (Penjor et al., 2021b) but largely driven by strong and coherent conservation policies. In keeping up with the mounting pressure of modernisation, paths and policies may go wrong at several places but this tiny Himalayan kingdom maintains steadfast balance and exemplary actions by implementing a holistic development model – the Gross National Happiness. In this model, environment conservation forms a solid foundational pillar, scrutinising infrastructure development so that minimal pressure is imposed on natural resources. This thesis aims to embellish this model by providing strong scientific evidence. The findings of this thesis have wider relevance and broader implications for biodiversity conservation and protected area management. The methodology can be easily replicated, and findings may be implemented with some caveats, at least in landscapes that share the similarity in terrain and species composition (i.e., across most of the eastern Himalayan landscapes). Using findings from this research, I relate the implications in the context of conservation themes *sensu lato* and expand on how they fill in the gap in existing knowledge and further our understanding of biodiversity conservation per se.

Conservation is shifting its focus from single-species, single-landscape to multi-species and multi-regions. Management interventions solely based on a single species may not be adequate and may not fully inform conservation. We may not be able to appreciate the importance of multi-species conservation without understanding: 1) the influence of anthropogenic disturbances on multiple species at multiple scales (Chapter 2). In species distribution modelling, scale is increasingly recognised as an important factor in determining the nuances in resource use (Kotliar and Wiens, 1990a). And 2) spatial patterns of multi-species interaction across human land-use gradient (Chapter 5).

The growing human footprint and concurrent increase in the demand for resources are making Himalayan natural landscapes more heterogeneous and complex (Weinzettel et al., 2018). It is essential that conservation and management of natural resources adapt to the change but at the same time strive for synthetic and integrated efforts. In Bhutan Himalaya, for example, to develop effective conservation strategies that address the trade-off between economic growth and biodiversity conservation would require identifying, prioritising, and optimising protection of critical habitat for megafauna (Chapter 2) and identifying the scale at which species respond (Chapter 3). The most biodiverse areas are those with the least economic development, but my findings show that it is also possible to protect the biodiversity that shares the landscape with humans (e.g., land-sharing approach, Chapter 5).

While aiming to meet the Aichi Target of conserving at least 17% land area by 2020, countries often designate sparsely populated, arid, and high-altitude biomes as protected areas (Pimm et al., 2018) whereas the need for protection is more imminent and urgent for lowland habitat that is productive but faces immense pressures from human activities (Li et al., 2020). The predilection to expand protection to areas with low human impact or similar (species)

communities to those already protected may offer little biodiversity protection and misdirect conservation targets (Zhu et al., 2021). My findings provide evidence that protection and prioritisation of conservation (or key biodiversity) areas require robust assessment of habitat suitability and richness at multiple spatial scales for multiple species (Chapter 2) and the need to further embellish these efforts by identifying spatially explicit multi-species core habitats and dispersal corridors (Chapter 3). My findings, thus, aspire to align management interventions with the Aichi Biodiversity Target of conserving ecologically representative areas through well-connected systems of protected areas (Pimm et al., 2018).

Protected areas in anthropogenically perforated matrix/landscape become increasingly isolated and this, in turn, affects animal movement and dispersal (Hofmann et al., 2021). Therefore, conservation efforts must prioritise connectivity as a strategy to facilitate movement and sustain ecological processes that are vital to ecosystem functioning and maintenance of biodiversity (Baldwin et al., 2018, Brennan et al., 2020, Dinerstein et al., 2019). Most connectivity assessments are centred around a single focal species with the assumption that it will support the connectivity needs of other species that share the landscape. This strategy, however, has failed to produce desired results of multispecies connectivity (Brennan et al., 2020). In Chapter 3, I showed that smaller multispecies movement paths may add to the connectivity value by helping to create more complete linkages between critical core habitats. My findings highlight the importance of multispecies consideration in corridor design and connectivity conservation within and beyond protected areas.

Although desirable (and feasible in the terms of management), single species (usually charismatic and those that captivate the public in general) often fail to protect (under the false

guise of umbrella) the non-charismatic but those that require urgent protection. The truth is charismatic and large-bodied species constitute only a very small fraction of the world's total biodiversity. In protecting the tiger, we certainly protect substantial fractions of other species in the tropical and temperate forests it inhabits, there is, however, very little compelling reason or evidence that tigers protect biodiversity in the alpine habitats. I provide evidence as well as the mechanism to identify multiple (but oft-ignored) species that are crucial in maintaining ecosystem processes, structure and stability and propose them as umbrella species because multiple umbrella species would provide more inclusive protection than any single species (Chapter 2). Management intervention aimed at protecting a single apex carnivore may need to consider the nature of interaction with other carnivores and their surrounding environments (Chapter 5). Further, Bhutan is known for rich carnivore diversity in the region (Tempa et al., 2013, Dorji et al., 2019, Penjor et al., 2020) and conservation of a multi-carnivore system would benefit from limiting the conversion of forests to other land-use types and the protection of natural habitat and prey (Chapter 5). My findings in Chapter 5 suggests the importance of protecting habitats adjacent to human settlements and therefore highlights the potential for conservation prioritisation outside protected forest reserves for multi-carnivore communities (also supported by the findings in Chapter 2, and 3).

As we mark an end to the 'decade of biodiversity' of ambitious Aichi Targets, global achievement still falls short of the target (16.64% of the global terrestrial land brought under protection) (Stokstad, 2020), and is largely seen as inadequate for halting the overall biodiversity declines (Watson et al., 2021). We have seen that biodiversity is on the tangents and to continue with our naively 'business as usual' means the global biodiversity will continue with the downward trend. A focus on merely protecting areas without ensuring quality and representativeness has yielded a rather perverse outcome for biodiversity (Barnes

et al., 2018). Post-2020 discussions are already underway (Williams et al., 2021) and recognise that this decade should focus on restoration of degraded land and sea and increase the areas for biodiversity conservation (Maron et al., 2021). This decade of ecosystem restoration must ensure that the restoration of targeted areas has potential gains for biodiversity. Securing and protecting areas with high conservation value (for example, the high net species richness areas identified in Chapter 2 and multispecies core habitat and corridor networks identified in Chapter 3) would be crucial to safeguarding biodiversity and perhaps fulfilling the Convention on Biological Diversity's 2050 vision of healthy planet that benefits all people (Allan et al., 2021). Besides species conservation, these areas will be crucial in the provisioning of food, materials, water, climate regulation and ecosystem services such as crop pollination and pest control as shown by the importance of functional traits and evolutionary diversity in Chapter 4 (Maron et al., 2021).

The community assembly process, ecosystem functioning, conservation value and ecosystem resilience are underpinned by functional traits and evolutionary history. Although the insurance hypothesis asserts that an ecosystem with high species richness (taxonomic diversity) will hold more species that can adapt to environmental fluctuations and maintain functioning (Yachi and Loreau, 1999), it is criticised on the grounds that richness alone provides little information about the changes in evolutionary relatedness of species and individuals within assemblages and/or functional trait variation (Cadotte et al., 2019, Cadotte et al., 2011, Cadotte et al., 2010, Violle et al., 2014). Therefore, it is of paramount importance to evaluate how community structure changes over time and how the change in the environmental surrounding affects them. In Chapter 4, I show that species' position in functional trait space is non-random and the loss of species whose functional roles cannot be easily replicated by other species in the community may impact long term ecological and

evolutionary processes. For example, Asian elephants occupy the boundary of the functional trait space in Bhutan and for any unfortunate reason, if Bhutan loses elephants in the future, we will lose the unique ecological functions such as grassland or forest regeneration. The loss of species that are vulnerable yet possesses unique ecological traits and occupy a precarious position in the trait space will create a lacuna and eventually impact the overall ecosystem structure, function, and processes (Flynn et al., 2009a). In Chapter 4, I further demonstrate that anthropogenic pressures result in low functional and phylogenetic diversity. This indicates that there is a possible loss of traits and evolutionary lineages and that vital ecosystem services may already be lost in some human-dominated areas. The ecological network is what Charles Darwin described as the "tangled bank" of complex species interaction inextricably linked with each other (Darwin, 1909). The ecological network and other aspects of biodiversity, that are vital to human wellbeing, will also be affected by the extrinsic global change, including forestry and timber management, fisheries, agronomy, pest and invasive species control or human and wildlife disease management (Bellard et al., 2012 and references therein).

Drivers of biodiversity decline at a local scale provide a fine scale understanding of the relationship between species and their environmental surroundings. For local management planning, this information is vital to enhancing local area knowledge to make conservation efforts effective and minimise local rates of species loss. There is a need for a paradigm shift from species-centred focus to a holistic view that encompasses species interaction networks (Chapter 5), and other aspects of biodiversity such as functional and phylogenetic diversity (Chapter 4, Devictor et al., 2010). Though it is prominent in academia, practical conservation management rarely considers these facets of biodiversity. Congruent with global studies, my findings show that the large variation of responses of different

species necessitates the use and integration of multiple approaches to enhance our understanding of the impacts of land use and climate change on biodiversity (Bellard et al., 2012, Dawson et al., 2011). Therefore, I recommend and encourage the incorporation of multiple facets (taxonomic, functional, and phylogenetic diversity) of biodiversity into mainstream monitoring programmes.

Finance for conservation is paltry in developing economies. The developing countries (mostly in the global south) are rapidly losing forests largely driven by relentless consumption in developed economies (Moran and Kanemoto, 2017) and thus the latter has a moral obligation to reduce consumptive demands or generously fund local conservation in the former (Allan et al., 2021). Global biodiversity funding per se is limited. We need frameworks that will help identify and fund the conservation of areas that are in dire need but also ensure that the ones already established are functional, sustainable, and serving the purpose. Biodiversity funding in developing nations must be increased. The current global biodiversity funding is estimated between $4 and $10 billion each year (Barbier et al., 2018, Dinerstein et al., 2017). Although it may seem huge, it is dwarfed when compared with the climate mitigation and adaptation fund in Europe, which is estimated at over $221 billion between 2014 and 2020 (Grzelbieluch et al., 2018). Therefore, if we are serious about the biodiversity and climate crises posing an existential threat to humankind, we need a balanced investment in developing countries where the rate of land-use change is higher than developed countries with a relatively higher rate of carbon and greenhouse gas emission.

There is an urgency for the scientific community to provide scientific guidance for the development of conservation strategies given the large projected impacts of land use and climate change on biodiversity at all levels (Bellard et al., 2012 and references therein).

Keeping the projected changes in mind, conservation planning must be done decades in advance (Hansen et al., 2010) and needs to be periodically revised. The differences in the impacts of land use and climate change on terrestrial vertebrates (Chapter 4) warrant a tailored but integrated approach under a unified framework to identify vulnerable species or ecosystems and accordingly adapt management interventions (Bellard et al., 2012). For instance, species or ecosystems projected to be primarily affected by inclement climate may require adaptive measures compared with species negatively affected by land-use change that could persist through land-sharing approaches (Hannah et al., 2007, Bellard et al., 2012). However, because the enormity of the problem of synergistic interaction between land use and climate change is greater than either factor alone, the mitigation measures must be integrative. One of the important strategies is to enhance landscape connectivity (Chapter 3) to enable species movement through interconnected habitat matrix to allow species to track climate (so to say) or escape the perils of unsuitable climatic conditions (Hannah et al., 2007).

Bhutan has a large proportion of the population depending directly on agriculture for subsistence but paradoxically on a meagre 4% of the total land. We need a legal framework that will guarantee the protection of biodiversity while practising agriculture. Laws that convivially obligate agricultural practices to protect soil and water and regulate the use of pesticides will be crucial to conserving biodiversity across human land-use gradients. It is important to recognise and incentivise biodiversity-friendly agriculture practices and encourage the land-sparing approach. Training on biodiversity-friendly agriculture developments will be vital to maintain and encourage farmers' motivation about successful conservation measures. Further, conservation can only be successful when all the stakeholders are content: adequate and sustainable compensation for the crop or livestock

loss to wild animals is needed (as a short-term measure). Finally, it will be helpful to reward farmers' commitment to biodiversity protection via subsidies (Mupepele et al., 2021).

Future conservation management should increasingly consider the co-benefits of biodiversity conservation and carbon trade. Protecting biodiversity and habitats can also help in achieving the climate targets. Conserving high forests that serve as carbon sinks also helps in offsetting carbon emissions. We can achieve the dual benefit of curtailing carbon emission in the atmosphere while also protecting biodiversity by prioritising and restoring tropical rainforests (Zhu et al., 2021). Thus, management strategies should aim to synergise biodiversity and carbon priorities (Zhu et al., 2021). However, carbon-only priority may not be a wise approach because of the risk of overemphasis on monoculture plantations that excludes biodiversity in the entirety (Lewis et al., 2019).

While the fate of global biodiversity remains grim through the 21st century, this thesis offers optimism. The findings from this thesis give us hope that human development and conservation can be harmonised. A gleam of light shimmers through this tiny Himalayan country and shows us the path to a balanced *middle path* (a term borrowed from Buddhism). Through this thesis, I aimed to provide insights into the broader picture of biodiversity (focusing on mammals and birds) in an understudied yet important global biodiversity hotspot. I have tried to make this thesis comprehensive by touching on a range of concepts from behavioural ecology to landscape connectivity and community ecology by applying state-of-the-art models. The findings are neither excessively novel nor a plain platitude but offer interesting insights (and unconventional) into the biodiversity scenario of Bhutan. Conservation beyond protected areas emerged as a recurring finding (Chapter 2 and 3) and multi-species conservation prioritisation seems rather inherently advantageous than a single

species approach (Chapter 2). Further, to improve our understanding of ecosystem services, we need an inclusive management approach that considers the multiple facets of biodiversity in mainstream management and Chapter 4 shows that anthropogenic pressures coupled with global climate change affect terrestrial vertebrates in a non-trivial way. Lastly, human modification of the landscape alters species interaction: large carnivores sharing the landscape with humans may have to trade-off between resource subsidy and escalating conflict (Chapter 5). I hope the findings of this thesis will stimulate debate and rational thinking in conservation managers in Bhutan and beyond.

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Appendices

Supplementary Chapter 1

Vulnerability of mammal communities to the combined impacts of anthropic land use and climate change in the Himalayan conservation landscape of Bhutan

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Abstract

Human land use and climate change drive biodiversity loss, precipitating the extinction crisis. The fragility of the Himalayas makes species in this landscape vulnerable to land-use and climate change. We aim to quantify the response of terrestrial mammal community to land use and climate scenarios in the Bhutan Himalaya. Using large-scale camera-trap dataset, we examine the effects of anthropic land-use and climate variables on the terrestrial mammal assemblage using Bayesian multi-species occupancy model. Most of the terrestrial mammals in our sample displayed a strong negative relationship with anthropic land-use variables (agriculture, roads and settlement). Further, the occurrence of most species decreased with likely projections for climate variables, illustrating threats to conservation if the current trend in global warming continues. Notably, we found that biodiversity conservation in this landscape can be achieved by protecting extensive forest cover. Our findings emphasize the importance of reconciling land use management and mammal conservation in the face of climate change and provide vital information which can be used to optimize future conservation and development plans.

Keywords

camera-trapping, climate, conservation landscape, Himalaya, land-use, mammals, multi-species occupancy model

1 Introduction

The impact of human activities on the current rate of global biodiversity decline will likely trigger the sixth mass extinction (Ceballos et al., 2015). The use and conversion of land have, throughout recorded history, been the pervasive, dominating force behind biodiversity loss

(Maxwell et al., 2016, Johnson et al., 2017). This crisis is aggravated by invasive species (Clavero and García-Berthou, 2005), disease (Daszak et al., 2000) and livestock expansion (Morand, 2020). With the human population projected to double by the end of this century, human-induced land-use and climate change will likely interact to repeat the mass extinction of wildlife of the geological past (Barnosky et al., 2011, Williams et al., 2007). It is fundamentally important to understand the impacts of anthropogenic land-use and climate change on species communities.

The global decline of biodiversity has been attributed mainly to agricultural expansion and encroachment into nature and wilderness areas (Tilman et al., 2001, Pereira et al., 2010, Rands et al., 2010, Venter et al., 2016). By 2070, the impact of land-use change is predicted to endanger ~1700 species of amphibians, birds and mammals globally, including species of high conservation value and functional importance, due mainly to habitat contraction (Barlow et al., 2016, Powers and Jetz, 2019). While agriculture is the backbone of socio-economic development, it often comes at the expense of biodiversity and ecosystem services (Kiffner et al., 2015, Newbold et al., 2015b, Usubiaga-Liaño et al., 2019). Ironically, human well-being is at stake because biodiversity loss disrupts crucial ecosystem services which are vital to human survival and recreation (Frishkoff et al., 2014, Mendenhall et al., 2014).

On the other hand, climate change threatens one in every six species, risking ~20-30% of the species to extinction (Warren et al., 2013, Urban, 2015). At the current rate of global greenhouse gas (GHG) emission and forest loss, ~34% of species with moderate dispersal ability and ~42% of species with limited dispersal ability, respectively, would lose >50% of their range by 2080 (Warren et al., 2013). Although, some species could shift their range in response to climate change (Chen et al., 2011), most endemic species would face extinction

due to disappearing local climate and habitat (Jackson and Overpeck, 2000, Beever et al., 2016). The synergy between land-use and climate change is expected to prompt a more profoundly negative impact on biodiversity than a single driver or their additive combination (Brodie, 2016, Newbold, 2018).

Eastern Himalaya is a biodiversity hotspot in south Asia (Myers et al., 2000, Dorji et al., 2018) and a critical part of Asia's water source and glacier ice repository outside the Poles (regarded as the 'Third Pole'), in the Himalayas (Sharma et al., 2019). But the biodiversity here is under siege from the threats of human land use and climate change (Tilman et al., 2017). Bhutan is a biodiversity hotspot in the Eastern Himalaya with ~70% forest cover and >50% of the land under protection (Myers et al., 2000, DoFPS, 2011b). The extreme altitudinal variation and topographical complexity influence weather pattern and create a unique microclimate which harbors a wide assemblage of plant and animal communities (Chettri et al., 2010). Yet, the fragility (erosion-prone landscape, melting glaciers and risk of flood) of the mountain ecosystem makes it vulnerable to the challenges of the Anthropocene (Chettri et al., 2010, Tse-ring et al., 2010, Kremen and Merenlender, 2018). We examined the effects of land-use and climate on the occurrence of terrestrial mammal assemblages in this landscape, using a multi-species occupancy model (MSOM). The central premise of this study is that the mammal community would be adversely affected by land use (agriculture, roads, settlement) changes, the factors which fragment and degrade habitat. Although the effect of climate might not be apparent in the overall mammalian assemblage in the shorter-term, the cumulative impact, however, could drastically compromise the species' ability to cope with the change (e.g. Bellard et al., 2012). On the other hand, we expected natural forest cover to be critical in maintaining biodiversity and perhaps mammalian community integrity in the fragile mountain ecosystem. Our study

quantifies the effects of land-use and climate on the mammal community of the hitherto understudied Himalayan landscape of Bhutan and proposes a generic paradigm to reconcile land management and biodiversity conservation.

2 Materials and Methods

2.1 Study area and camera-trap survey

Bhutan is a small (38394 km^2) country landlocked between India and China. The vegetation types vary along the altitudinal gradient and are broadly classed under agro-ecological zones namely sub-tropical, warm broadleaved, cool broadleaved, temperate, sub-alpine and alpine (DoFPS, 2011b). The elevation characterizes temperature and precipitation: lower foothills with high summer temperature and heavy rainfall during monsoon while the higher mountains receive scant rainfall and experience low temperature. The elevation ranges between 100m and 7000m. The annual temperature ranges between 10°C and 24°C and annual precipitation between 300m and 6000m across Bhutan (NSB, 2020). Bhutan is sparsely populated with a mean density of 19 people km^{-2} (NSB, 2020). The topography, in general, is steep terrain, deep gorges, and narrow river valleys.

We collected detection/non-detection data of mammals through camera trap survey between 2014 and 2015 which was part of the national tiger survey (Table S1). The national tiger survey comprised 1129 paired, unbaited, passive infra-red camera-traps (models used HCO Scoutguard, Bushnell, Cuddeback, Reconyx and U-way; see Table S2 for modelled performance on detection probability) installed across the country. Each camera station was placed within a 5 km x 5 km grid, based on the putative home range size of a female tiger (Karanth and Nichols, 2002) at an average distance of 2.9km (1.2km SD) ensuring there were no more than two camera stations per grid. These grids excluded areas of high-density

settlement, large river network, and areas above 4500m (DoFPS, 2015b). The camera traps were randomly placed but following animal trails or frequently used sites such as mineral licks and water holes but in the context of accessibility. For logistical convenience, the camera-traps were installed in two survey blocks: north (n=681) and south (n=448) (Figure 1). The south block was surveyed between March 2014 and June 2014 and the north block between October 2014 and March 2015. Survey teams monitored the stations every 30 days to retrieve data, replace batteries and clear bushes obstructing camera lenses.

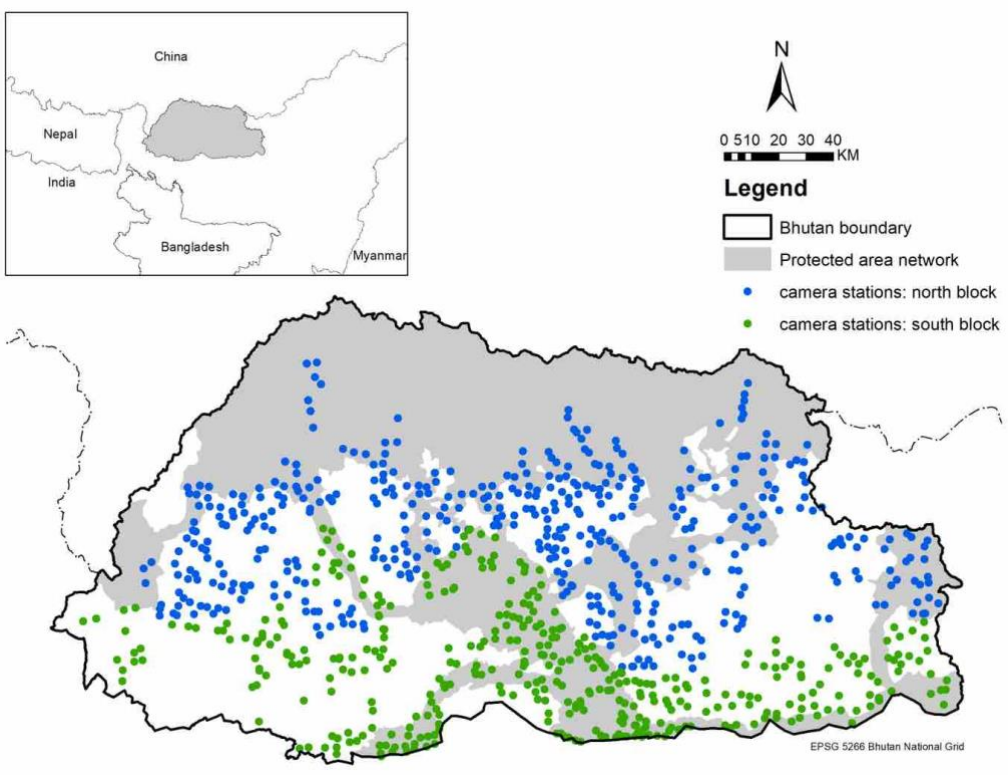


Figure 1. The location of the study area (Bhutan) in south Asia (inset) with camera stations. Camera stations in the north are indicated by blue points and in the south by green points. The grey polygons represent protected area network (national parks, wildlife sanctuaries and biological corridors) which constitute ~51% of the total geographical area

2.2 Land-use and climate variables

The land-use variables at the landscape scale were selected based on our *a priori* hypotheses. We hypothesized that agriculture expansion, road density, and proximity to settlement (a proxy of human disturbance) would negatively affect mammalian species occurrence and richness while forest cover would positively influence both occurrence and richness. We considered sampling unit as an area within 1km buffer of each camera station, roughly corresponding to less than half of the mean distance between neighboring camera stations (Sollmann et al., 2012) and extracted covariates within this buffer. This buffer was chosen to represent the average site characteristic surrounding camera traps. We accessed the land use data from the local forest department and calculated the percentage of land area for agriculture, and distance to feature for road and settlement. Mean forest cover was obtained from the Global Forest Change data (Hansen et al., 2013). We derived annual mean precipitation and temperature from the WorldClim 1.4 database at $1km^2$ resolution (1960 to 1990; Hijmans et al., 2005). Responses of species to climate forecast were based on projections of Global Climate Models (GCM) for three representative concentration pathways (RCP 2.6, 4.5 and 8.5) for the year 2070. Since both the climate variables (temperature and precipitation) were highly correlated with each other (Pearson's $|r| > 0.8$; Figure S1), we built separate models for each variable to disentangle the effects separately which otherwise would be confounded by multicollinearity (Dormann et al., 2013). All covariates were standardized to mean 0 and standard deviation 1 before analysis. We provide our model specifications in the Supplementary Material.

2.3 Modelling framework

We assessed the effects of land use and climate variables on the mammalian community using a Bayesian hierarchical MSOM (Dorazio and Royle, 2005). MSOMs provide a convenient framework which allows for composite analysis of communities or group of

species while accounting for observation heterogeneity (detection probability, (Dorazio et al., 2010, Kéry and Royle, 2016). By rationalizing detections of species in a community, it improves inference even for a rare and cryptic species otherwise impossible with a single species model (Zipkin et al., 2009b).

The latent ecological process underlying the true pattern of occurrence for species *k* at camera site *i*, z_{ik} is considered a Bernoulli random variable, $z_{ik} \sim Bernoulli(\psi_{ik})$ with the probability of occupancy ψ_{ik} (z_{ik} = 1 if species is present, 0 otherwise). The measurement of actual observation, y_{ik} is another random variable conditional on the occurrence z_{ik} such that, $y_{ik}|z_{ik} \sim Bernoulli(z_{ik} * p_{ik})$, where species present (z_{ik} = 1) is detected with probability p_{ik}. At a site where the species does not occur, z_{ik} = 0 and y_{ik} = 0 and cannot be falsely detected. Thus, hierarchical occupancy models can be described as Bernoulli-Bernoulli mixture models (Kéry and Royle, 2016). The sum of Bernoulli trials yields a Binomial distribution and the observation y_{ik} can be rewritten as, $y_{ik} \sim Binomial(z_{ik} * p_{ik}, n_i)$, where *n* is the total number of trials (i.e. the number of active camera-trap days at site *i*). We introduced the effects of covariates (cov_i) at each site *i* using the logistic ("logit") link function as $logit(\psi_{ik}) = \beta_{0k} + \beta_{xk} * cov_i$, where β_{0k} is the normally distributed species-specific random effect (intercept), $\beta_{0k} \sim Normal(\mu_{\beta_{0k}}, \sigma^2_{\beta_{0k}})$, $\sigma^2_{\beta_{0k}}$ is the variance which specifies the occupancy probability of species *k* at site *i*, and β_{xk} is the effect (slope) of site covariate on species *k* with a prior from a normal distribution, $\beta_{xk} \sim Normal(\mu_{\beta_{xk}}, \sigma^2_{\beta_{xk}})$. The detection probability was also modelled using the logit link function as $logit(p_{ik}) = \alpha_{0k} + \alpha_{xk} * cov_i$, where α_{0k} is a normally distributed species-specific random effect, $\alpha_{0k} \sim Normal(\mu_{\alpha_{ok}}, \sigma^2_{\alpha_{0k}})$, and α_{xk} is the specific-specific effect of covariates on detection probability. We modelled polynomial terms for agriculture, temperature and precipitation to allow for non-linear responses. Detection probability was modelled as a function of camera-

traps placed on- or off-trail and camera models to assess the nuances in capture success due to different operative capabilities and durability of camera models. We used normal priors for means of hyperparameter, $\mu_{\beta_{0k}} \sim Normal(0, 0.001)$ for intercept and, $\mu_{\beta_{xk}} \sim Normal(0, 0.001)$ for slopes and weakly informative folded Student-*t* priors with four degrees of freedom (ν = 4) for standard deviations of hyper-parameters, $\tau_{\beta_{0k}} \sim t(0, 2.25, \nu = 4)$ for the intercept where precision, $\tau_{\beta_{0k}} = 1/(\sigma_{\beta_{0k}} * \sigma_{\beta_{0k}})$ and, $\tau_{\beta_{xk}} \sim t(0, 2.25, \nu = 4)$, $\tau_{\beta_{xk}} = 1/(\sigma_{\beta_{xk}} * \sigma_{\beta_{xk}})$ for the slopes which are proper but provides very weak information than any prior knowledge available (Gelman, 2006; model code in Supplementary Material S1).

We implemented the model in JAGS 4.3 (Plummer, 2003) called through R 3.6.1 (R Core Team, 2021) using the package jagsUI (Kellner, 2019). We ran three parallel chains of 200000 Markov Chain Monte Carlo (MCMC) iterations each, discarding 100000 during the adaptation phase and thinned by 20 for the economy of computer space. We drew inferences on species-specific and community response from 30000 posterior samples and interpret the covariate effect based on the overlap of credible intervals (but see Ogle et al., 2019). The model convergence was assessed by visually inspecting the trace plots and by ensuring that the Gelman-Rubin statistic for all parameters was <1.1 (Gelman et al., 2013).

3 Results

We recorded 54 mammal species in 849 camera stations (out of 1129 stations) over a total survey effort of 73 259 trap days during 2014 and 2015. We only included terrestrial mammals with bodyweight >180g (the smallest species in our study was mountain weasel *Mustela altaica*) and discarded rodent (squirrels and mice) and semi-aquatic species (otters;

Table S3). The number of species detected per site ranged from 0 to 17. The naïve mean number of species per site was 5.49 (SD = 3.79). The mean estimated richness per site is seven (95% Bayesian credible interval (CRI) 5.65 to 9.30). We achieved convergence for all parameters in land use and climate models. The mean occupancy probability across the mammal community was 0.15 (0 – 0.70) and the mean community detection probability was 0.02 (0.004 – 0.25). The mean community detection probability was positive on trails ($\hat{\beta}$ = 0.32, 0.09 – 0.55) and variable for different camera models (Table S2). The mean occupancy probability was highly variable among species, ranging from 0.004 for takin *Budorcas taxicolor* to 0.62 for muntjac *Muntiacus muntjak* (Figure S2, Table S4). Similarly, detection probability dramatically varied among species with lowest for binturong *Arctictis binturong* (0.004) and highest for muntjac (0.12, Figure S2, Table S4).

3.1 Species-level response

Thirty-eight out of 45 species displayed negative response to agriculture, and this response was strong for nine species (CRIs exclude zero). Asian elephant, Asiatic brush-tailed porcupine *Atherurus macrourus*, common palm civet *Paradoxurus hermaphroditus*, crab-eating mongoose, gaur *Bos gaurus*, masked palm civet *Paguma larvata*, large Indian civet *Viverra zibetha*, small Indian mongoose *Herpestes auropunctatus*, and small Indian civet *Viverricula indica* displayed the strongest response (Figure 2 & 3; Table S4). Only wild pig *Sus scrofa* displayed a significant positive association with agriculture ($\hat{\beta}$ = 0.16, 0.07– 0.27, Figure 2). Forty-one out of 45 species displayed negative response to distance to road, of which three showed strong avoidance (CRIs exclude zero). The three species that showed strong avoidance of road were gaur ($\hat{\beta}$ = 0.23, 0.03 – 0.46), red panda *Ailurus fulgens* ($\hat{\beta}$ = 0.23, 0.01 – 0.50) and marbled cat *Pardofelis marmorata* ($\hat{\beta}$ = 0.30, 0.11 – 0.52, Figure 3). The response to settlement was highly variable: 21 out of 45 species showed avoidance, of

which only three, that is, Asian elephant ($\hat{\beta}$ = 0.53, 0.24 – 0.84), tiger ($\hat{\beta}$ = 0.33, 0.11 – 0.55), and crab-eating mongoose ($\hat{\beta}$ = 0.63, 0.27 – 1.02) displayed strong relationship. Thirty-five species showed a positive association with forest cover, of which 17 were strongly associated. The species strongly affiliated with forest cover were Asian elephant, Asiatic brush-tailed porcupine, Assamese macaque *Macaca assamensis*, clouded leopard *Neofelis nebulosa*, common palm civet, gaur, Asiatic black bear *Ursus thibetanus*, Malayan porcupine *Hystrix brachyura*, masked palm civet, yellow-throated marten *Martes flavigula*, large Indian civet, leopard cat *Prionailurus bengalensis*, marbled cat, muntjac, sambar deer *Rusa unicolor*, spotted linsang *Prionodon pardicolor*, and wild pig (Figure 2 & 3). Thirty-seven species negatively responded to an increase in precipitation and temperature, respectively. Further, 15 of those species displayed a strong negative association with precipitation and temperature (CRIs exclude zero), respectively (Table S5). Masked palm civet, Himalayan serow *Capricornis thar*, yellow-throated marten, muntjac, red fox *Vulpes vulpes*, red panda, spotted linsang and wild pig showed a strong negative relationship to both temperature and precipitation (Figure S3). Most species displayed a negative response to all three RCP scenarios indicating vulnerability to future climate extremes (Figure 5).

3.2 Community-level response

The terrestrial mammal communities exhibited an overall negative response to agriculture (Figure 4A, decrease in mean occupancy probability with an increase in land under agriculture cultivation, overall community response, $\widehat{\beta_{community}}$ = -0.10, -0.16 – -0.05) and distance to road ($\widehat{\beta_{community}}$ = 0.10, 0.04 – 0.18, the overall community occupancy probability tend to increase farther from roads (Figure 4B), and to a lesser extent to distance to settlement ($\widehat{\beta_{community}}$ = 0.04; -0.08 – 0.16, the overall community occupancy probability tend to increase farther from settlements, Figure 4C). The weak relationship between distance

to settlement and occupancy implies that there is the variability of responses of different species to human habitation. For example, Asian elephant *Elephas maximus*, tiger *Panthera tigris* and crab-eating mongoose *Herpestes urva* strongly avoided human settlement (increasing occupancy probability away from human settlement) while masked palm civet *Paguma larvata* was present near the human settlement (higher occupancy probability closer to settlement). Community-level mean occupancy probability was strongly and positively associated with forest cover ($\hat{\beta}$ = 0.21, 0.04 – 0.38, Figure 4D). Community-level mean occupancy probabilities were strongly and negatively associated with precipitation ($\hat{\beta}$ = -0.25, -0.40 – -0.11) and temperature ($\hat{\beta}$ = -0.25, -0.43 – -0.08) under all RCP scenarios (Figure 5).

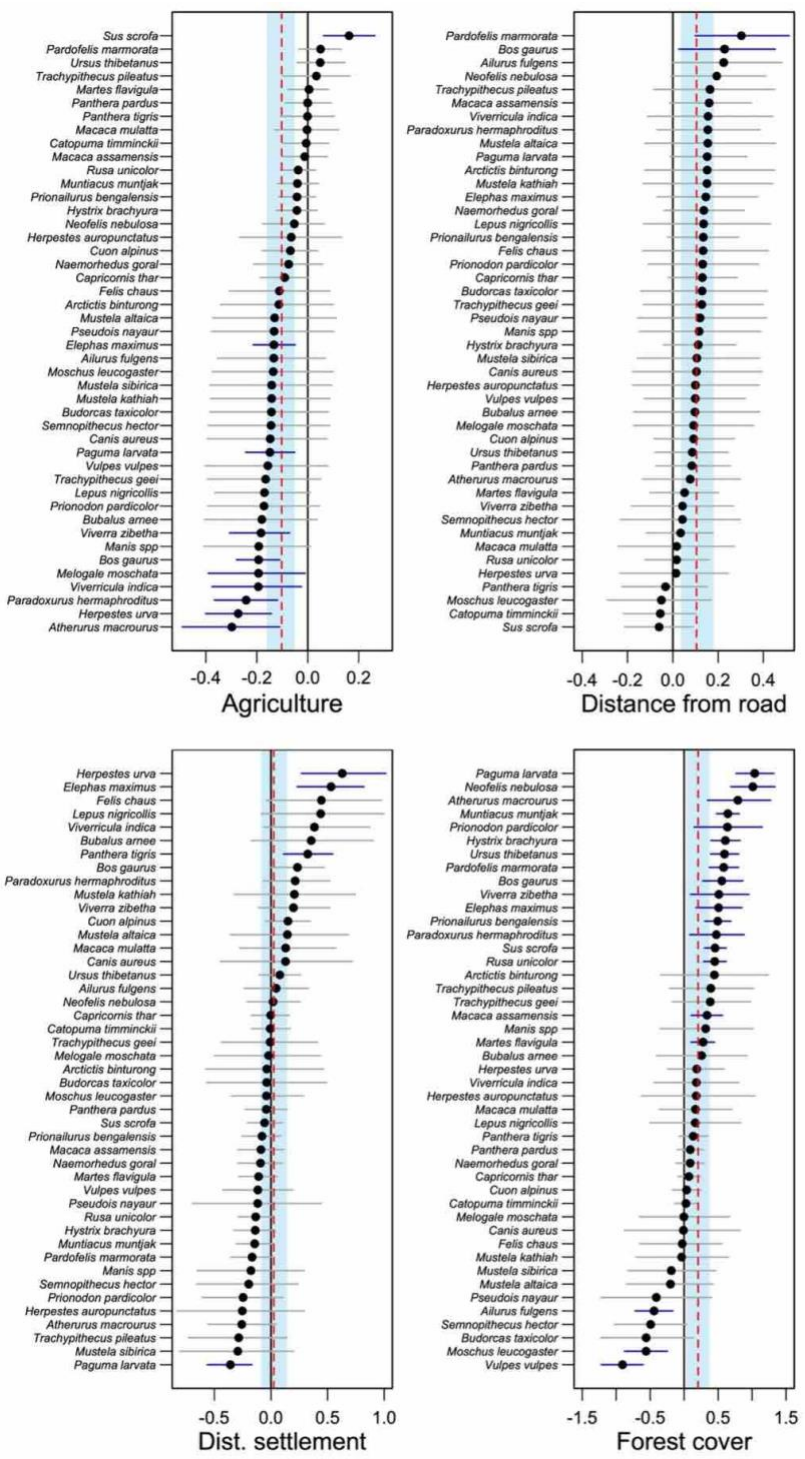


Figure 2. The community mean and individual species' response to land-use variables (agriculture, roads, settlement and forest cover) in Bhutan. The red dashed lines indicate the posterior means and the light blue vertical bars are the 95% credible intervals. The black points are the posterior means of the individual species' response and the grey lines are 95%

credible intervals. The dark blue horizontal lines represent species with a strong response (95% credible intervals non-overlapping zero)

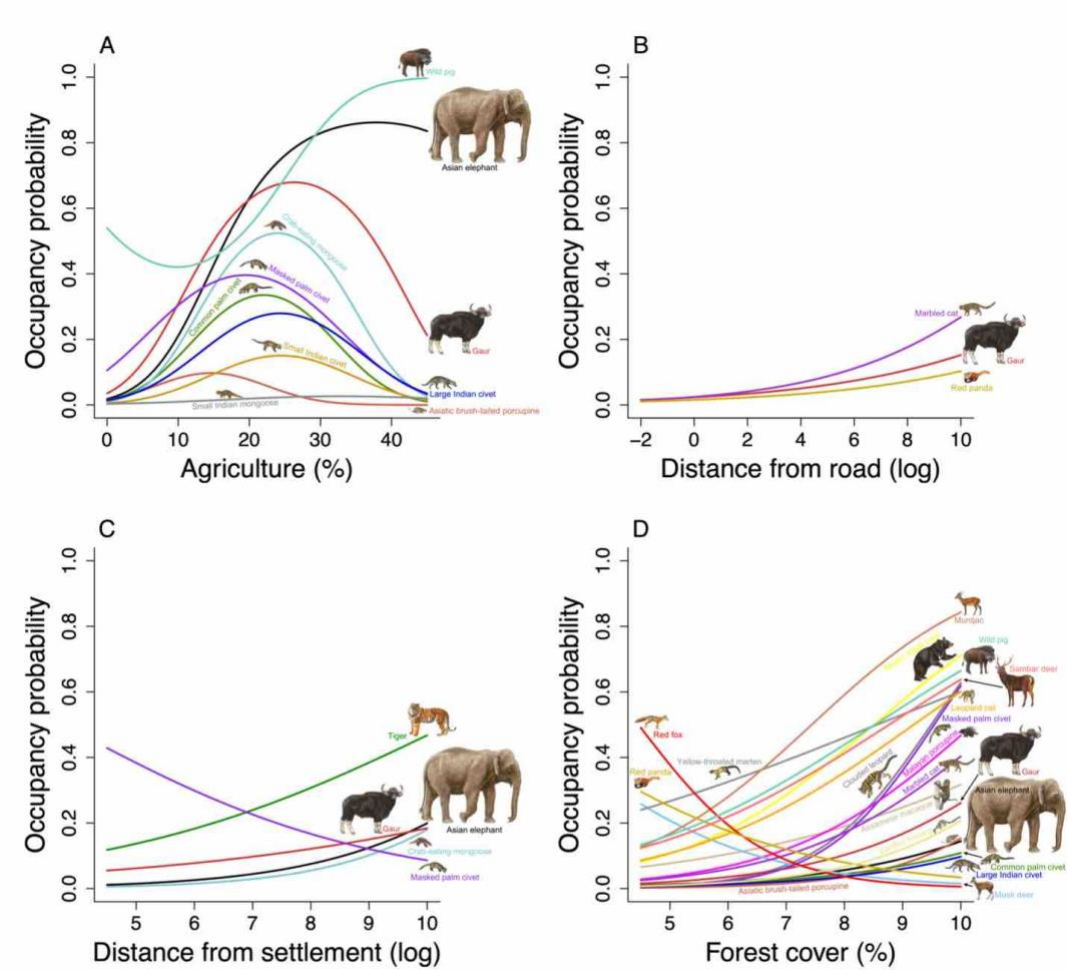


Figure 3. Posterior occupancy probabilities of species displaying strong (95% credible intervals non-overlapping zero) association (positive/winner or negative/loser) with agriculture, distance to road, distance to settlement and forest cover in Bhutan. Image courtesy: (Francis, 2019)

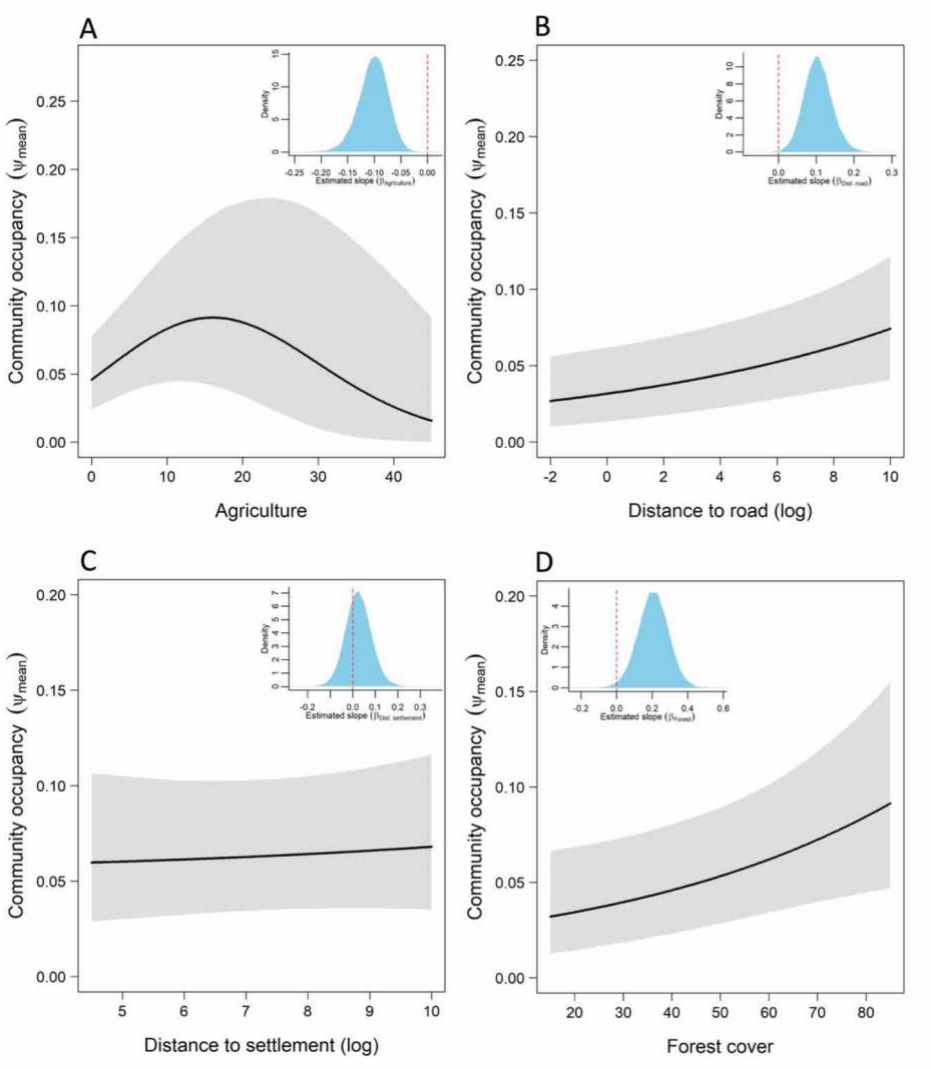


Figure 4. The response of the mammal community to land-use variables (A, B, C, D) and their posterior probability densities of beta coefficients (insets) in Bhutan. The overall mammal assemblage shows decreasing mean occupancy probability with the increase in agriculture land (A), increases further away from the road (B), settlement (C) and in areas with a high percentage of forest cover (D). The solid black lines indicate the mean probability and grey polygons represent the 95% CRIs

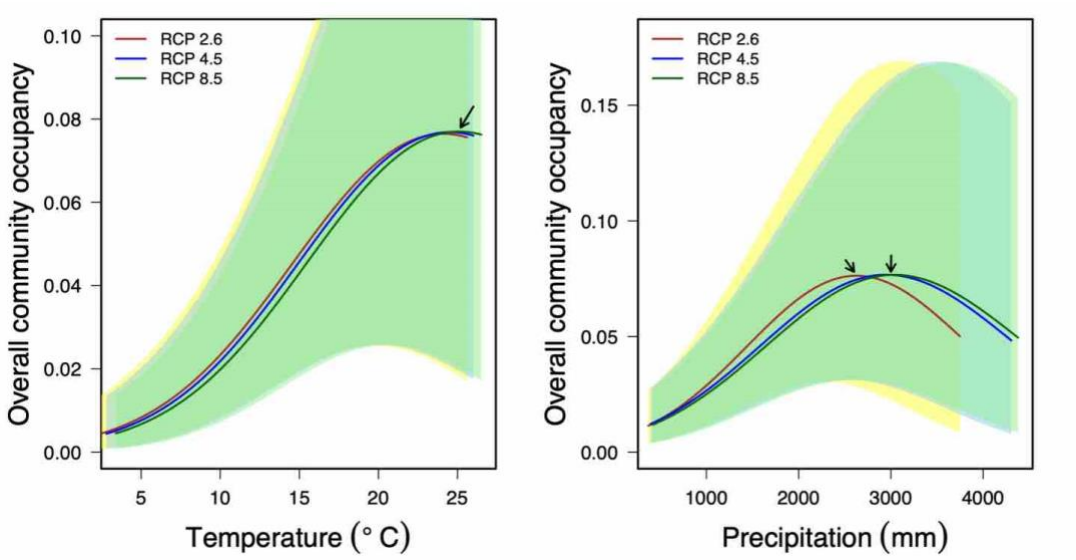


Figure 5. Estimated effects of temperature and precipitation on terrestrial mammal community under RCP scenarios (RCP 2.6, 4.5 and 8.5) in the year 2070. The arrows indicate the threshold beyond which the overall community occupancy begins to dip. The coloured curves indicate different scenarios and the corresponding 95% credible intervals by the shaded polygon

4 Discussion

In a fragile mountainous landscape, human land-use pressure can interact synergistically with climate change to further aggravate the decline in biodiversity. We found that all anthropogenically induced land-use changes like agriculture, roads and settlement were associated with decreased species richness and were avoided by a large number of species (Figure 2). The impact of climate change may not be instantly apparent, but our findings show the inherent vulnerability of mammal communities concerning the future extremes of climate as indicated by the relationship between mean community occupancy and precipitation and temperature under all RCP scenarios (Figure 5, S3).

Congruent with our hypothesis that most of the terrestrial mammals would avoid agriculture land use, we found that mammals in the montane subtropical and temperate landscape are negatively associated with agricultural land. Although we found that the probabilities, across mammals, of using agricultural land are consistently low, we speculate that the mechanisms underlying this generalization may vary between species and probably include aspects of dispersal, colonization and the tolerance of stress (Flynn et al., 2009b). The terrestrial mammals that we studied are forest-affiliated species and can be easily affected by habitat loss and degradation. For example, Asian elephant, Asiatic brush-tailed porcupine, common palm civet, crab-eating mongoose, gaur, large Indian civet, masked palm civet, small Indian civet and small Indian mongoose were clear losers. The only winner was wild pig, an agriculture-adept species (Schley et al., 2008). However, wild pigs are notoriously known for crop raid (Wang et al., 2006, Schley et al., 2008) and thus, agriculture development may escalate the conflict (Liu et al., 2019).

The agricultural land-use change in the long term could lead to decreased habitat, isolated population and increased conflict with humans (Laurance, 1991). In addition to decreasing species richness, land use intensification can, and generally does, reduce functional diversity of mammals (Flynn et al., 2009b), which seems likely to be detrimental to ecosystem function and the provision of ecosystem services. While this impact may be subtle for some species, in aggregate the decrease in species richness associated with the increasing proportion of land under agriculture is a threat to biodiversity conservation. The shrinkage and fragmentation of natural habitat are also likely to increase the interface between humans and wildlife and thereby exacerbate conflict (Acharya et al., 2017). Further, edge effects at the ecotone of the forest-agriculture interface worsen conservation threats (Balme et al., 2010), including the transmission of zoonotic disease (Faust et al., 2018). Our

findings tend to a pessimistic view of the hope that land-sharing can deliver the conservation of some large carnivores such as snow leopard (Johansson et al., 2016). Many of the mammalian species sampled by camera-trapping require largely forested habitat and maybe seriously ill-adapted to the agricultural matrix (Ceballos et al., 2005, Kinnaird et al., 2003). In this regard, we see merit in Green et al.'s (2005) argument for intensifying agricultural production on land already converted, while prioritizing the protection from the conversion of remaining forest (land-sparing).

The negative association of mammal community to roads illustrates a portent environmental cost associated with road development. Although only two species (marbled cat and gaur) displayed strong negative response, the majority tend to avoid roads (Figure 2). A major loss of forest, both inside and outside protected areas, in Bhutan in recent years is attributed to the rapid expansion of the road network (WMD, 2017). Such losses could be a malign indicator of wildlife habitat loss. Penetrating natural forest with new roads leads inevitably to a proliferation of secondary and tertiary road networks, opening avenues for deforestation, degradation and conduits for timber theft, poaching, encroachment and conversion (Laurance et al., 2014, Bennett, 2017) culminating in reduced mammal abundance (Vanthomme et al., 2013). Roads, in general, have been associated with cascading effects like overexploitation, habitat conversion, fire, farming and invasive species (Laurance et al., 2015, Ibisch et al., 2016). Although the effect was statistically weak, the human settlement had a generally negative association with mammalian diversity, an ominous association considering the growing human footprint (Torres et al., 2016, Gaynor et al., 2018). Asian elephant, tiger and crab-eating mongoose selected sites farther from human settlement. This corroborated the findings of previous studies, in Bhutan and elsewhere, that tiger and elephant avoided dense human settlement (Rood et al., 2010, Bishnu Prasad and Pavel, 2018,

Penjor et al., 2019). Most of the conflicts associated with tiger and elephant occur proximate to human settlement. Our finding suggests that proximity to human habitation could aggravate the human-wildlife conflict. One species (i.e. masked palm civet) displayed a peculiar response to human settlement- high occupancy probability near human settlement. It is unclear why masked palm civet shows affinity to human habitation, but we surmise probable high density of rodents and fruit trees may provide easy pickings for this omnivorous species (Zhou et al., 2008).

The effects of land-use change can be limited only by setting aside protected forest. Our model shows that mammal community occupancy increases with an increase in forest cover. The strongest effects on Asian elephant, Asiatic brush-tailed porcupine, tiger, clouded leopard, common palm civet, gaur, Asiatic black bear, Malayan porcupine, masked palm civet, yellow-throated marten, large Indian civet, leopard cat, marbled cat, muntjac, sambar deer, spotted linsang and wild pig highlight the importance of forest in maintaining functional assemblages and/or diversity, and ecological integrity besides provision of the basic need such as food, shelter and cover (Cassano et al., 2014). Further, such protection delivers reduced carbon emissions (Daily and Matson, 2008, Mendenhall et al., 2014, Frishkoff et al., 2014).

A strong negative response displayed by mammal communities to temperature and precipitation for the current (Figure S3), as well as future predictions (Figure 5), resonates with global apprehension regarding likely impacts of climate change for biodiversity and, in this case, terrestrial mammals. Novel climates result in habitat shifts mostly toward upper latitude and elevation (Chen et al., 2011). Species with limited ability to track this change may be imperiled. For instance, the Asian elephant is a tropical species and migration to

upper latitudes may not be possible due to steep topography of Bhutan. This situation is aggravated by growing human settlement and agriculture expansion across the border further constricting their range. Although habitat generalists like common leopard *Panthera pardus*, dhole *Cuon alpinus*, goral *Naemorhedus goral*, Himalayan serow *Capricornis thar* and primates may adapt to habitat shifts induced by climate change, the synergistic effect of climate and land use can be far-reaching (Brodie, 2016) and needs evaluation. It underscores the need to conserve large connected landscapes, facilitating species movement (McGuire et al., 2016). No less concerning is the threat to the livelihoods of people living in these landscapes, resulting from compromised ecosystem services, decreased agriculture production through decreased rainfall (Newbold et al., 2016, Roxy et al., 2017). Economic development is entwined with ecosystem services, and economies dependent on natural capital such as hydropower and tourism, are particularly at risk (Williams et al., 2007).

4.1 Management implications

The most effective approach to conserving biodiversity is to minimize the impacts of extrinsic factors such as human impacts on unfragmented natural wildlands (Barlow et al., 2016). A judicious approach to land management, with changing patterns of consumption and increasing agriculture productivity and concomitant reduction of land conversion to agriculture, is necessary (Stehfest et al., 2019). To cope with climate change, species will require contiguous habitat and linking corridor, together with providing refuges and facilitating movement (Chen et al., 2011, Tilman et al., 2017). Further, the synergy between land use and climate is not only interactive but also correlative (Tilman et al., 2017). For example, climate change is not only caused by greenhouse gas (GHG) emission but also significantly worsened by agricultural imperatives to clear land, deploy chemical fertilizer and methane gas associated with livestock production (Balmford et al., 2009, Tilman et al.,

2017). While, where it is feasible, conservation has much to gain from land-sharing (Feber et al., 2015a), in many of the areas we have studied in this paper, land-sparing is more appropriate to deliver the conservation of the terrestrial vertebrates we have studied. In a landscape where the human footprint is growing, long-term species persistence requires minimizing and mitigating anthropogenically-induced land-use change (e.g. Petracca et al., 2019). Besides land-use change, inadequately regulated hunting and ineffective enforcement regarding wildlife trade are amongst burgeoning issues that threaten local, regional and global biodiversity conservation and require a scrupulous examination (Ripple et al., 2016, Benítez-López et al., 2017).

5 Conclusions

We provide sufficient evidence for the need of preemptive and proactive conservation measures such as increased land protection and preservation of natural habitat which can further be coupled with scaled-up anti-poaching patrols and community engagement to achieve maximum conservation benefits. Considering the likelihood that global forest cover will decline due to climate change, in Bhutan, as elsewhere, both the protection of ecologically rich areas and the restoration of damaged ecosystems are crucially important (Bastin et al., 2019, Dorji et al., 2019).

Conservation is shifting its focus from single- to multi-species considerations. Our analyses demonstrate that communities of terrestrial mammals, sampled by camera-trapping, in a fragile mountain landscape are susceptible to land use and future climate change. We further show how individual species respond to these changes when considered under a multi-species framework. A clear conclusion is that conservation of this component of biodiversity necessitates minimizing conversion of natural wildlands and protecting inviolate

forest cover. A co-benefit of these recommendations will be safeguarding human wellbeing, insofar as this is inextricably linked to the natural ecosystem. The need to reconcile land use management and conservation is heightened in the face of the stochasticity of climate change. Our results on mammal assemblages, and the factors affecting their diversity and abundance in Bhutan, provide insight into the drivers of community dynamics and provide policy-relevant evidence germane to the impacts of land-use and climate change on biodiversity.

6 Authors' contributions

Ugyen Penjor: Conceptualization, Data curation, Methodology, Formal analysis, Validation, Writing - original draft, Writing - review & editing. **Sonam Wangdi:** Project administration, Resources. **Tandin Tandin:** Data curation. **David W. Macdonald:** Conceptualization, Funding acquisition, Resources, Supervision, Validation, Writing - review & editing.

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Supplementary Chapter 2

Anthropogenic land-use change shapes bird diversity along the eastern Himalayan altitudinal gradient

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Abstract

1. Globally, the conversion of natural forest into agricultural land and human settlement has altered avian diversity and structure often leading to functional and/or phylogenetic homogenisation. While the effects of land-use change on avian functional and phylogenetic diversity is well studied in the tropics, it is poorly understood and scarcely studied in the Himalayas let alone in the eastern Himalayan bird communities.

2. Using data from replicated transect surveys, we investigated the effects of land-use change (agriculture, settlement, and forest) on the community diversity and structure of 336 bird species while accounting for imperfect detection across 679-point count locations along the elevational gradient in the eastern Himalayan biodiversity hotspot of Bhutan.

3. The main findings of our study are 1) bird community occupancy along the elevational gradient is negatively associated with human land use (agriculture and settlement), 2) bird assemblages at higher elevations were functionally and phylogenetically clustered, and 3) agriculture and settlement harboured disproportionately higher functional and phylogenetic diversity whereas forest had phylogenetically diverse communities within functionally convergent traits.

4. *Synthesis and applications.* Our findings suggest that high functional diversity in agriculture and settlement offers an opportunity for a broad range of ecosystem services such as pollination, insect- and rodent-pest control. Agricultural practices that protect and improve bird-friendly habitats (particularly for insectivores) should be promulgated. To facilitate coexistence, educational programmes on the importance of the functional roles of birds should be implemented to sensitise farmers about the importance of farmland biodiversity. Management intervention should seek to integrate bird conservation and farm production. Safeguarding edge habitats and forests abutting human settlements would be key to

promoting phylogenetically diverse assemblages and ecological functions in the Himalayan working landscapes.

Keywords: altitudinal gradient, anthropogenic land use, detectability, Eastern Himalaya, functional diversity, multi-species occupancy model, phylogenetic diversity

1 Introduction

Global biodiversity is threatened by increasing anthropogenic pressure (Maxwell et al., 2016), escalating species extinction risk and corresponding loss of ecosystem services (Flynn et al., 2009a). Human pressure not only reduces species richness (Brawn et al., 2001) but affects other aspects of biodiversity such as functional and phylogenetic diversity (Flynn et al., 2009a, Naeem et al., 2012). This results in altered community diversity and structure (Simons et al., 2016, Thorn et al., 2016) often leading to functional and phylogenetic homogenisation (Devictor et al., 2007, Ibáñez-Álamo et al., 2017). The decline in biodiversity of forest communities concurrently leads to a substantial loss of ecological functions and thus impinges on the overall ecosystem functioning and processes (Cadotte et al., 2011, Betts et al., 2017). One of the biggest conservation challenges is to maintain a balance between biodiversity loss and agriculture and urban development (Johnson et al., 2017, Kehoe et al., 2017). This challenge is complicated along the elevational gradients where land-use intensity and patterns vary substantially (Bellard et al., 2012, de Oliveira Roque et al., 2018) such as the Himalayas. Thus, understanding the interaction between biodiversity and land-use change along the elevational gradient is particularly important in the context of the Himalayan landscape.

Phylogenetic diversity (PD) in conjunction with functional diversity (FD) is used to evaluate community response to environmental disturbances. Phylogenetic diversity reflects the evolutionary history and patterns of evolutionary relationships (Faith, 1992), while FD helps understand the functional uniqueness and patterns of functional trait distribution in a community (Cadotte et al., 2011). Generally, agriculture and urban habitats harbour less FD or PD than natural forests due to filtering of specific traits and lineages allowing to persist perturbation-tolerant species and resulting in redundant communities (Cannon et al., 2019). Further, on tropical mountains, FD and PD are low at higher elevations because only specialised traits inherited in phylogenetic lineages (phylogenetic niche conservatism) survive colder climates (Dehling et al., 2014, Montaño-Centellas et al., 2021). Thus, the interplay between elevation and land use has shaped many biotic communities across the globe (Santillán et al., 2019).

Bhutan, entirely within the Eastern Himalayan biodiversity hotspot (Myers et al., 2000), is a biologically diverse country with species composition from two biogeographic realms, the Palearctic and the Indo-Malayan (Olson et al., 2001). The extreme altitudinal variation (100m to >7000m) and topographical complexity that characterises the Himalayan landscape influence weather patterns and create a unique macroclimate which, in turn, harbours a wide spectrum of biodiversity (Chettri et al., 2010). However, rapid socio-economic development and urbanisation are modifying ecosystems and creating novel habitats, thus affecting species diversity and structure (Flynn et al., 2009a). Bhutan's ca.70% agrarian population depends on a mere 3% cultivable land (FRMD, 2017a). Achieving food self-sufficiency would require expansion of agricultural land which might impose additional pressure on natural resources. A large number of studies in the past investigated the effects of climate (Ruggiero and Hawkins, 2008, Kissling et al., 2010) and vegetation structure (Ferger

et al., 2014, Zhang et al., 2013) on bird diversity along tropical elevational gradients (Sreekar et al., 2021), but studies on the impacts of anthropogenic factors on the bird FD and PD along the eastern Himalayan altitudinal gradient are scarce or rather none. Himalayan mountain systems, due to the differences in stability, climate regimes, and topography, serve as an excellent natural laboratory to study the influence of interactions between geographic, environmental, and biotic factors in shaping bird community diversity and structure (Graham et al., 2014).

Birds play an important role in ecosystem functioning through pollination (Anderson et al., 2011), pest control (Bael et al., 2008, Martínez-Salinas et al., 2016), fruit and seed dispersal (Breitbach et al., 2012) and nutrient deposition (Wenny et al., 2011, Morante-Filho et al., 2018) and are known to respond strongly to changes in their environment (Canterbury et al., 2000, Gagné and Fahrig, 2011). Hence, they serve as an important indicator of ecological changes (Gardner et al., 2008) and ideal taxa to assess changes in FD and PD across the Himalayan landscape. Bird species richness has been shown to display a unimodal pattern along the global altitudinal gradient (Quintero and Jetz, 2018). The mid-domain hypothesis posits that species richness, irrespective of the influence of biotic and abiotic factors would peak at mid-elevations (Colwell and Lees, 2000, McCain, 2005). However, human intervention across elevational gradients is nuanced (Nogués-Bravo et al., 2008) and biotic factors are known to mediate variation in species diversity and richness (Jankowski et al., 2013). Gauging biodiversity change solely based on species richness or taxonomic diversity (TD) is inadequate to capture changes in evolutionary history or functional traits of species and individuals within assemblages (Swenson, 2013, Violle et al., 2014), overlooking crucial aspects of community ecology and conservation. For example, studies have shown that even when functionally important species are lost from the community, the TD remains

stable (Ernst et al., 2006, Spaak et al., 2017). Thus, understanding the intricacies of ecosystem functioning and services and evolutionary history requires evaluation of the impacts of human disturbance on FD and PD. Further, quantifying functional and phylogenetic responses of bird assemblages also helps us understand factors that drive community assembly mechanisms such as competitive exclusion or environmental filtering (Stevens et al., 2012).

In this study, we aim to establish a link between avian community diversity and structure and environmental (elevation and forest cover) and anthropogenic (agriculture and settlement) variables across the altitudinal gradient in this hitherto understudied landscape. We used data from point count surveys to examine the effects of land-use change (agriculture, human settlement, and forest cover) on the community assembly of 336 bird species. We hypothesised that bird community diversity and structure at high elevations and in presence of anthropogenic disturbances would be functionally and/or phylogenetically clustered (Hanz et al., 2019, Montaño-Centellas et al., 2021) while the structural complexity of vegetation would enhance bird diversity. Specifically, our aims were: 1) to quantify the response of community assembly to environmental and anthropogenic variables, and 2) to evaluate the factors mediating the variation of community diversity and structure along the elevational gradient. We show that human-mediated disruptions have a negative impact on bird community occupancy but not on diversity and structure and are highly variable among species.

2 Materials and Methods

2.1 Study site and survey protocol

We conducted point count surveys in three different locations across Bhutan (Figure 1). Site Narphu-Samdrup Jongkhar (NSJ) is in south-eastern Bhutan and spans altitudes from 150m and 1900m with subtropical and warm broad-leaved vegetation. Site Shechamthang-Waklaytar (SWK) is in south-central Bhutan with predominantly subtropical broad-leaved and dry chir pine (*Pinus roxburghii*) forest and elevation ranges between 300m and 1960m. Site Rimchu-Gasa (RGS) is in north-west Bhutan within the altitudinal ranges from 1345m to 2817m and vegetation is mostly composed of warm and cool broad-leaved forests.

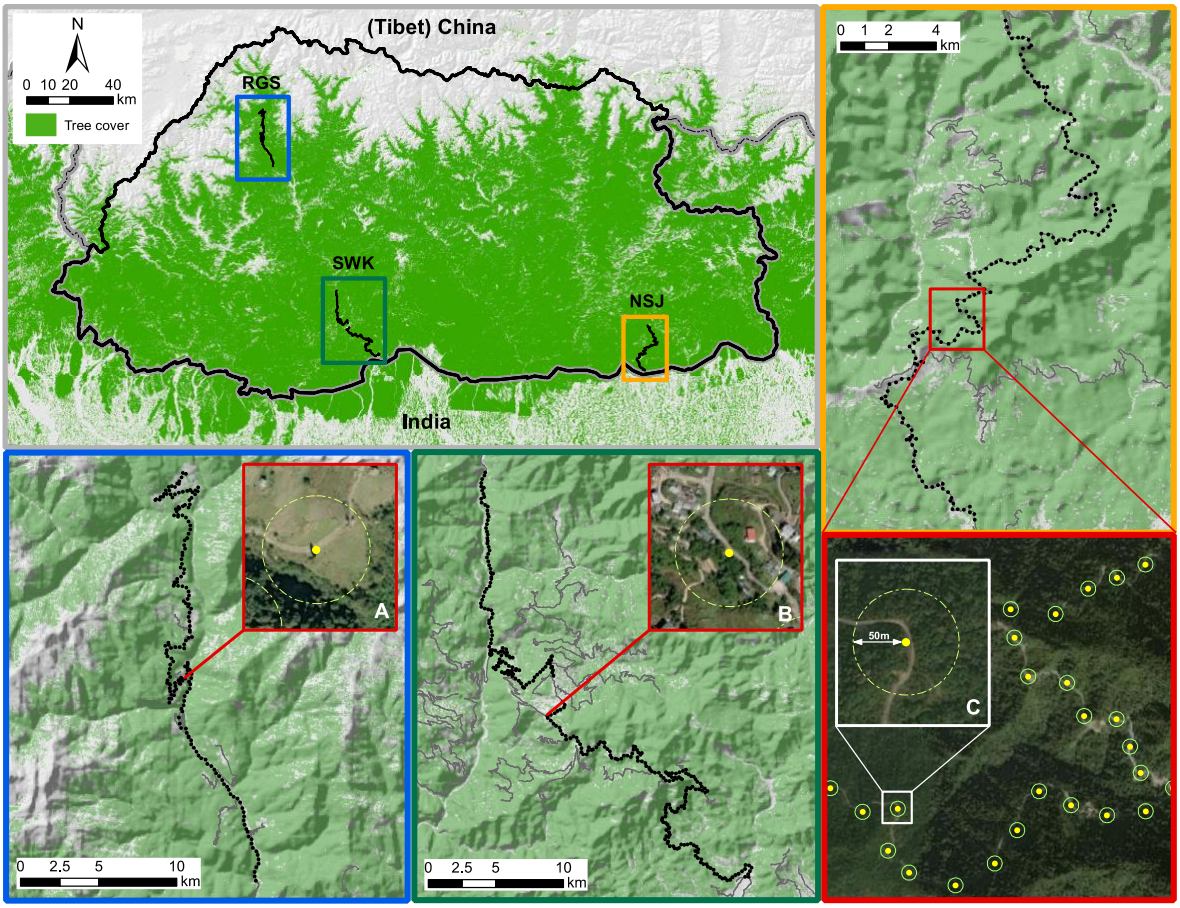


Figure 1. Map of Bhutan showing study sites and transects with point count locations. The insets show the plot design

We laid transects along the highway assisted by trained field observers who were familiar with the species composition across study sites. NSJ had 185-point count locations along 56km transect, SWK had 303 along 91km and RGS had 191 along 58km. Points were located at least 300m apart. We visited these sites on three separate occasions between October 2019 and March 2020. During the 15-min observation at each location, we recorded the presence of all species seen or heard within a 50m fixed radius of a point-count location. Resident birds flying overhead were also recorded. We conducted surveys in the early hours of the day coinciding with the increased activity of birds. We recorded a total of 373 bird species in 66 families across the survey. For our analysis, we removed migrant and vagrant species (Table S8), leaving us with 336 species from 679-point count locations.

2.2 Data analyses

2.2.1 Multispecies occupancy model

We used a multi-species occupancy model (MSOM) to estimate species richness (taxonomic diversity) for each site (Dorazio et al., 2006). MSOMs allow modelling variation in richness and diversity by teasing apart the latent ecological (state) process from the observation (detection) process. Using data from repeated sampling design, MSOM distinguishes non-detection from point-level absence and yields an unbiased estimate of occupancy (Dorazio et al., 2011).

The latent (ecological) process underlying the true pattern of occurrence of species k at site i is modelled as a Bernoulli random variable, $z_{ik} \sim Bernoulli\ (\psi_{ik})$ with the occupancy parameter ψ. The observation y of species k at site i on occasion j is another Bernoulli random variable conditional on the occurrence, $y_{ijk}|z_{ik} \sim Bernoulli\ (z_{ik} * p_{ijk})$. If the species is truly present, $z_{ik} = 1$ with detection probability p_{ijk}. For $z_{ik} = 0$, the

resulting observations are fixed zeros and false detections are not allowed. Probabilities of occupancy and detection can be modelled as functions of covariates through logistic link functions: $\text{logit}(\psi_{ik}) = \beta_{0k} + \beta_{\text{x}ik} \times cov_i$ for occupancy probability and $\text{logit}(p_{ijk}) = \alpha_{0k} + \alpha_{\text{x}ijk} \times cov_{ij}$ for detection probability, respectively. The β_{0k} and α_{0k} are the species-specific intercept parameters, $\beta_{\text{x}ik}$ is the slope parameter for site-level covariate x and $\alpha_{\text{x}ijk}$ is the slope for survey covariate x at each site i on occasion j indexed for each species k. We modelled occupancy as a function of elevation (linear and squared), per cent forest cover, per cent agricultural land and human settlement density and detection as a function of date (linear and squared) and survey duration and habitat type (categorical: warm broadleaf, cool broadleaf, subtropical dry chirpine and subtropical broadleaf forest). The site covariates were extracted within a 100m buffer of each point count location and standardised before analyses (all were continuous except habitat type). The correlation between occurrence and detection probability (common and abundant species are easily detected) (Royle and Nichols, 2003, Zipkin et al., 2009a) was accommodated by modelling a joint distribution of species-specific random effects (β_{0k} and α_{0k}) using a correlation parameter ρ, which also enables us to obtain estimates for rare species (Dorazio et al., 2011).

Species-specific parameters were modelled as draws from normal distributions, $\beta_k \sim Normal(\mu_{\beta_k}, \tau_{\beta_k})$ with community-wide means (μ) and precision (τ). We used weakly informative half-Cauchy priors with σ=2.25 on the standard deviation of hyperparameters (Gelman, 2006b, Dorazio et al., 2011). Models were implemented in JAGS 4.3 (Plummer, 2003) called through R 4.0 (R Core Team, 2020) using the package jagsUI (Kellner, 2019). We ran three parallel chains of 50,000 iterations each, discarding 10,000 during burn-in and retaining every 20th sample of the posterior distribution. We inspected model convergence by visually checking trace plots of parameters and ensuring that the Gelman-Rubin statistics ($\hat{R}$)

for all parameters were below 1.1 (Gelman et al., 2013). We used k-fold cross-validation for model selection and assessed model fit using posterior predictive checks (Hooten and Hobbs, 2015, Broms et al., 2016).

2.2.2 Functional and phylogenetic diversity

We used the detection-corrected true occurrence *z*-matrix to estimate community diversity metrics. Site-level TD was estimated as the sum of occurrence probability of species at each site (Jarzyna and Jetz, 2016). Functional diversity (FD) was calculated using detection-corrected site × species and species × trait matrices. Trait data were extracted from the global dataset (Wilman et al., 2014). We used Gower's distance (due to the presence of a binary and continuous variable in our trait data) to calculate multivariate trait dissimilarity for a pairwise combination of 336 species by assigning equal weights to each trait category (Jarzyna and Jetz, 2017). We then constructed a master functional dendrogram using the UPGMA (Unweighted Pair Group Method with Arithmetic mean) method and calculated FD as the sum of branch lengths of the dendrogram for all species in a community (Petchey and Gaston, 2002). Phylogenetic diversity was calculated using a sample of 100 global phylogenetic trees downloaded from birdtree.org (Jetz et al., 2012). The global trees were averaged and pruned to the observed species list and PD was calculated by summing branch lengths linking species in a community (Faith, 1992).

We used the null model approach to calculate standardised effect size (SES) by comparing observed communities with 1000 simulated communities to account for the influence of species richness on FD and PD metrics (Swenson, 2014, Cadotte et al., 2019). We computed four abundance-weighted metrics each for FD and PD: 1) SES.FD and SES.PD as the proportionate difference between observed and null expectations to measure

community diversity. Positive values suggest higher FD/PD than expected by chance and negative the opposite (Swenson, 2014). 2). The SES of mean pairwise distance (SES.fMPD and SES.MPD) between species in a community with positive values indicating overdispersion while negative indicating clustering relative to null communities (Webb et al., 2002). All analyses were performed in R using packages picante (Kembel et al., 2010), fundiv (Bartomeus, 2016), FD (Laliberté et al., 2014a), and phytools (Revell, 2012).

To determine the effects of anthropogenic and environmental variables (elevation, forest, agriculture and settlement) on functional and phylogenetic diversity and structure, we used a linear mixed-effect model in R package nlme (Pinheiro et al., 2017). For each diversity metric, we built a set of 16 models (with a biologically plausible combination of predictors) and used Akaike Information Criterion (corrected for sample size, AIC_c) in the MuMIn package (Barton, 2016) to select the most parsimonious model (Table S2-S6). This model was then analysed under the Bayesian framework with Gaussian error distribution to estimate posterior median and uncertainty. We assessed the significance of coefficient estimates with 95% credible intervals (CRI) and model fit using Bayesian R^2 (Gelman et al., 2019).

3 Results

We recorded a total of 28605 individuals from 66 families at 1937-point locations (across three temporal replicates, J_1= 590 locations, J_2= 668 locations, J_3= 679 locations) along 642 km transect during the 2019-2020 period. The numbers of species recorded along NSJ, SWK and RGS transects were 262, 291 and 204, respectively. The number of detections per species ranged from 1 to 366.

3.1 Relationship between occupancy and environmental and anthropogenic variable

Model selection criteria rendered support to the occupancy model consisting of four covariates (elevation and its squared term, forest, agriculture, and settlement) (Figure S2, Table S1). Across the bird community, the overall posterior median occupancy and detection probability were very low (median [95% CRI], $\hat{\psi}$=0.08[0.06, 0.12], $\hat{p}$=0.04[0.03, 0.04]). The occupancy probability was highly variable among species, ranging from 0.0004 (0, 0.005) for Asian fairy bluebird (*Irena puella*) to 0.93 (0.88, 0.97) for great barbet (*Megalaima virens*). Similarly, detection probability among the species varied to a considerable degree: lowest for dark-sided flycatcher (*Muscicapa sibirica*) (0.003[0, 0.008]) and highest for red-vented bulbul (*Pycnonotus cafer*) (0.42[0.35, 0.49]).

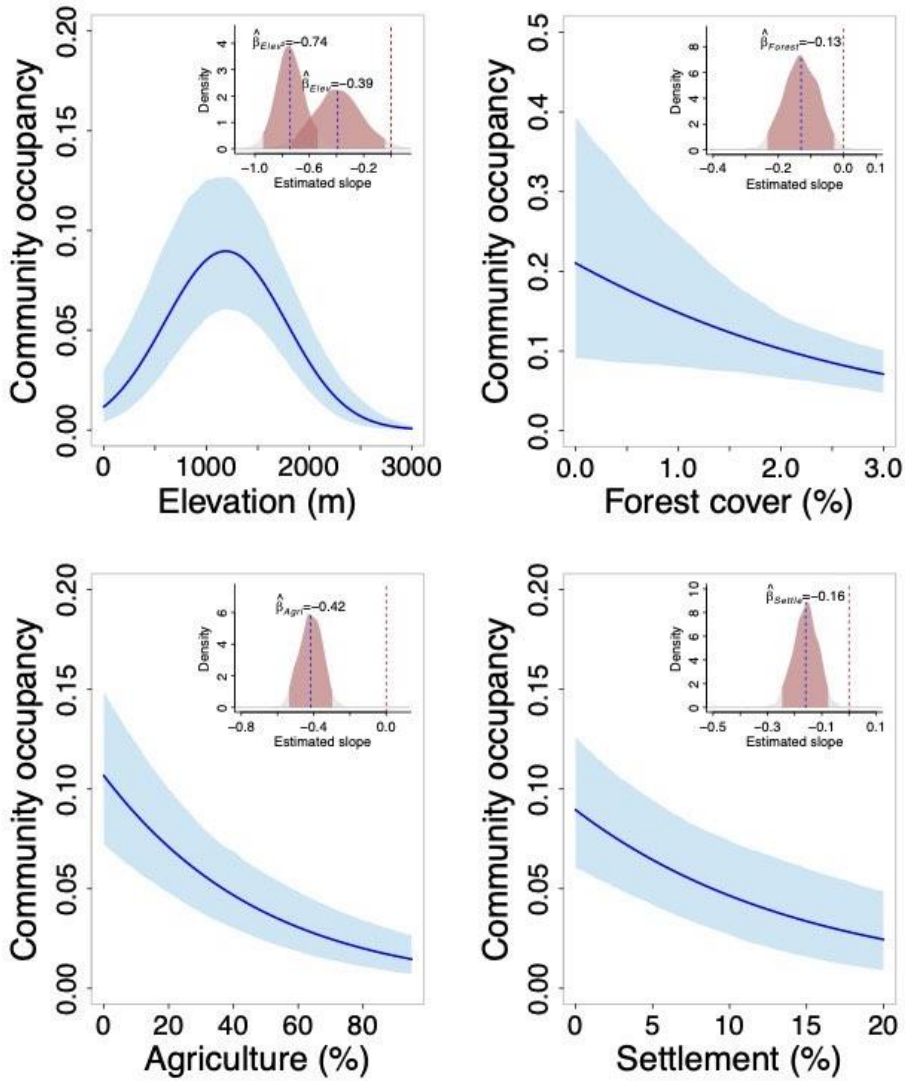


Figure 2. Response of community occupancy probability to elevation, forest cover, agriculture, and settlement. The blue lines show posterior means, and light blue shades show 95% CRI. Insets show the posterior distribution of slopes with 95% CRIs shaded in red and median values indicated by blue dotted vertical lines. While plotting the prediction of one covariate, others were held at their mean

The overall community occupancy strongly decreased with elevation (β_{ele}=-0.39[-0.73, -0.04]; β_{ele^2}=-0.74[-0.94, -0.54], Figure 2). Likewise, community occupancy was

negatively associated with forest cover (β_{tree}=-0.13[-0.23, -0.03]), agriculture (β_{agri}=-0.42[-0.54, -0.30]) and settlement (β_{set}=-0.16[-0.25, -0.08]). The overall detection probability was high during the initial surveys (α_{date}=0.49[0.39, 0.58]) but gradually decreased towards the end of the survey (α_{date^2}=-0.06[-016, 0.05]) probably due to the decline in the activity level of birds with the breeding season drawing to an end. The time spent at each site tends to increase the probability of detecting a species (α_{dur}=0.50[0.47, 0.53]). The detection probability was positively associated with warm broad-leaved (α_{WBLF}= 0.10[0.05, 0.16]) and subtropical broad-leaved forests (α_{SBLF}=0.25[0.18, 0.32]), and negatively with dry chir pine forest (α_{DCPF}=-0.35[-0.44, -0.26]).

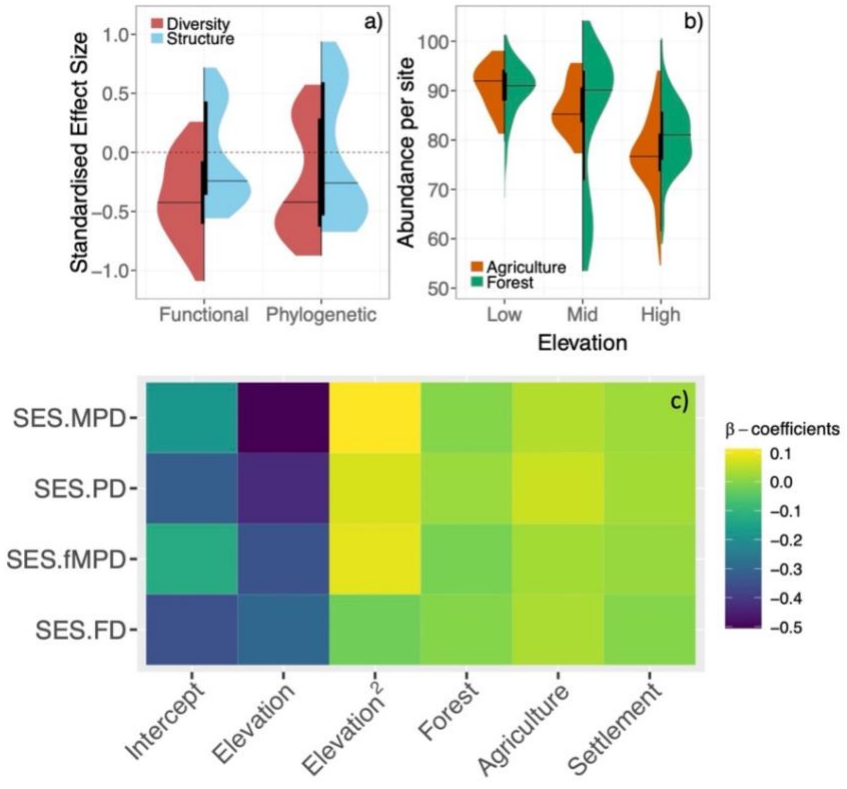


Figure 3. (a) Estimates of functional and phylogenetic diversity presented as abundance-weighted standardised effect sizes (SES) for the bird communities. (b) Posterior abundance per site across the elevational gradient in agriculture and forest sites. The horizontal lines indicate the median value, and the thick vertical lines indicate the first and third quartile

range. (c) Posterior coefficient estimates of slopes of functional (SES.FD) and phylogenetic diversity (SES.PD) and structure (SES.fMPD & SES.MPD) in response to environmental and anthropogenic variables

3.2 Community diversity and structure

Elevation and agriculture were strong predictors of functional and phylogenetic diversity (SES.FD and SES.PD). Further, the variation in SES.PD was additionally explained by forest and settlement (model containing forest and settlement, R^2= 0.92). The functional and phylogenetic structures (SES.fMPD and SES.MPD) were strongly predicted by elevation, agriculture, and settlement. Additionally, forest explained a significant amount of variation in SES.fMPD (model containing forest, R^2= 0.93).

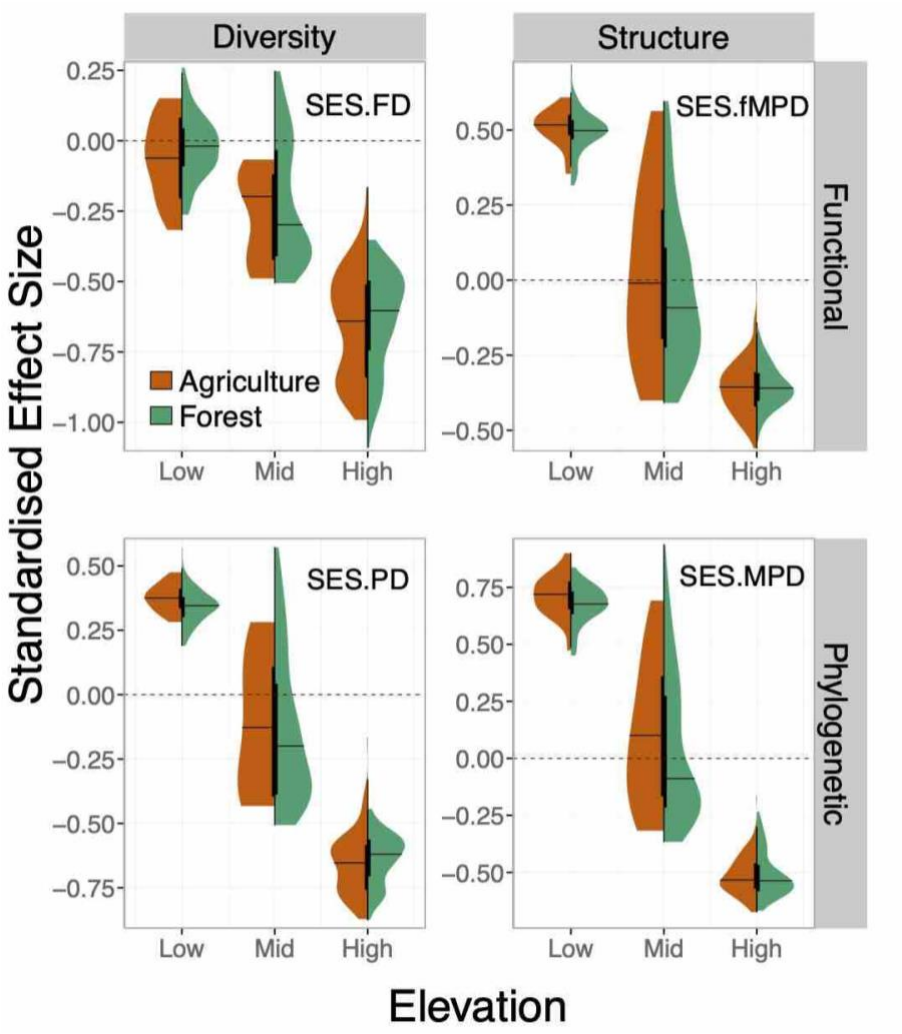


Figure 4. The variation in bird functional and phylogenetic diversity across an elevational gradient. Bird community diversity and structure were similar in both land-use types at low and high elevation but marginally higher in agriculture than forest at middle elevation. The horizontal lines indicate the median value, and the thick vertical lines indicate the first and third quartile range

The overall diversity and structure across the study area were lower than expected by chance indicating that bird communities were functionally and phylogenetically clustered (Figure 3). However, the diversity and structure were markedly different between land-use types (agriculture and forest) along the elevational gradient (Figure 4). The SES.FD and SES.PD (i.e., diversity) patterns mirrored each other across the elevational gradient showing

high values at low elevations compared with middle and high elevations. The SES.FD values in the forest were higher than agriculture at low and high elevations but lower than agriculture at middle elevation. At low and middle elevations, SES.PD in agriculture was higher than forest but lower at high elevation. The functional diversity tended towards a net clustering irrespective of the elevational gradient while the phylogenetic diversity was overdispersed at low elevation but clustered at middle and high elevations. Similarly, the functional and phylogenetic structures (SES.fMPD and SES.MPD) mirrored each other across the elevational gradient. Both SES.fMPD and SES.MPD in agriculture habitat were higher than forest at low and middle elevations but similar at high elevation. The functional and phylogenetic structure showed net overdispersion at low elevation, net clustering at high elevation and indifference from null communities at middle elevation (Figure 4).

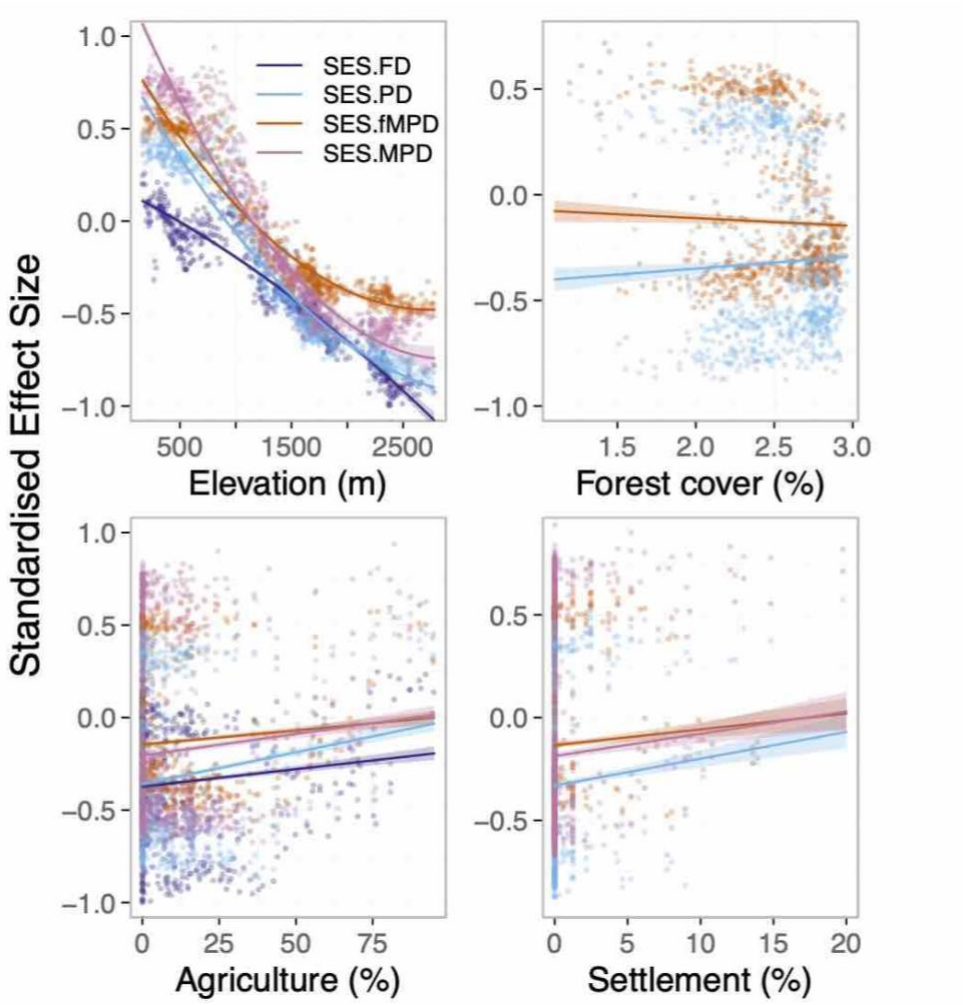


Figure 5. Relationship between elevation, forest, agriculture, and settlement and community diversity metrics. The mean response is indicated by solid lines and shading represents 95% CRI. The relationship is based on the predicted values from the top-ranked models of each metric

3.3 Effects of environmental and anthropogenic variables on community diversity and structure

The regression analysis revealed a precipitous decline in both functional and phylogenetic diversity (SES.FD and SES.PD) and structure (SES.fMPD and SES.MPD) with elevation, showing a sharp decrease (steeper slope) as elevation ascends from 300m to 2800m (Figure 5). Forest cover had an opposing effect on functional structure (SES.fMPD) and phylogenetic

diversity (SES.PD). The SES.fMPD decreased when the surrounding sites had a higher proportion of forest but SES.PD increased, while others showed a non-significant relationship (Figure 5). Agriculture had a positive effect on both functional and phylogenetic metrics (SES.FD, SES.fMPD, SES.PD and SES.MPD). The settlement had a strong positive effect on all metrics except SES.FD (Figure 3 & 5; Table S7).

4 Discussion

Using data from a temporally replicated transect survey, we examined the effects of environmental and anthropogenic factors on bird community assembly in the eastern Himalaya while accounting for imperfect detection. Our findings show that all three facets of biodiversity (taxonomic, functional, and phylogenetic) decreased with elevation, and that changes in forest cover, agriculture, and settlement mediate this pattern. There was a clear pattern of decline in community diversity and structure with bird assemblages tending to cluster in trait and phylogeny at higher elevations. There was no evidence that this pattern differed between natural forest and human settlement with the latter showing a marginally higher functional diversity and structure than the former but the former supporting higher phylogenetic diversity. Our study demonstrates the importance of bird diversity in human land-use settings to maintain ecological networks and crucial ecosystem processes.

The community assembly pattern across agriculture and forest shows evidence of clustering at higher elevations. The decline in functional diversity (SES.FD) and structure (SES.fMPD) and the concomitant decline in phylogenetic metrics (SES.PD and SES.MPD) with an increase in elevation irrespective of the land use type suggest the dominant role of abiotic filters in driving montane bird assemblages (Montaño-Centellas et al., 2021). The physiological and energetic constraints imposed by the low temperature at higher elevations

might exclude climate-intolerant traits and filter for species adapted to specific environments through similar ecological strategies and/or phylogenetic histories (Graham et al., 2014, Laliberté et al., 2014b, Laiolo et al., 2018, Hanz et al., 2019, Montaño-Centellas et al., 2021) as evidenced in this study by a decrease in the distance between functional pairs of species (SES.fMPD) at higher elevations. The decrease in SES.MPD with elevation is consistent with studies elsewhere (Dehling et al., 2014, Hanz et al., 2019, Montaño-Centellas et al., 2021) and suggests that the effect of harsh conditions and decreasing structural complexity of vegetation at higher elevations prevents species from colonising or persisting (Graham et al., 2014). At evolutionary timescale, as niches are conserved (phylogenetic niche conservatism), this leads to a decrease in PD (Webb et al., 2002). In contrast, the functional overdispersion in lowland assemblages might be driven by niche partitioning and interspecific competition (Pigot et al., 2016, Montaño-Centellas et al., 2021). There was a conspicuous difference between community occupancy and FD, and PD and elevation. The former showed a hump-shaped relationship corroborating the mid-elevation hypothesis (McCain, 2009), whereas the latter (FD and PD) consistently declined. This suggests that a single metric approach to assessing community assembly mechanisms may be inadequate (Violle et al., 2014) and a complementary approach combining all three metrics would be required (Ding et al., 2021).

Contrary to our expectations, bird communities showed patterns of increase in functional diversity and structure (overdispersion) with agriculture and settlement. The relatively easy accessibility of resources in agriculture habitat and settlement (e.g., food and nesting substrate) may favour species with traits that are tolerant of perturbation to survive and colonise but may not necessarily increase the overall diversity. This was supported by the contrasting relationship between FD and community occupancy and agriculture and settlement indicating that the overall community avoids human-dominated habitats and that

only a few species from recently diverged clades tolerate disturbances, suggesting that agriculture and settlement can act as ecological filters (Frishkoff et al., 2014). For example, species, often associated with disturbed habitats, such as spotted dove (*Stigmatopelia chinensis*), large-billed crow (*Corvus macrorhynchos*) and common iora (*Aegithina tiphia*) belonging to different family clades (Columbidae, Corvidae and Aegithinidae, respectively) and trophic guilds (granivore, omnivore and insectivore, respectively) were consistently detected in both agriculture and settlement, contributing to the overall functional and phylogenetic diversity (Figure 6). Although a wide array of clades across the avian phylogeny thrive in human-modified environments, the so-called 'winners' tend to be disproportionately over-represented in a few families (Sol et al., 2017) like the one we observed in this study (e.g., crows, pigeons, doves).

Studies have shown that human-altered habitats provide more niche opportunities for different life-history traits of some plant species, supporting higher phylogenetic diversity than expected (Uchida et al., 2019). Considering the bottom-up effects of plants on animal communities (Vollstädt et al., 2017), a higher FD and PD may not be idiosyncratic in some human land-use settings (García-Navas and Thuiller, 2020), though the generality of this finding needs further assessment. Since these metrics were corrected for species richness, the positive relationship between diversity and human land-use variables implies that communities in human-dominated landscapes tended to have a higher functional richness than expected by the number of species present (Sol et al., 2017). Therefore, functional overdispersion suggests that human-altered habitats may have created novel niches (habitat filters) that allow functionally distinct, though mostly non-forest, species to occupy, survive, and competitively exclude species that are not well adapted to disturbances (Cavender-Bares et al., 2009, Matuoka et al., 2020). Further, nuances in effects of anthropogenic disturbances

may affect species differently, with some ecological traits (e.g., specialised in habitat use) rendering higher vulnerability than others (Clavel et al., 2011). However, after a certain threshold, agriculture and settlement may act as ecological traps beyond which the benefit of being near them is outweighed by costs such as conflict, and reduced fitness and reproduction (Battin, 2004, Cooke et al., 2020).

We found contrasting effects of forest cover on the functional and phylogenetic diversity of bird communities. Surprisingly, we detected a negative effect of forest cover on the functional structure (SES.fMPD), implied by decreasing distances in functional traits between species at sites with a higher percentage of forest cover. Phylogenetic diversity (SES.PD), on the other hand, increased with forest cover. This may be due to several reasons. 1) Forest interior harbours mostly foraging and habitat specialists within distinct evolutionary lineages (e.g., insectivores such as red-headed trogon (*Harpactes erythrocephalus*), yellow-rumped honeyguide (*Indicator xanthonotus*), yellow-bellied fantail (*Chelidorhynx hypoxantha*), sultan tit (*Melanochlora sultanea*) – all from divergent families, were positively associated with forest) thus increasing the phylogenetic diversity but concurrently increasing functional redundancy and clustering (decreasing SES.FMPD) due to the similarity in functional traits (all insectivores, trait conservatism) (Cavender-Bares et al., 2009, Clavel et al., 2011). 2) Conversely, forest edge may favour generalists with divergent foraging traits (e.g., common myna (*Acridotheres tristis*) (omnivore), large-billed crow (*Corvus macrorhynchos*) (omnivore), Eurasian tree sparrow (*Passer montanus*) (granivore), oriental magpie robin (*Copsychus saularis*) (invertivore)), thus increasing the trait diversity compared with forest interior but within recently diverged clades (Figure 6). Further, forest edges, due to higher accessibility and/or visibility, might allow birds to easily locate prey thereby attracting species with a wider variety of traits to congregate, hence increasing functional

diversity than interiors (Barbaro et al., 2014). This suggests that forests surrounding agriculture and settlement may promote functional redundancy. Although functional redundancy may buffer against future species extinction (debt), forests adjacent to human perturbations are less resilient, and thus species loss can easily compromise ecosystem services provided by birds in these habitats (Flynn et al., 2009a, Matuoka et al., 2020)

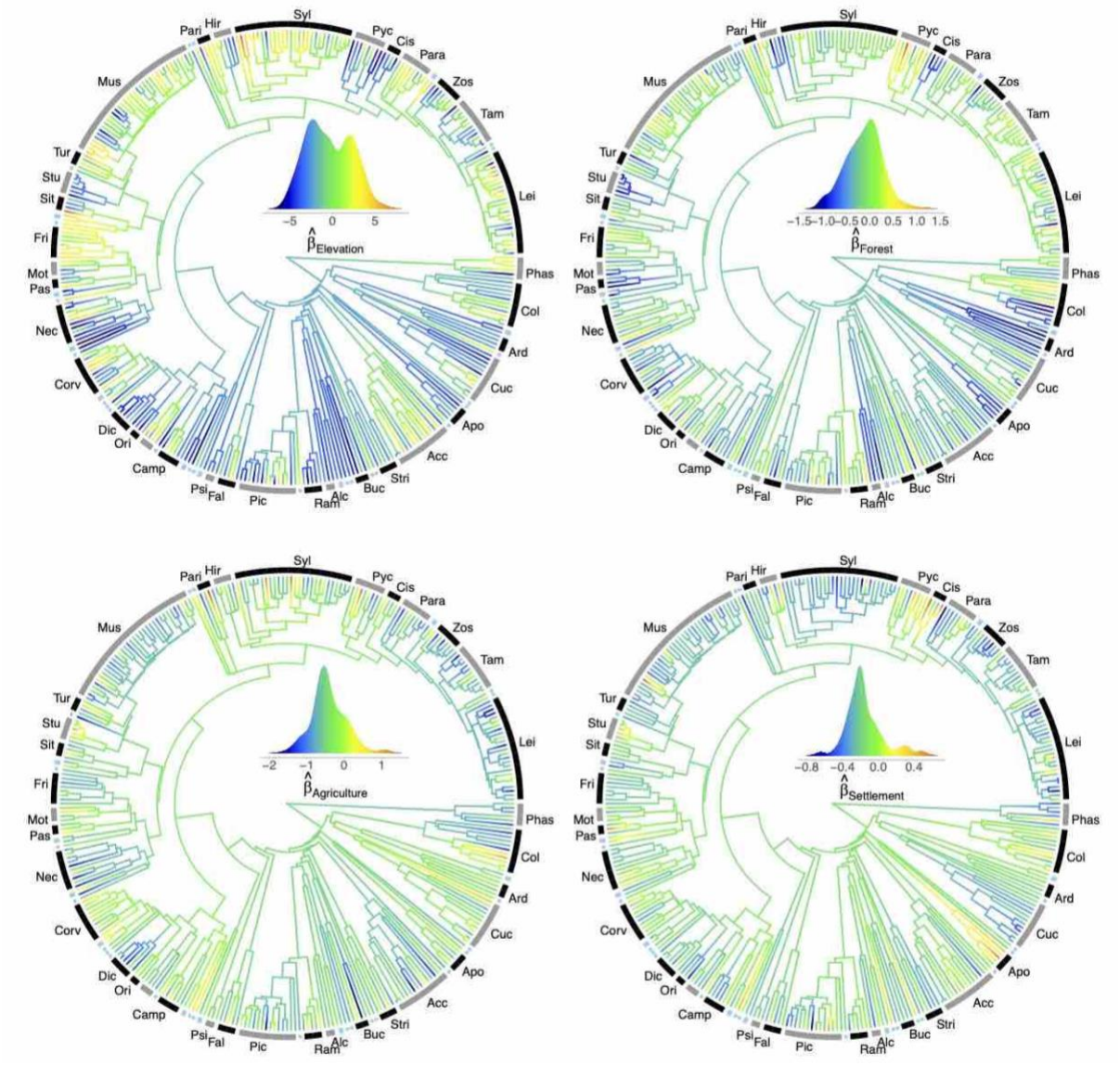


Figure 6. Response of 336 species across the phylogenetic tree to elevation, agriculture, forest, and settlement. Branches are coloured by the magnitude of response (heat = positive; cool = negative). Density plots show the overall posterior distribution of slopes with shading

corresponding to branch colour. Families with less than 2 species are shown as blue circles and rectangles. Clades are labelled with contracted family names for readability: Acc, Accipitridae; Apo, Apopidae; Alc, Alcedinidae; Ard, Ardeidae; Buc, Bucerotidae; Camp, Campephagidae; Cis, Cisticolidae; Col, Columbidae; Corv, Corvidae; Cuc, Cuculidae; Dic, Dicrudidae; Fal, Falconidae; Fri, Fringillidae; Hir, Hirundinidae; Lei, Leiothrichidae; Mot, Motacillidae; Mus, Muscicapidae; Nec, Nectariniidae; Ori, Orilidae; Para, Paradoxornithidae; Pari, Paridae; Pas, Passeridae; Phas, Phasianidae; Pic, Picidae; Psi, Psittacidae; Pyc, Pycnonotidae; Ram, Ramphastidae; Sit, Sittidae; Stri, Strigidae; Stu, Sturnidae; Syl, Sylviidae; Tam, Tamiliidae; Tur, Turdidae; Zos, Zosteropidae

4.1 Limitations

Our transects were placed entirely along the road. Road traffic may affect the singing or feeding behaviour of birds but also the observer's ability to detect or hear bird calls (Lituma and Buehler, 2016) and hence may induce variability in detection. We suspect that this might have resulted in the disproportionate detection of some traits in this survey (e.g., more detection of invertivores [n=204] than nectarivores [n=5]). Studies looking into the differences in detection between transects on-road and other natural habitats are therefore highly advised. Detection probability can vary during the breeding season: high detection at the beginning when birds are settling and building the nest and later in the season when most birds have laid eggs and started brooding, the detection will be low (Chambert et al., 2012). Our survey took place towards the end of the breeding season which might have resulted in heterogeneity in detectability. Future studies could compare detectability at the start and end of the season to elucidate the difference.

4.2 Conservation implications

Agriculture and settlement harboured diverse functional traits that reflect the opportunity for a broad range of ecosystem services. For example, the northern armyworm (*Mythimna separata* larvae) infestation destroys crops and results in economic losses to farmers in Bhutan annually. This can be mitigated by promoting insectivore diversity, which will eventually act as biological control (avian predators) (Hooks et al., 2003, Jones et al., 2005), by providing nesting sites and planting native (roost) trees. We advocate implementing agricultural practices that safeguard and promote habitats to attract insectivorous birds. Management should also aim to increase public awareness on the importance of functional roles of birds and integrate bird conservation with farm production. We recommend the protection of forest surrounding agriculture and settlement for cover and vegetation complexity. This will act as a buffer zone between natural areas and agriculture/settlement matrix, provide edge habitat and facilitate spillover of species and preserve greater evolutionary diversity (Frishkoff et al., 2014). Managing landscape heterogeneity to conserve birds and their multiple functions is a valuable prospect for farmers and private landowners living in these landscapes to potentially offset disservices of bird pests (e.g., granivores) and predators (e.g., raptors). To boost the conservation value of working landscapes in the Himalayas, policy should capitalise on avitourism opportunities (Biggs et al., 2011) which is currently in its infancy in Bhutan. This entails considering multiple facets of bird diversity and we provide an unequivocal approach to doing so using all three metrics (TD, FD, PD) in the context of eastern Himalayan bird communities. We encourage the use of trait- and phylogeny-based approaches to gauge the impacts of land-use change on biodiversity (Cannon et al., 2019). Thus, we recommend incorporating FD and PD assessments into the mainstream monitoring programmes.

5 Conclusions

This study offers insights into the community assembly process in a hitherto understudied eastern Himalayan landscape and the factors mediating avian diversity and structure. An unconventional yet novel finding of this study, at least in this landscape, is the functional and phylogenetic overdispersion of bird communities in agriculture and settlement. Although it may seem at odds with studies elsewhere, it suggests that bird communities in anthropic environments are relatively stable and provide a greater opportunity for ecosystem services by the remaining traits. We demonstrate that at a medium level of disturbance (i.e., intermediate disturbance hypothesis) in human-dominated landscapes, it might be possible to conserve functionally diverse traits and perhaps reap ecosystem benefits.

6 Authors' contributions

U.P. and S.S. conceived the study, S.S. designed the survey and collected the data; U.P. analysed the data and interpreted results; U.P. led the writing of the manuscript; S.S. contributed to the initial draft. All authors contributed to the drafts and gave final approval for publication.

7 Data availability statement

Data and scripts (software tab under 'Related works') are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.cnp5hqc5v or https://datadryad.org/stash/share/t6r3bumqdVd22ehC9_CEmFzeGfx6MMBXoYpNHaizjQA.

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Supplementary material for Chapter 2

Table S1. Details of national tiger survey (camera trap) 2014-15 in Bhutan. PAs are protected areas and TDs are territorial divisions or non-protected areas

Study area	Category	Block	Year	Number of stations	Trap days	Mean trap days (SD)
Jigme Khesar Strict Nature Reserve (JKSNR)	PA	North	2014-15	20	1701	85(37.2)
Paro Division	TD	North	2014-15	40	2775	69.4(31.7)
Jigme Dorji National Park (JDNP)	PA	North	2014-15	38	1997	52.5(31.1)
Thimphu Division	TD	North	2014-15	21	1825	86.9(48.1)
Wangdue Division	TD	North	2014-15	81	5393	66.6(40.1)
Wangchuck Centennial National Park (WCNP)	PA	North	2014-15	31	1091	35.2(24.5)
Bumthang Division	TD	North	2014-15	37	3914	105.8(36.8)
Mongar Division	TD	North	2014-15	30	1931	64.4(24.5)
Phrumsengla National Park (PNP)	PA	North	2014-15	26	1873	72(40.6)
Bumdelling Wildlife Sanctuary (BWS)	PA	North	2014-15	29	3369	116.2(45.8)
Trashigang Division	TD	North	2014-15	25	2419	96.8(30.3)
Sakteng Wildlife Sanctuary (SWS)	PA	North	2014-15	22	1908	86.7(53.7)
Samtse Division	TD	South	2014	8	762	95.2(25.2)
Gedu Division	TD	South	2014	34	2655	78.1(38.0)
Tsirang Division	TD	South	2014	37	4020	108.6(38.1)
Phipsoo Wildlife Sanctuary (PWS)	PA	South	2014	20	2353	117.6(20.2)
Sarpang Division	TD	South	2014	39	3807	97.6(24.3)
Jigme Singye Wangchuck National Park (JSWNP)	PA	South	2014	58	6264	108(23.1)
Royal Manas National Park (RMNP)	PA	South	2014	73	7728	105.9(27.4)
Zhengang Division	TD	South	2014	102	8637	84.7(33.0)
Samdrupjongkhar Division	TD	South	2014	78	6837	87.6(33.8)
				849	73259	

Table S2. The list of terrestrial mammal species. Ranking based on IUCN conservation status

Rank	Common name	Scientific name	IUCN Red List	
1	Bengal tiger	*Panthera tigris tigris*	Endangered	EN
2	Asian elephant	*Elephas maximus*	Endangered	EN
3	Dhole	*Cuon alpinus*	Endangered	EN
4	Common leopard	*Panthera pardus*	Vulnerable	VU
5	Clouded leopard	*Neofelis nebulosa*	Vulnerable	VU
6	Gaur	*Bos gaurus*	Vulnerable	VU
7	Asiatic black bear	*Ursus thibetanus laniger*	Vulnerable	VU
8	Sambar	*Rusa unicolor*	Vulnerable	VU
9	Asiatic golden cat	*Catopuma timminckii*	Near Threatened	NT
10	Marbled cat	*Pardofelis marmorata*	Near Threatened	NT
11	Leopard cat	*Prionailurus bengalensis*	Least Concern	LC
12	Himalayan serow	*Capricornis thar*	Near Threatened	NT
13	Indian muntjac	*Muntiacus muntjak*	Least Concern	LC
14	Masked palm civet	*Paguma larvata*	Least Concern	LC
15	Yellow-throated marten	*Martes flavigula*	Least Concern	LC
16	Wild pig	*Sus scrofa*	Least Concern	LC

Table S3. Model averaged coefficients of habitat suitability models for 16 terrestrial mammals in Bhutan. Parameters presented area mean, standard error, 95% confidence intervals, p-values and summed model weights of each covariate

Asiatic black bear							
Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-0.820	0.085	-0.987	-0.653	0.000	
agriculture (GYRATE_AM)	0.5	**-0.244**	**0.109**	**-0.459**	**-0.029**	0.026	0.870
compound topographic index (FM)	1	**-0.310**	**0.089**	**-0.485**	**-0.135**	0.001	0.990
meadow (PD)	2	-0.187	0.097	-0.378	0.004	0.140	0.720
river (FM)	32	0.144	0.089	-0.031	0.319	0.260	0.570
non-forest (PLAND)	8	**-0.559**	**0.126**	**-0.807**	**-0.312**	0.000	1.000
built-up (PD)	32	0.050	0.089	-0.125	0.224	0.860	0.300
roughness (FM)	32	0.032	0.084	-0.132	0.196	0.900	0.300
slope position (FM)	4	-0.030	0.096	-0.219	0.159	0.920	0.270

Asian elephant							
Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-10.743	4.389	-19.355	-2.131	0.014	
agriculture (PD)	8	**-0.658**	**0.259**	**-1.166**	**-0.150**	0.011	0.900
broadleaf forest (PD)	16	**-0.985**	**0.424**	**-1.817**	**-0.153**	0.020	0.800
elevation (FM)	32	**-2.087**	**0.680**	**-3.420**	**-0.753**	0.002	1.000
river (FM)	16	-0.236	0.139	-0.508	0.037	0.090	0.670
roughness (FM)	2	**-0.684**	**0.299**	**-1.271**	**-0.097**	0.022	0.870
slope position (FM)	1	-0.290	0.193	-0.670	0.090	0.134	0.560
snow cover (GYRATE_AM)	32	-12.722	8.473	-29.352	3.908	0.133	0.640
protected area (FM)	0.5	-0.325	0.235	-0.787	0.137	0.167	0.410
open-forest (GYRATE_AM)	4	0.152	0.281	-0.399	0.703	0.588	0.280

Asiatic golden cat							
Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-0.894	0.080	-1.050	-0.737	0.000	
conifer forest (PD)	2	**0.255**	**0.080**	**0.098**	**0.412**	0.002	0.980
roughness (FM)	16	**0.308**	**0.083**	**0.144**	**0.472**	0.000	0.990
slope position (FM)	4	0.128	0.081	-0.031	0.286	0.412	0.550
land cover all (CWED)	8	-0.127	0.089	-0.302	0.049	0.509	0.500
agriculture (GYRATE_AM)	32	-0.114	0.096	-0.303	0.075	0.660	0.400
broadleaf forest (PD)	32	0.098	0.086	-0.070	0.266	0.680	0.380
non-forest (GYRATE_AM)	32	-0.069	0.087	-0.239	0.100	0.850	0.300

Common leopard							
Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-2.441	0.159	-2.753	-2.128	0.000	
compound topographic index (FM)	16	**0.608**	**0.224**	**0.168**	**1.048**	0.007	0.900
elevation (FM)	4	**-0.692**	**0.215**	**-1.114**	**-0.270**	0.001	0.980
protected area (FM)	0.5	**1.055**	**0.150**	**0.760**	**1.350**	0.000	1.000
river (FM)	32	-0.243	0.133	-0.503	0.017	0.176	0.610
roughness (FM)	32	0.264	0.143	-0.017	0.546	0.198	0.570
non forest (GYRATE_AM)	32	**-0.397**	**0.202**	**-0.793**	**-0.001**	0.090	0.620
tree cover (PD)	16	0.200	0.150	-0.094	0.495	0.566	0.480
broadleaf forest (PD)	32	0.226	0.159	-0.086	0.538	0.558	0.500
settlement (FM)	16	0.169	0.145	-0.115	0.454	0.749	0.380
agriculture (PD)	8	0.184	0.169	-0.148	0.515	0.764	0.350
road (FM)	32	0.124	0.128	-0.128	0.376	0.837	0.310
land cover (PD)	16	0.130	0.183	-0.230	0.489	0.926	0.310
built-up (PD)	32	0.107	0.198	-0.281	0.495	0.919	0.280
slope position (FM)	32	0.048	0.134	-0.216	0.312	0.945	0.280

Clouded leopard							
Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-2.566	0.171	-2.902	-2.231	0.000	
broadleaf forest (PLAND)	32	**0.839**	**0.172**	**0.502**	**1.177**	0.000	1.000
land cover (PD)	4	**-0.364**	**0.150**	**-0.663**	**-0.065**	0.017	0.880
protected area (FM)	4	**0.423**	**0.120**	**0.191**	**0.655**	0.000	1.000
river (FM)	8	-0.119	0.120	-0.395	0.036	0.330	0.620
non-forest (GYRATE_AM)	0.5	**-0.353**	**0.160**	**-0.659**	**-0.048**	0.020	0.870
built-up (PLAND)	8	-0.193	0.300	-1.025	0.210	0.520	0.510
road (FM)	8	0.101	0.160	-0.102	0.553	0.520	0.480
broadleaf forest (PD)	4	-0.029	0.085	-0.493	0.208	0.810	0.370
roughness (FM)	16	0.002	0.031	-0.217	0.275	0.960	0.280

Dhole							
Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-1.333	0.098	-1.526	-1.140	0.000	
agriculture (GYRATE_AM)	1	-0.173	0.129	-0.424	0.079	0.510	0.540
land cover (CWED)	4	-0.136	0.099	-0.330	0.059	0.560	0.440
river (FM)	2	**-0.250**	**0.113**	**-0.472**	**-0.028**	0.030	0.860
road (FM)	1	**-0.511**	**0.194**	**-0.892**	**-0.129**	0.009	0.990
slope position (FM)	4	**0.208**	**0.098**	**0.016**	**0.400**	0.033	0.800
open-forest (GYRATE_AM)	8	**0.211**	**0.088**	**0.037**	**0.384**	0.020	0.840
land cover (GYRATE_AM)	1	0.139	0.100	-0.057	0.335	0.500	0.450

bare area (GYRATE_AM)	2	-0.125	0.103	-0.327	0.077	0.610	0.440
broadleaf forest (PD)	32	0.062	0.092	-0.118	0.242	0.820	0.340
built-up (GYRATE_AM)	4	-0.060	0.104	-0.263	0.144	0.860	0.300

Gaur

Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-3.791	0.334	-4.446	-3.136	0.000	
elevation (FM)	32	**-2.262**	**0.293**	**-2.837**	**-1.687**	0.000	1.000
protected area (FM)	0.5	**0.362**	**0.138**	**0.092**	**0.632**	0.009	0.920
roughness (FM)	8	-0.338	0.245	-0.819	0.143	0.170	0.500
closed forest (PD)	4	-0.444	0.304	-1.041	0.154	0.150	0.590
river (FM)	16	-0.146	0.115	-0.372	0.080	0.210	0.460
open-forest (GYRATE_AM)	4	0.177	0.212	-0.239	0.593	0.400	0.310

Himalayan Serow

Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-0.764	0.083	-0.927	-0.602	0.000	
bare area (GYRATE_AM)	32	0.192	0.108	-0.021	0.405	0.080	0.630
broadleaf forest (PD)	32	**0.454**	**0.095**	**0.268**	**0.641**	0.000	1.000
built-up (PLAND)	8	**-0.241**	**0.112**	**-0.460**	**-0.023**	0.030	0.720
compound topographic index (FM)	4	**-0.391**	**0.113**	**-0.613**	**-0.170**	0.005	0.990
meadow (GYRATE_AM)	0.5	**-0.268**	**0.094**	**-0.452**	**-0.084**	0.004	0.900
river (FM)	16	**-0.173**	**0.082**	**-0.334**	**-0.013**	0.004	0.750
roughness (FM)	32	0.149	0.089	-0.026	0.324	0.090	0.580
built-up (GYRATE_AM)	4	-0.135	0.110	-0.351	0.081	0.220	0.580
broadleaf forest (GYRATE_AM)	8	0.142	0.118	-0.090	0.374	0.230	0.420
slope position (FM)	0.5	0.087	0.082	-0.073	0.247	0.290	0.370
agriculture (PD)	32	0.095	0.100	-0.101	0.291	0.340	0.320
land cover (PD)	0.5	-0.043	0.096	-0.233	0.146	0.650	0.330
land cover (CWED)	4	0.041	0.093	-0.142	0.224	0.660	0.350
protected area (FM)	32	-0.037	0.094	-0.221	0.148	0.700	0.270
tree cover (CWED)	0.5	0.023	0.089	-0.151	0.197	0.790	0.280

Leopard cat

Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-0.972	0.087	-1.143	-0.801	0.000	
elevation (FM)	0.5	**-0.716**	**0.095**	**-0.902**	**-0.529**	0.000	1.000
protected area (FM)	4	**0.302**	**0.082**	**0.141**	**0.463**	0.000	1.000
open-forest (GYRATE_AM)	4	**-0.208**	**0.103**	**-0.411**	**-0.005**	0.044	0.740
settlement (FM)	1	0.096	0.077	-0.051	0.248	0.220	0.440
roughness (FM)	8	0.075	0.090	-0.102	0.253	0.410	0.320

river (FM)	2	0.035	0.081	-0.124	0.194	0.670	0.280
non-forest (GYRATE_AM)	0.5	-0.035	0.094	-0.220	0.150	0.710	0.300

Marbled cat							
Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-2.090	0.142	-2.368	-1.812	0.000	
agriculture (PD)	32	**0.295**	**0.123**	**0.053**	**0.536**	0.020	0.850
built-up (PLAND)	8	**-0.517**	**0.205**	**-0.919**	**-0.116**	0.010	0.960
protected area (FM)	4	**0.416**	**0.119**	**0.183**	**0.649**	0.001	0.990
river (FM)	2	**-0.388**	**0.133**	**-0.649**	**-0.127**	0.004	0.980
roughness (FM)	4	**0.483**	**0.100**	**0.286**	**0.680**	0.000	1.000
slope position (FM)	0.5	**0.584**	**0.117**	**0.355**	**0.813**	0.000	1.000
snow cover (PLAND)	0.5	**0.676**	**0.255**	**0.175**	**1.176**	0.008	0.990
tree cover (PD)	2	**-0.539**	**0.124**	**-0.836**	**-0.350**	0.000	1.000
broadleaf forest (PD)	4	-0.182	0.141	-0.459	0.095	0.200	0.460
closed forest (GYRATE_AM)	16	-0.134	0.138	-0.404	0.136	0.330	0.350
closed forest (PD)	32	0.059	0.116	-0.169	0.287	0.610	0.280
open forest (GYRATE_AM)	32	-0.031	0.110	-0.246	0.184	0.780	0.300

Masked palm civet							
Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-2.245	0.180	-2.598	-1.892	0.000	
conifer forest (PLAND)	8	**-1.848**	**0.210**	**-2.261**	**-1.436**	0.000	1.000
road (FM)	2	0.056	0.083	-0.106	0.219	0.500	0.320
roughness (FM)	8	0.045	0.110	-0.171	0.260	0.690	0.290
broadleaf forest (PD)	0.5	0.021	0.137	-0.249	0.290	0.880	0.270

Muntjac							
Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		0.377	0.079	0.221	0.532	0.000	
broadleaf forest (PLAND)	2	**0.919**	**0.110**	**0.703**	**1.136**	0.000	1.000
road (FM)	4	0.156	0.084	-0.009	0.321	0.064	0.710
slope position (FM)	32	-0.155	0.089	-0.329	0.020	0.082	0.650
open-forest (GYRATE_AM)	0.5	-0.143	0.085	-0.310	0.023	0.092	0.600
meadow (PD)	0.5	-0.090	0.089	-0.265	0.084	0.310	0.390
agriculture (PD)	32	0.112	0.114	-0.112	0.335	0.320	0.350

Sambar							
Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-0.433	0.076	-0.583	-0.284	0.000	
built-up (GYRATE_AM)	4	**0.187**	**0.088**	**0.014**	**0.359**	0.033	0.720
elevation (FM)	4	**-0.496**	**0.092**	**-0.678**	**-0.315**	0.000	1.000
meadow (PD)	0.5	**-0.261**	**0.093**	**-0.443**	**-0.079**	0.005	0.940

river (FM)	32	0.125	0.081	-0.033	0.284	0.120	0.560
settlement (FM)	2	0.112	0.083	-0.051	0.276	0.180	0.460
road (FM)	4	0.137	0.094	-0.048	0.321	0.150	0.550
slope position (FM)	32	-0.107	0.081	-0.266	0.052	0.190	0.440
open forest (GYRATE_AM)	0.5	-0.085	0.081	-0.245	0.074	0.300	0.380
non forest (GYRATE_AM)	0.5	-0.082	0.088	-0.255	0.090	0.350	0.370
built-up (PD)	32	0.090	0.100	-0.107	0.287	0.370	0.380
agriculture (PD)	32	-0.043	0.084	-0.208	0.121	0.610	0.290

Tiger

Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-2.034	0.127	-2.283	-1.785	0.000	
agriculture (PD)	4	**-0.309**	**0.139**	**-0.583**	**-0.035**	0.030	0.890
broadleaf forest (PD)	32	**-0.371**	**0.137**	**-0.640**	**-0.101**	0.007	0.840
meadow (PD)	16	**-0.344**	**0.128**	**-0.596**	**-0.093**	0.007	0.830
protected area (FM)	32	**0.493**	**0.124**	**0.249**	**0.736**	0.000	1.000
river (FM)	32	**0.239**	**0.110**	**0.023**	**0.455**	0.030	0.810
open-forest (GYRATE_AM)	16	**0.270**	**0.109**	**0.056**	**0.484**	0.010	0.890
roughness (FM)	1	-0.101	0.105	-0.307	0.106	0.340	0.380
compound topographic index (FM)	2	0.069	0.095	-0.118	0.256	0.470	0.370
tree cover (CWED)	32	-0.099	0.158	-0.409	0.211	0.530	0.430

Wild pig

Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-0.143	0.076	-0.292	0.006	0.060	
agriculture (PD)	32	-0.234	0.141	-0.511	0.042	0.100	0.540
bare area (GYRATE_AM)	8	**-0.222**	**0.098**	**-0.414**	**-0.030**	0.020	0.870
broadleaf forest (GYRATE_AM)	2	**0.369**	**0.124**	**0.126**	**0.612**	0.003	0.980
protected area (FM)	32	**-0.253**	**0.105**	**-0.460**	**-0.046**	0.020	0.840
river (FM)	16	**-0.289**	**0.080**	**-0.447**	**-0.132**	0.000	1.000
road (FM)	32	**0.300**	**0.118**	**0.069**	**0.531**	0.010	0.930
roughness (FM)	32	**0.300**	**0.082**	**0.139**	**0.460**	0.000	1.000
slope position (FM)	32	**-0.307**	**0.096**	**-0.496**	**-0.119**	0.001	0.980
agriculture (GYRATE_AM)	8	0.116	0.087	-0.054	0.286	0.180	0.530
non-forest (PD)	0.5	-0.074	0.082	-0.234	0.086	0.370	0.340
open-forest (GYRATE_AM)	0.5	-0.068	0.080	-0.226	0.089	0.400	0.320

Yellow-throated marten

Covariates	**scale (km)**	**mean**	**SE**	**LCI**	**UCI**	***p***	**SMW**
Intercept		-0.567	0.078	-0.719	-0.414	0.000	
agriculture (GYRATE_AM)	16	-0.166	0.096	-0.356	0.023	0.085	0.620

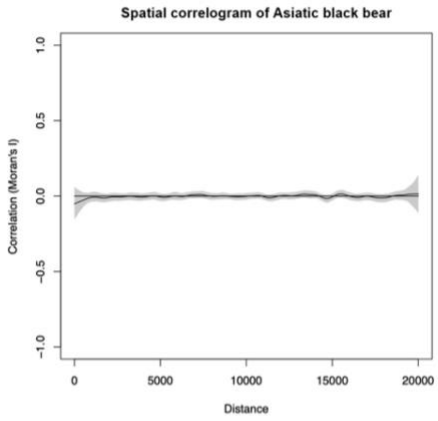
broadleaf forest (PLAND)	16	**0.290**	**0.094**	**0.105**	**0.474**	0.002	0.880
compound topographic index (FM)	2	**-0.234**	**0.103**	**-0.435**	**-0.032**	0.023	0.880
land cover (CWED)	0.5	**-0.166**	**0.084**	**-0.331**	**0.002**	0.050	0.700
roughness (FM)	4	**0.247**	**0.084**	**0.082**	**0.412**	0.003	0.970
slope position (FM)	4	0.094	0.082	-0.066	0.255	0.250	0.420
river (FM)	0.5	-0.108	0.095	-0.293	0.078	0.260	0.420
broadleaf forest (PD)	0.5	0.065	0.090	-0.111	0.242	0.470	0.340
closed forest (PLAND)	32	0.085	0.114	-0.140	0.309	0.460	0.390
conifer forest (PD)	0.5	-0.028	0.122	-0.227	0.171	0.780	0.330

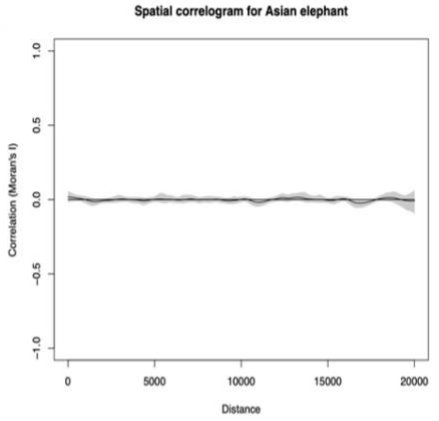
SE = standard error; LCI = lower 95% confidence interval; UCL = upper 95 %confidence interval; p = p-value; SMW = summed model weight; GYRATE_AM: radius of gyration area weighted mean; FM = focal mean; PLAND = percentage of land; CWED = contrast weighted edge density; PD = patch density

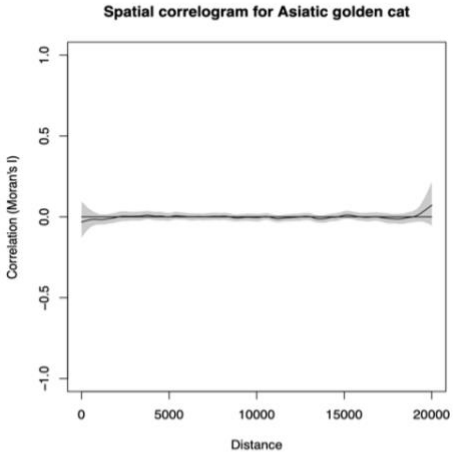
Table S4. Percentage of variables selected at different scales across all 16 species.

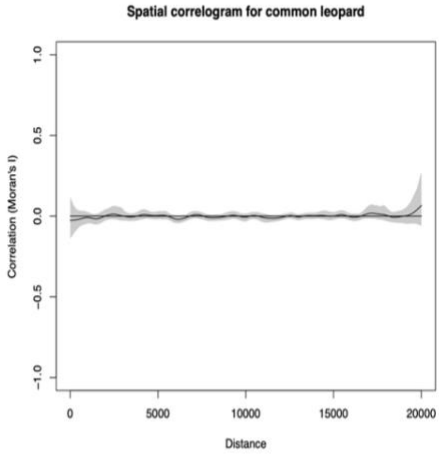
Scale (km)	Number of variables across all species	% in each scale	% in scale category[§]
0.5	27	17.42	
1	6	3.87	30.97
2	15	9.68	
4	29	18.71	30.32
8	18	11.61	
16	16	10.32	38.71
32	44	28.39	

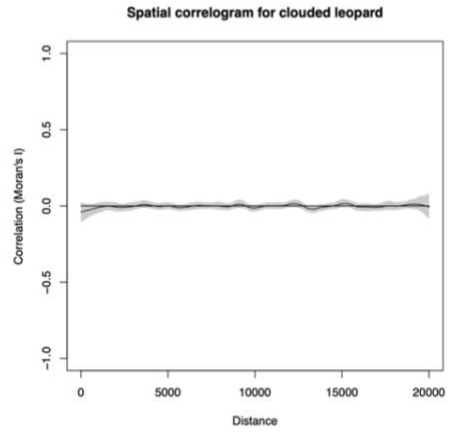
§ *small (500m, 1km and 2km); medium (4km and 8km); broad (16km and 32km)*

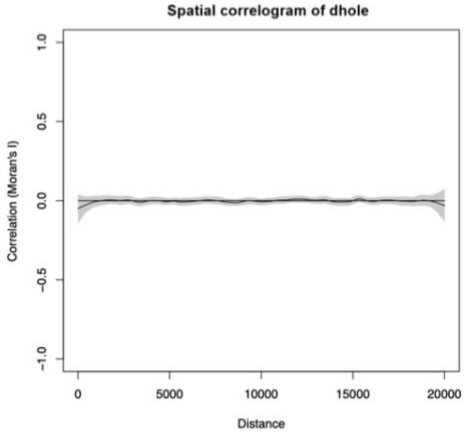

Spatial correlogram of Asiatic black bear
Correlation (Moran's I)
1.0
0.5
0.0
−0.5
−1.0
0
5000
10000
15000
20000
Distance

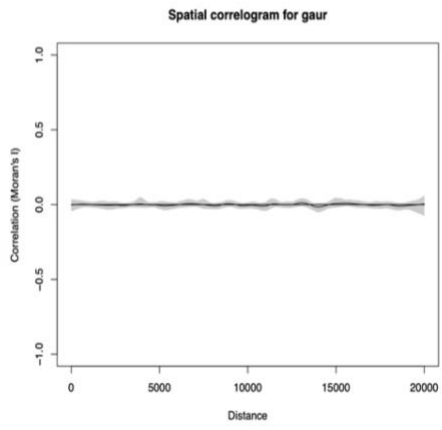

Spatial correlogram for Asian elephant
Correlation (Moran's I)
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0.5
0.0
−0.5
−1.0
0
5000
10000
15000
20000
Distance

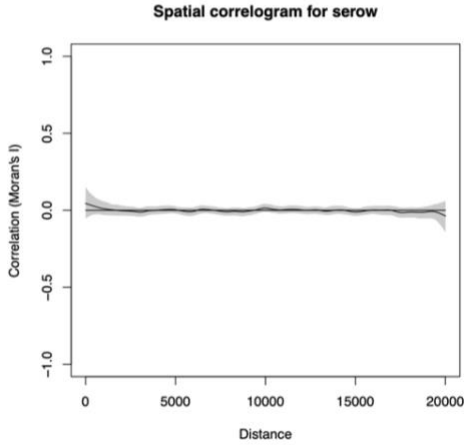

Spatial correlogram for Asiatic golden cat
Correlation (Moran's I)
1.0
0.5
0.0
−0.5
−1.0
0
5000
10000
15000
20000
Distance


Spatial correlogram for common leopard
Correlation (Moran's I)
1.0
0.5
0.0
−0.5
−1.0
0
5000
10000
15000
20000
Distance


Spatial correlogram for clouded leopard
Correlation (Moran's I)
1.0
0.5
0.0
−0.5
−1.0
0
5000
10000
15000
20000
Distance


Spatial correlogram of dhole
Correlation (Moran's I)
1.0
0.5
0.0
−0.5
−1.0
0
5000
10000
15000
20000
Distance


Spatial correlogram for gaur
Correlation (Moran's I)
1.0
0.5
0.0
−0.5
−1.0
0
5000
10000
15000
20000
Distance


Spatial correlogram for serow
Correlation (Moran's I)
1.0
0.5
0.0
−0.5
−1.0
0
5000
10000
15000
20000
Distance

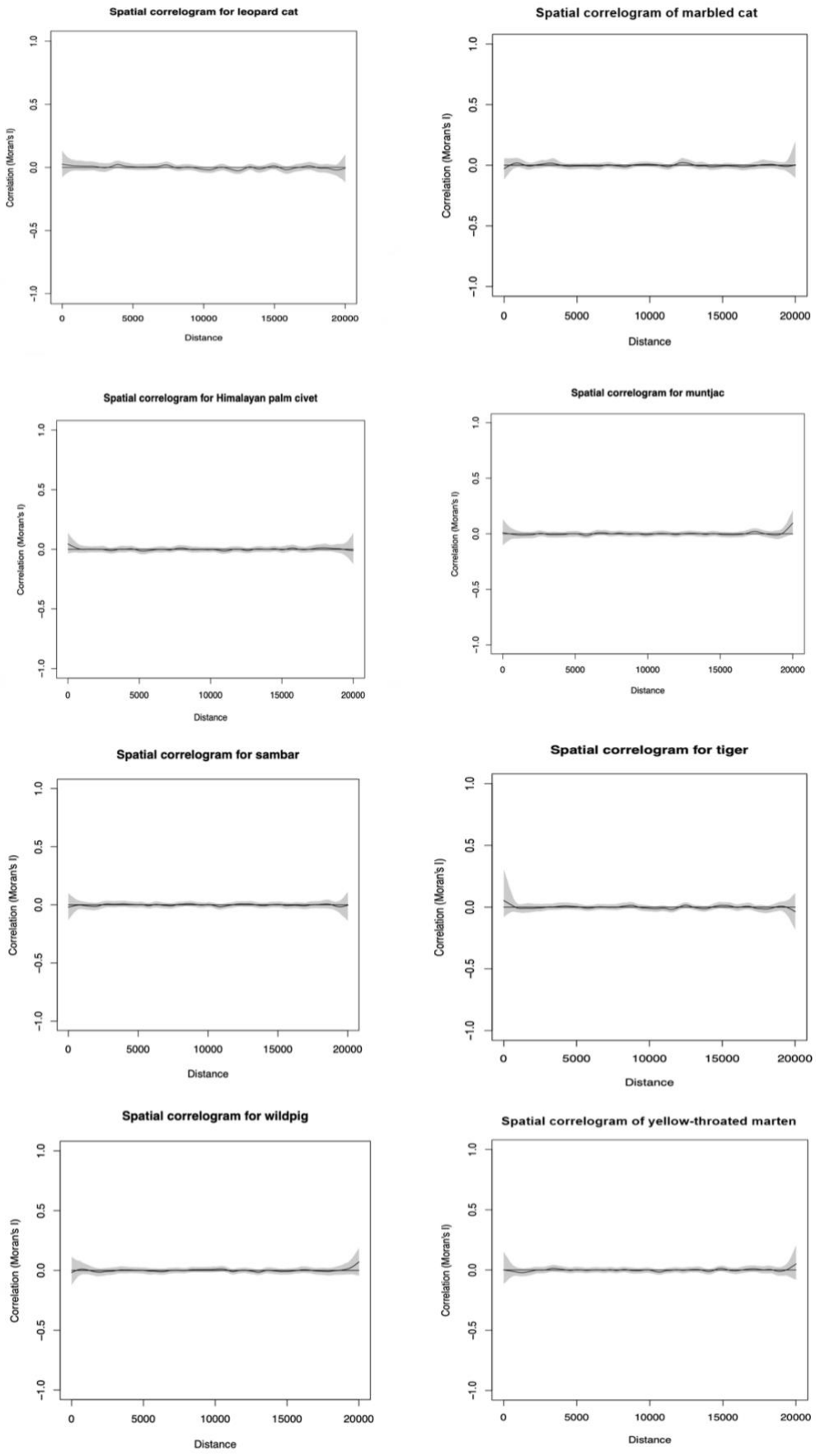


Figure S1. Spatial correlograms for the 16 study species

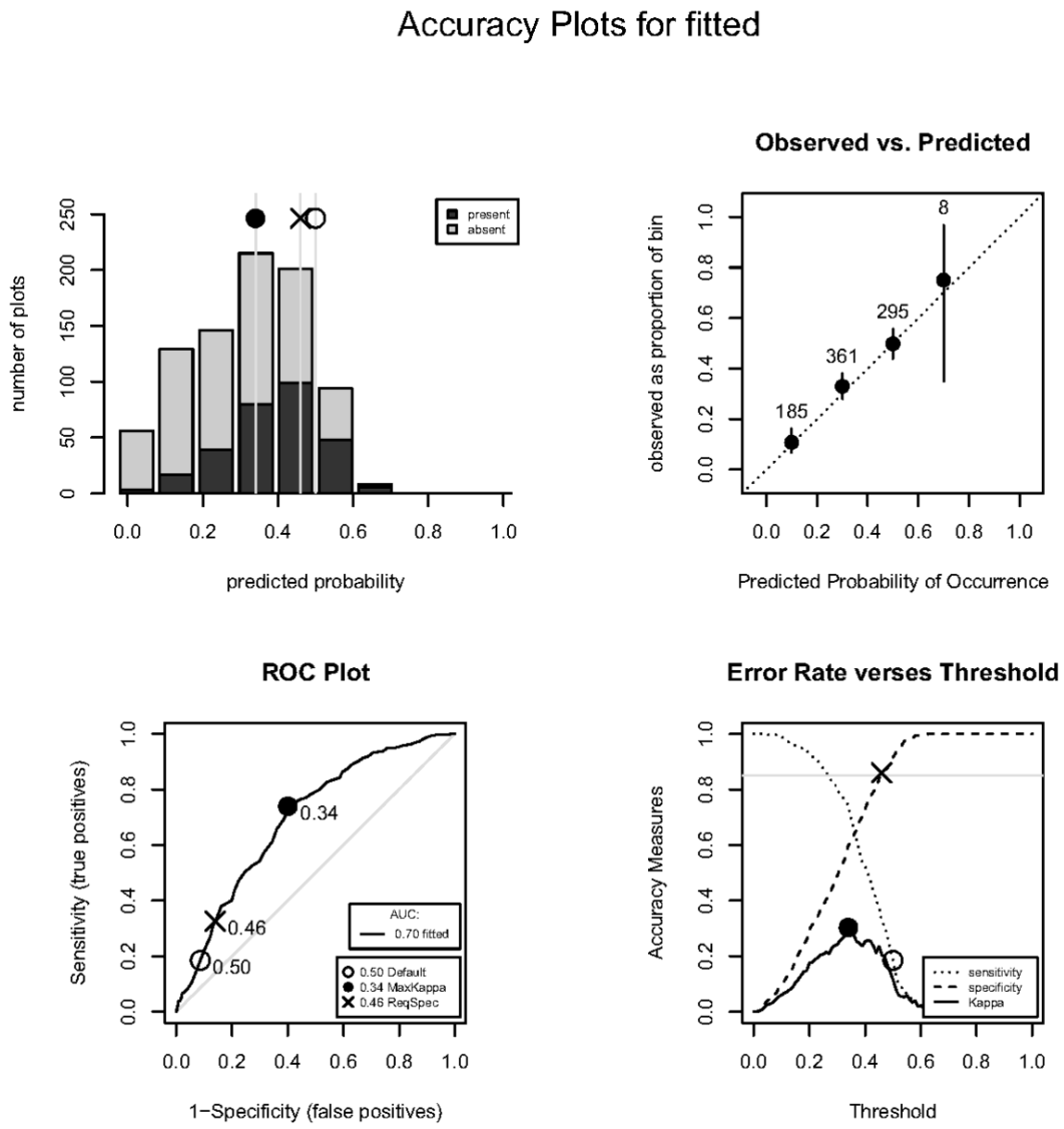


Figure S2. Model validation results for Asiatic black bear

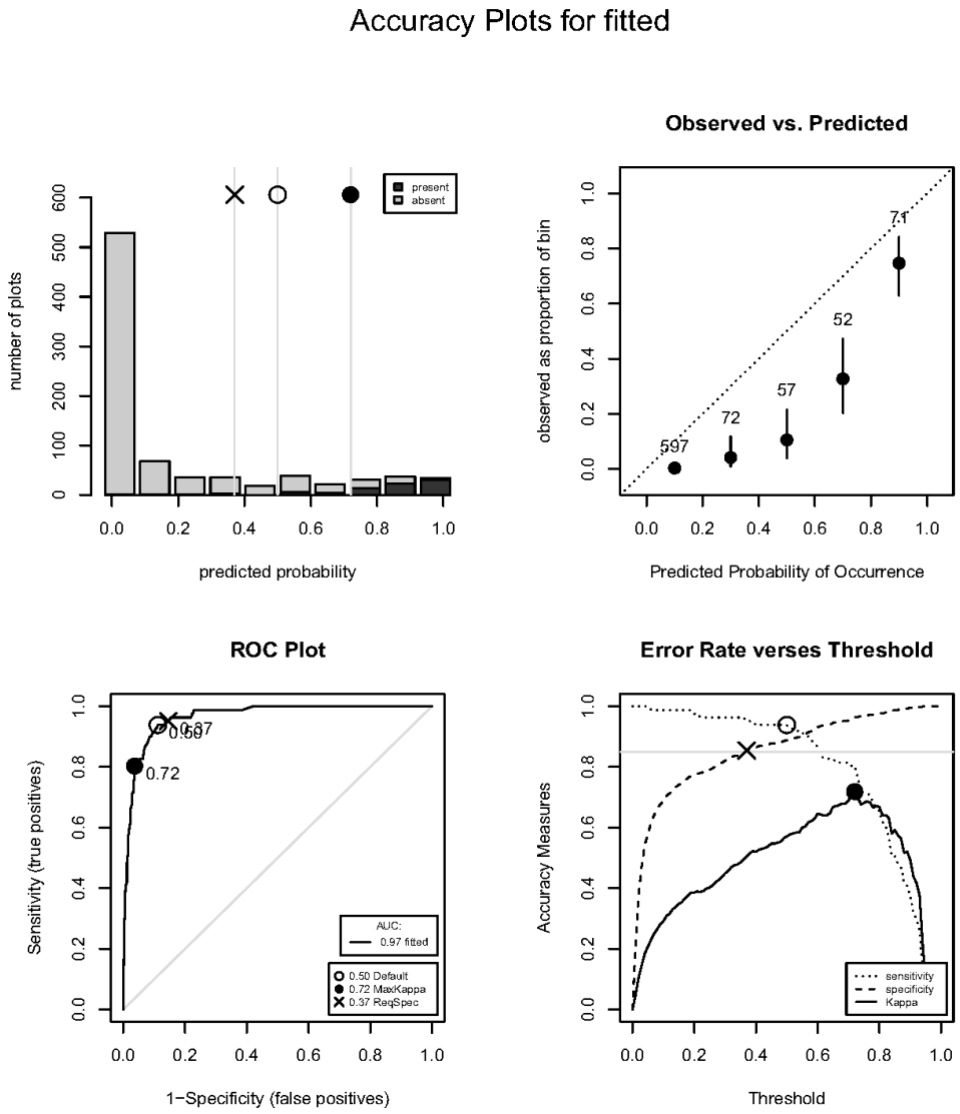


Figure S3. Model validation results for Asian elephant

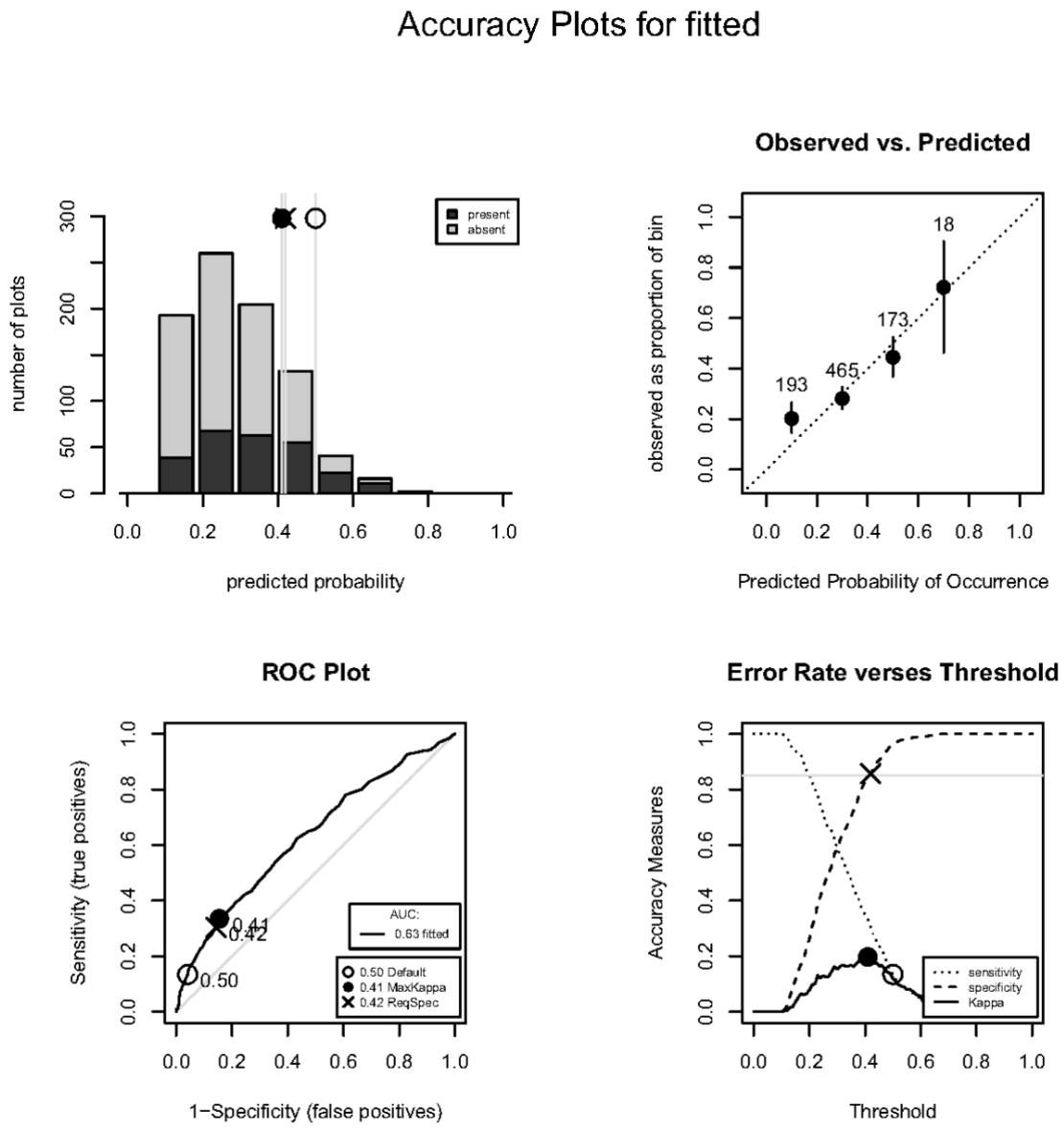


Figure S4. Model validation results for Asiatic golden cat

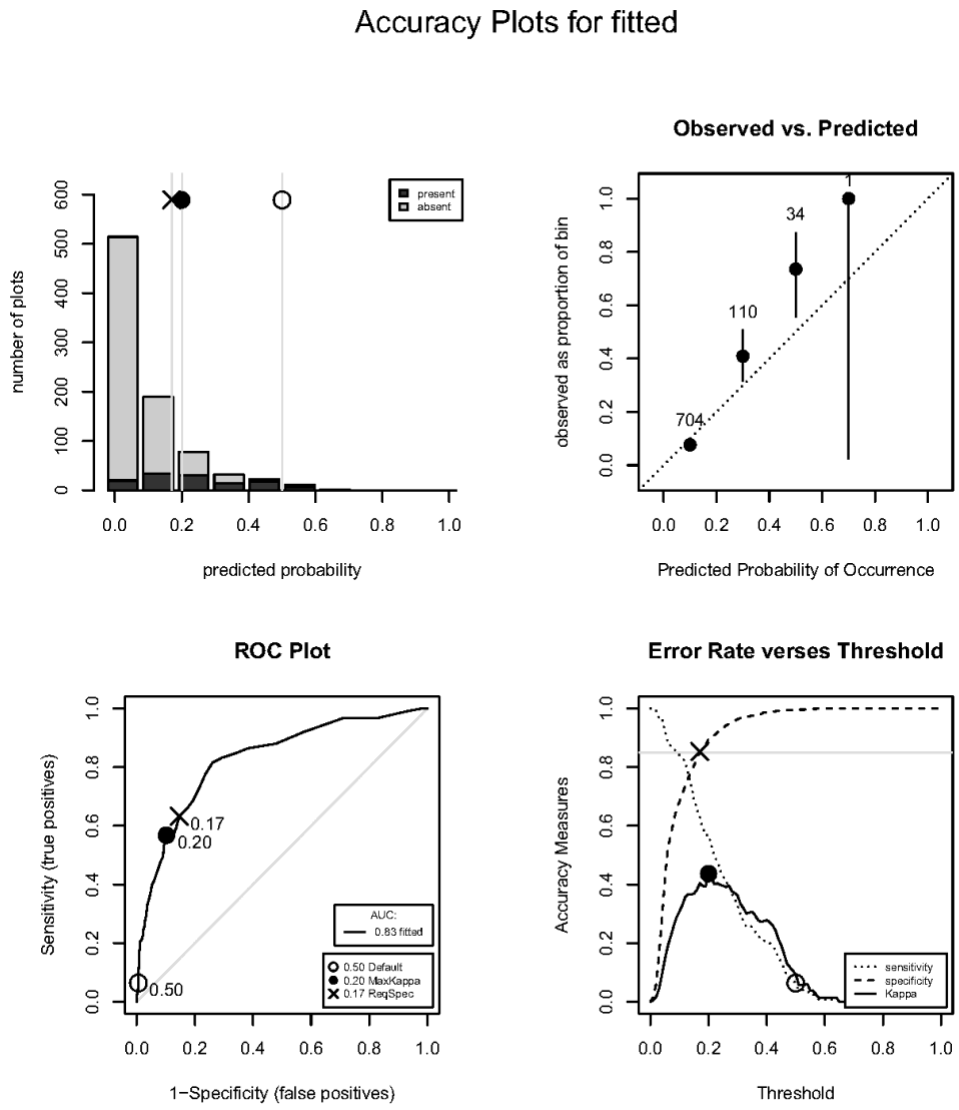


Figure S5. Model validation results for common leopard

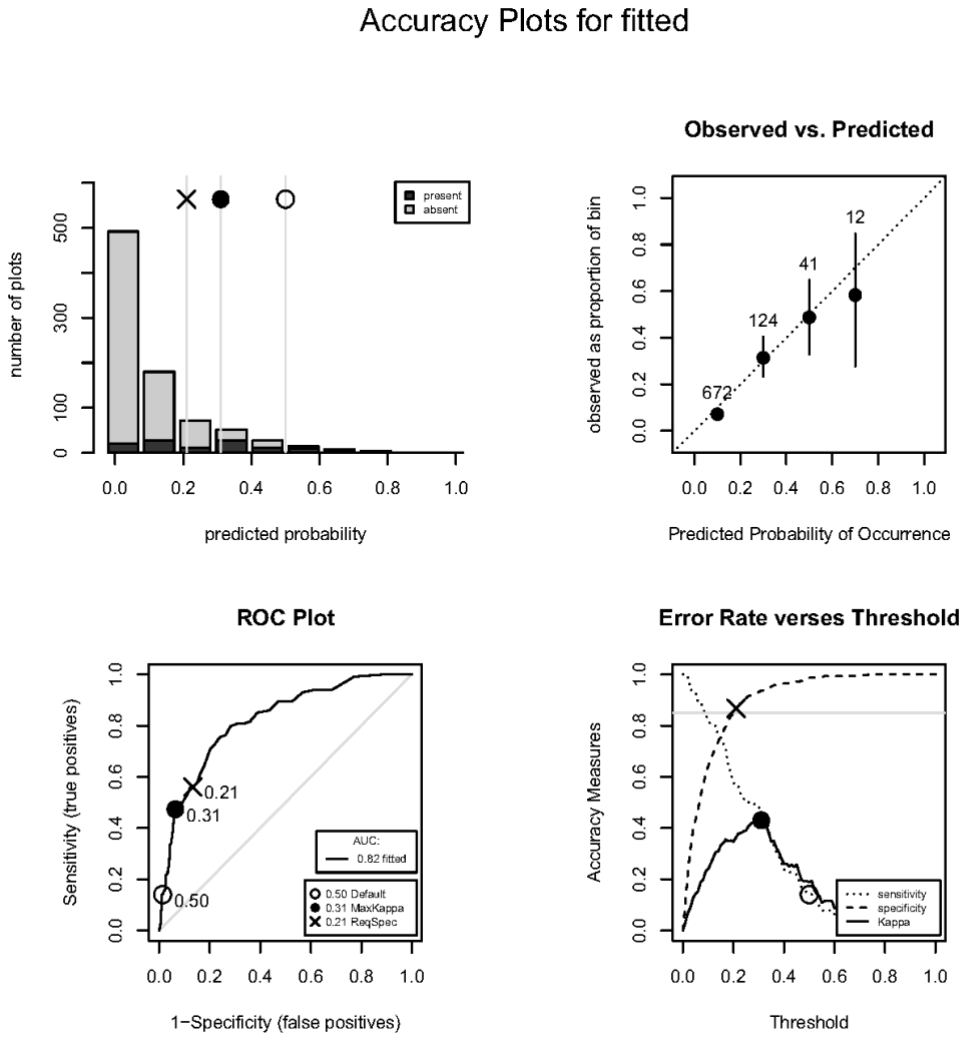


Figure S6. Model validation results for clouded leopard

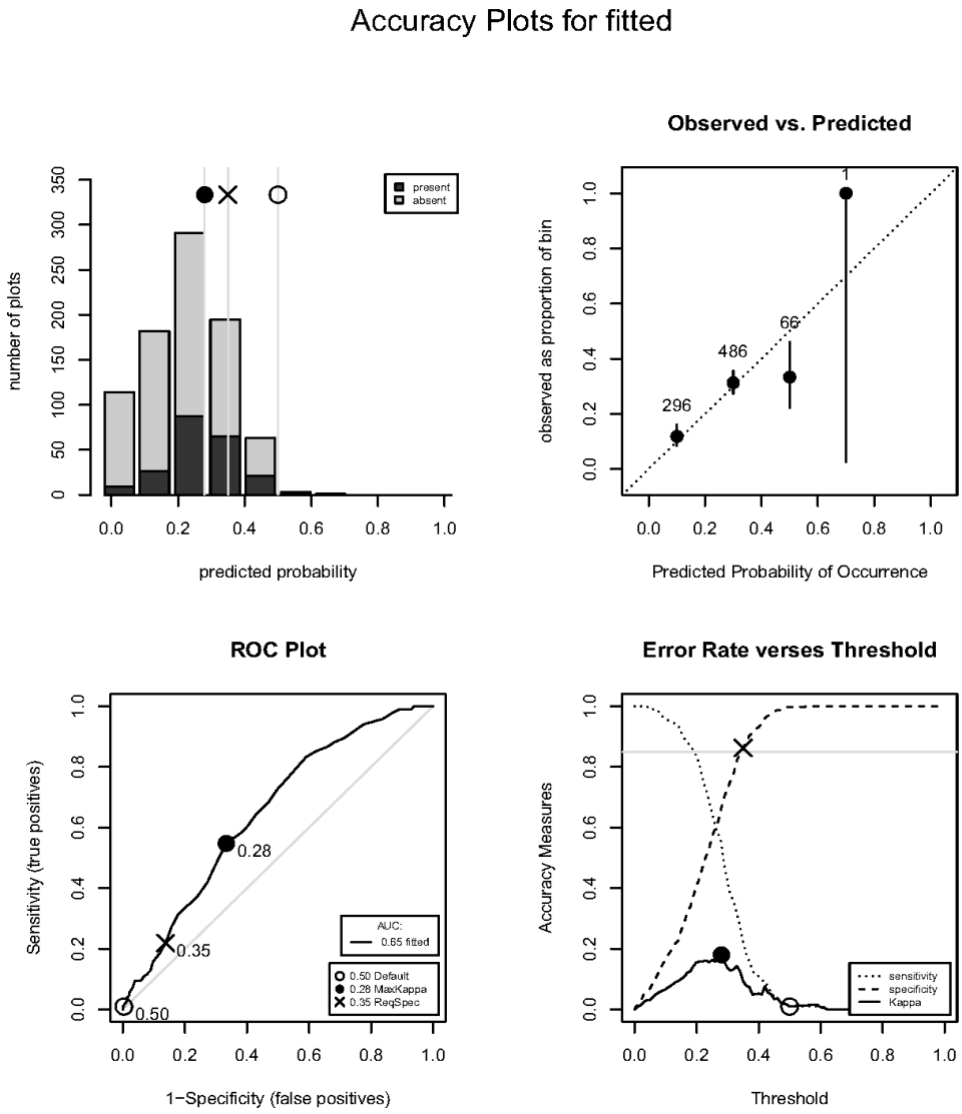


Figure S7. Model validation results for dhole

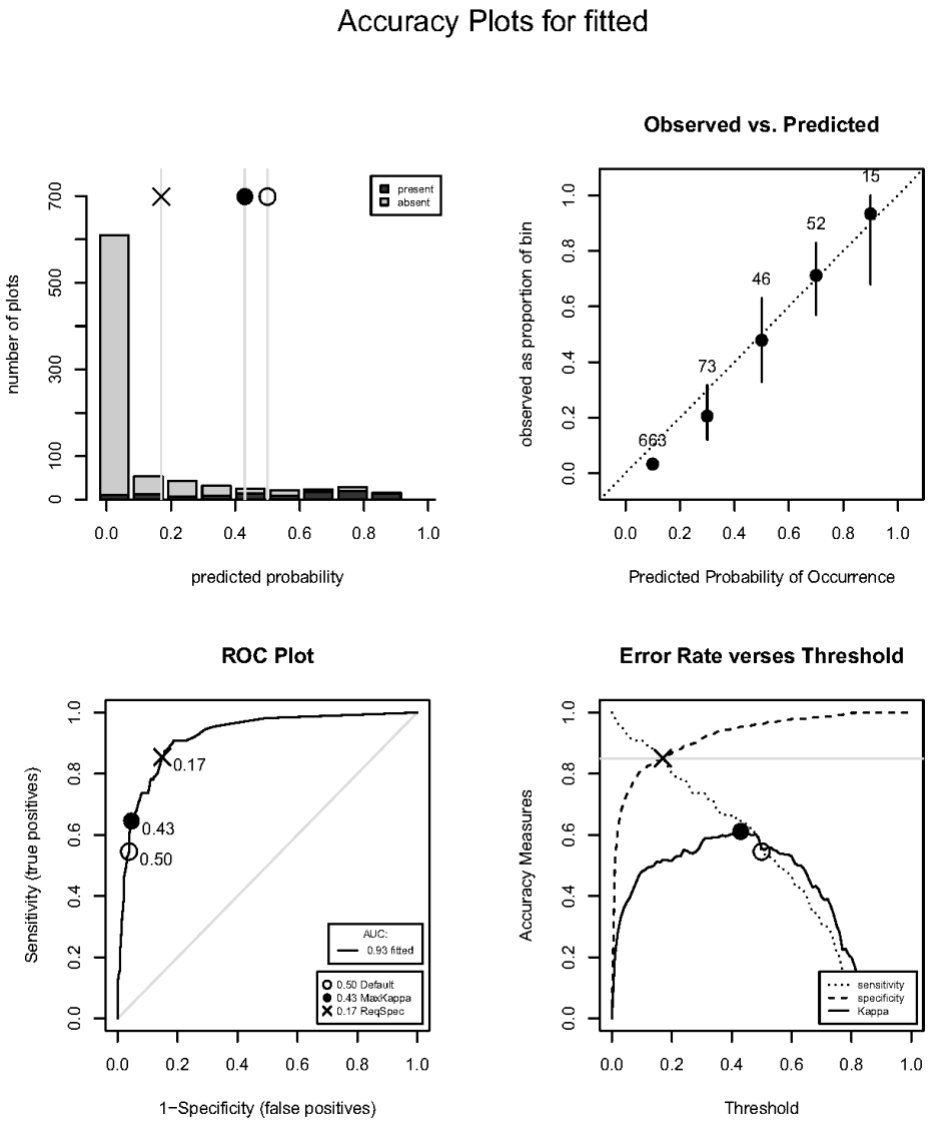


Figure S8. Model validation results for gaur

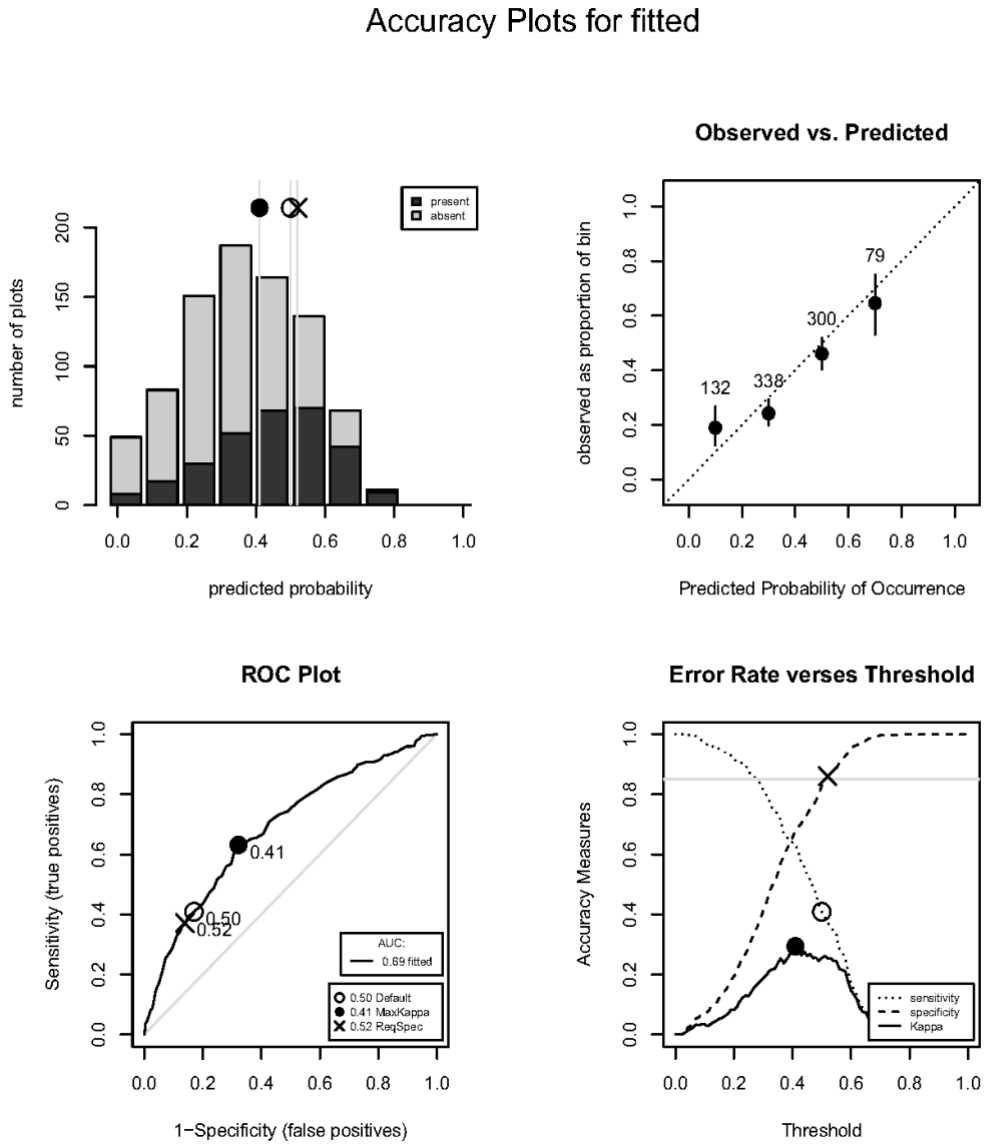


Figure S9. Model validation results for Himalayan serow

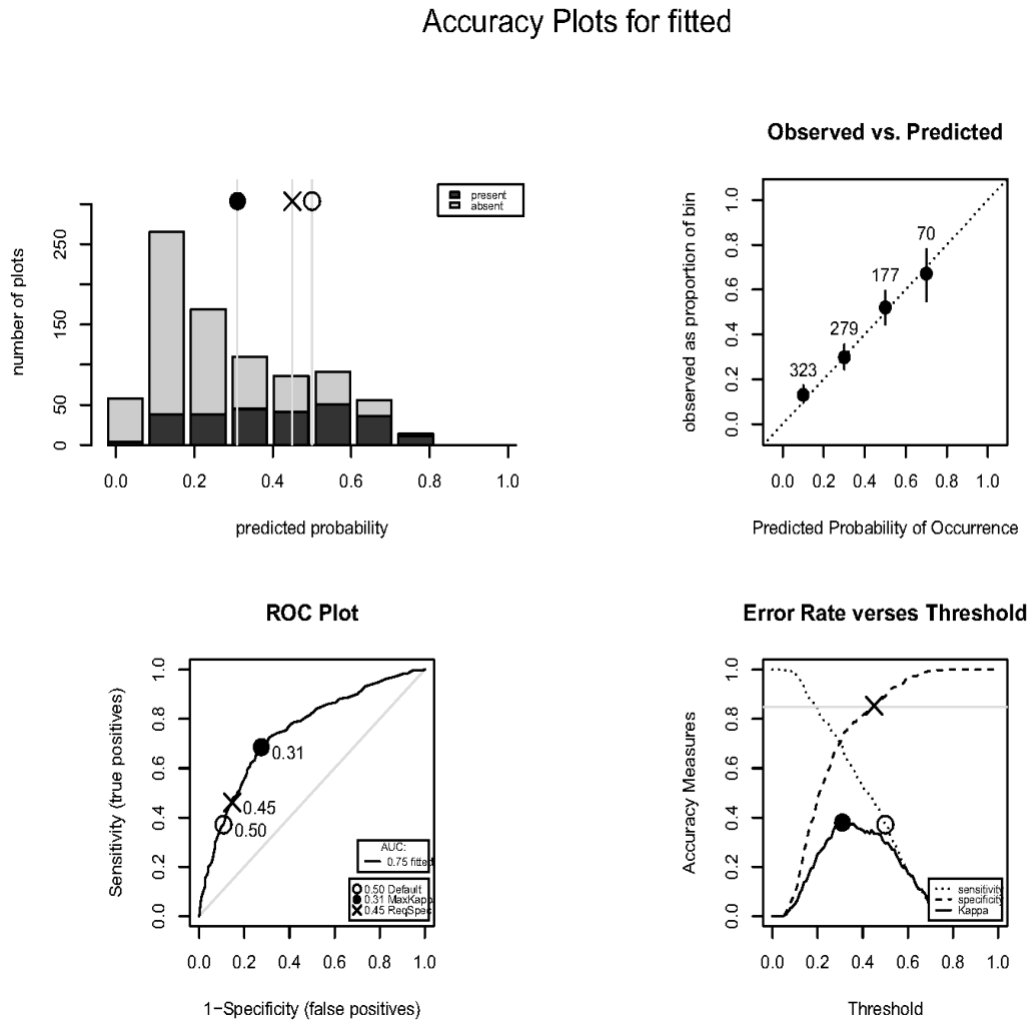


Figure S10. Model validation results for leopard cat

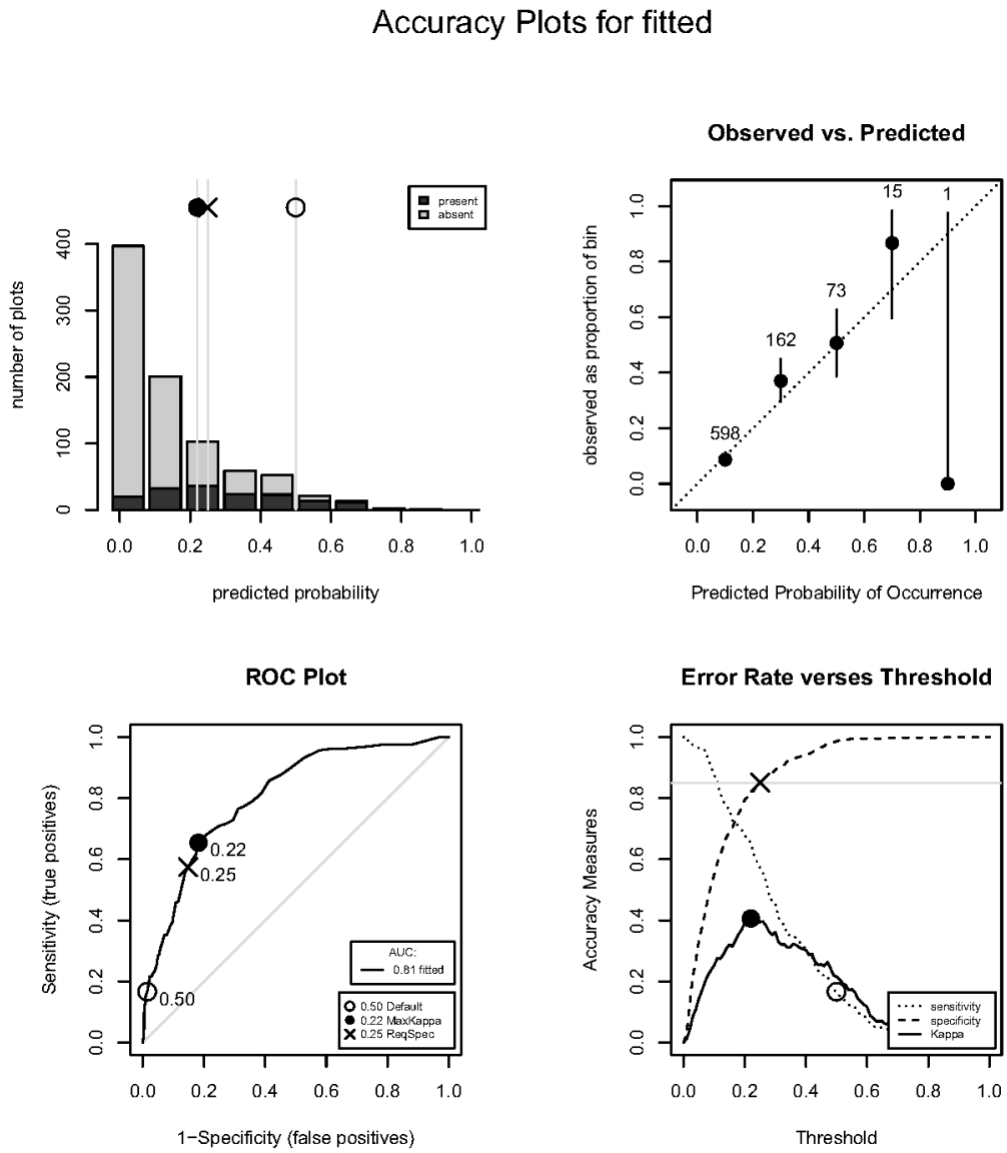


Figure S11. Model validation results for marbled cat

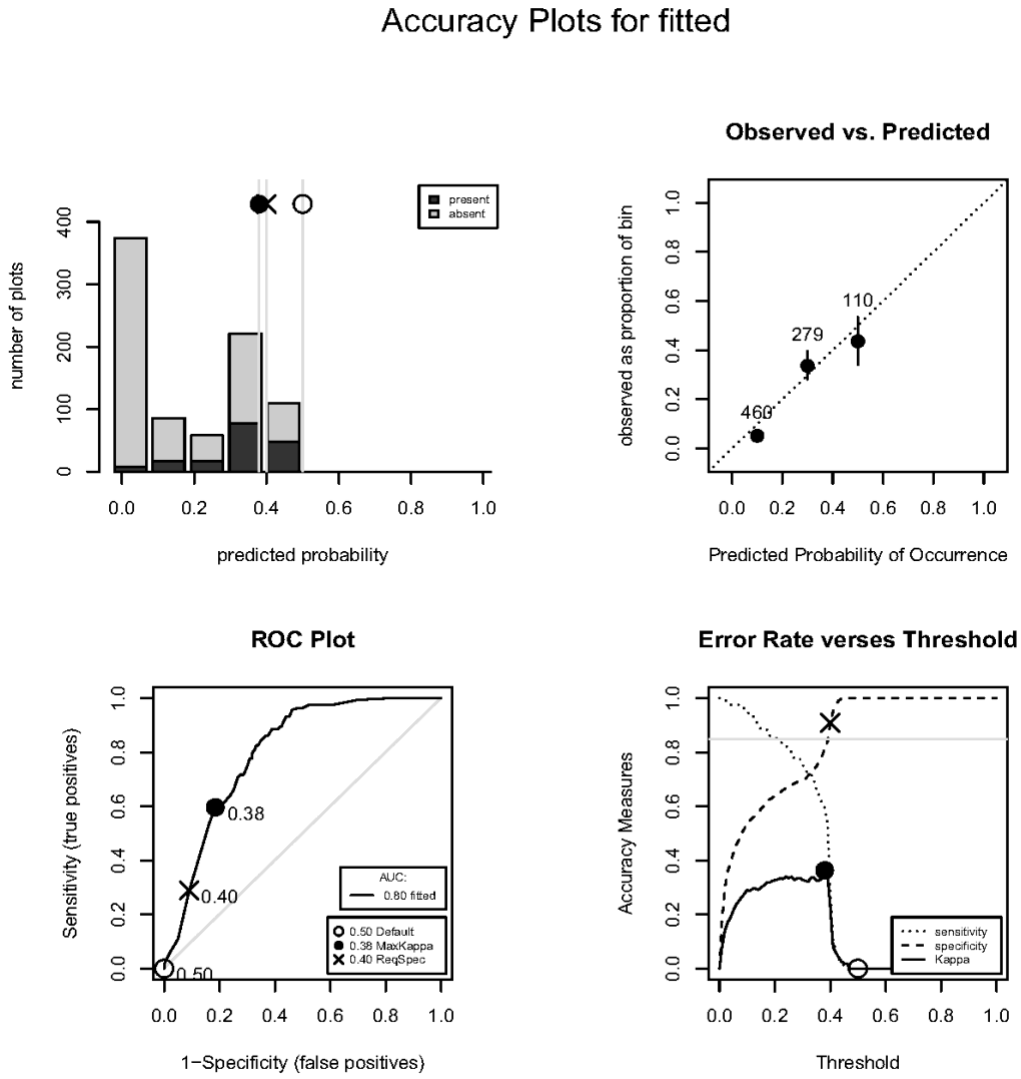


Figure S12. Model validation results for masked palm civet

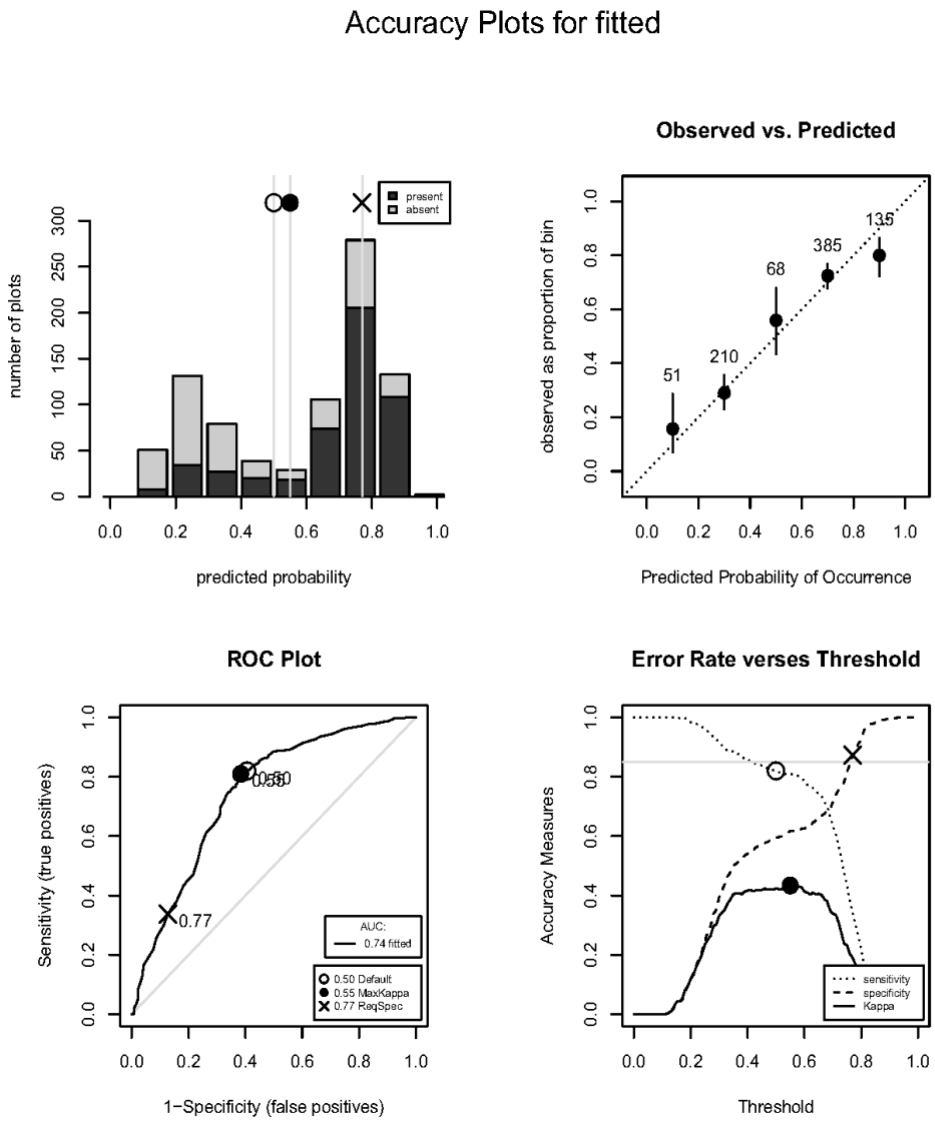


Figure S13. Model validation results for muntjac

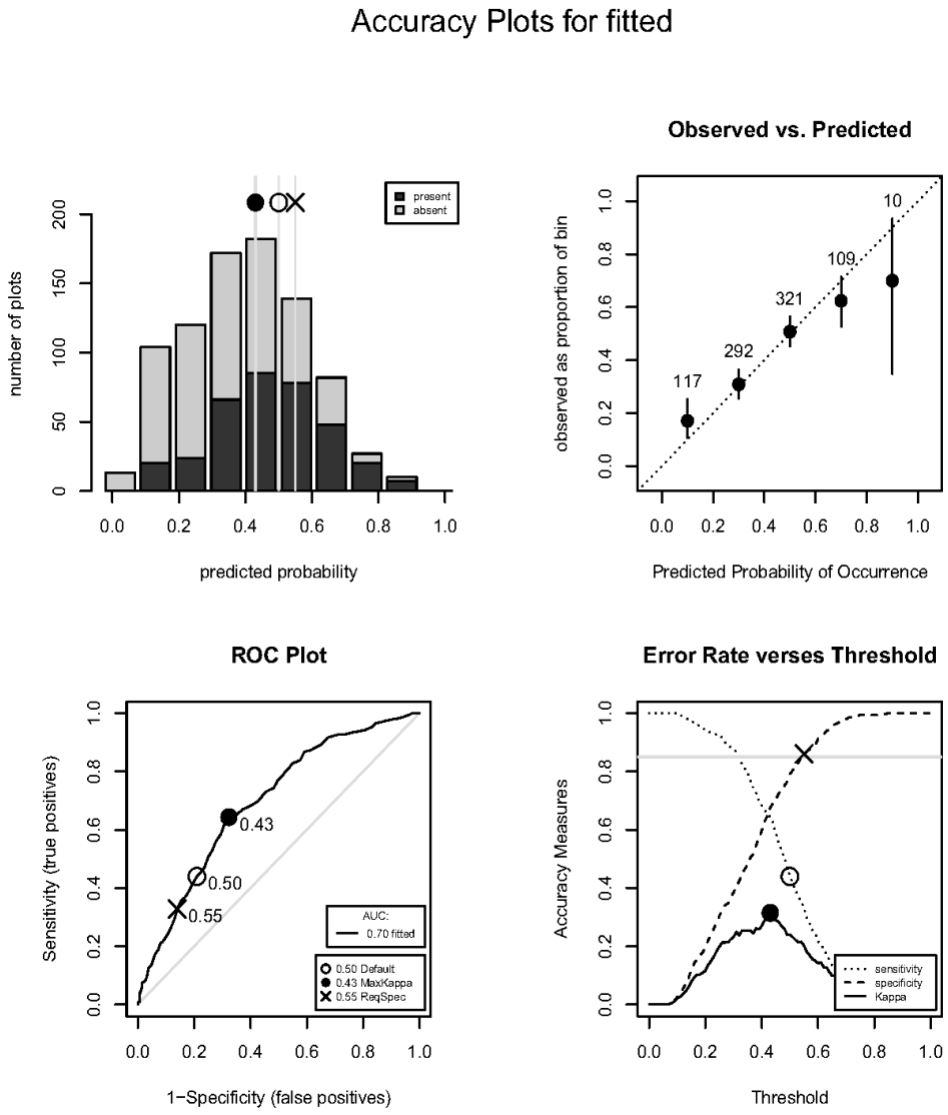


Figure S14. Model validation results for sambar

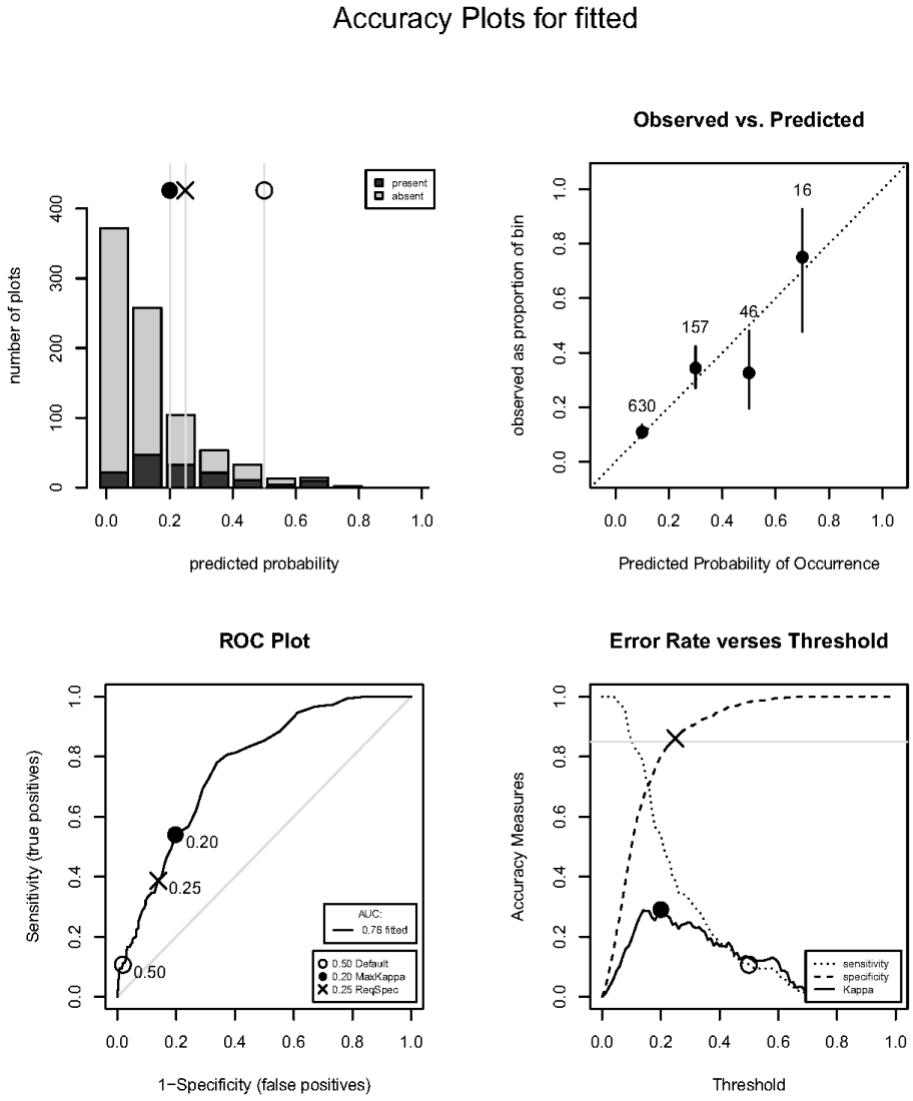


Figure S15. Model validation results for tiger

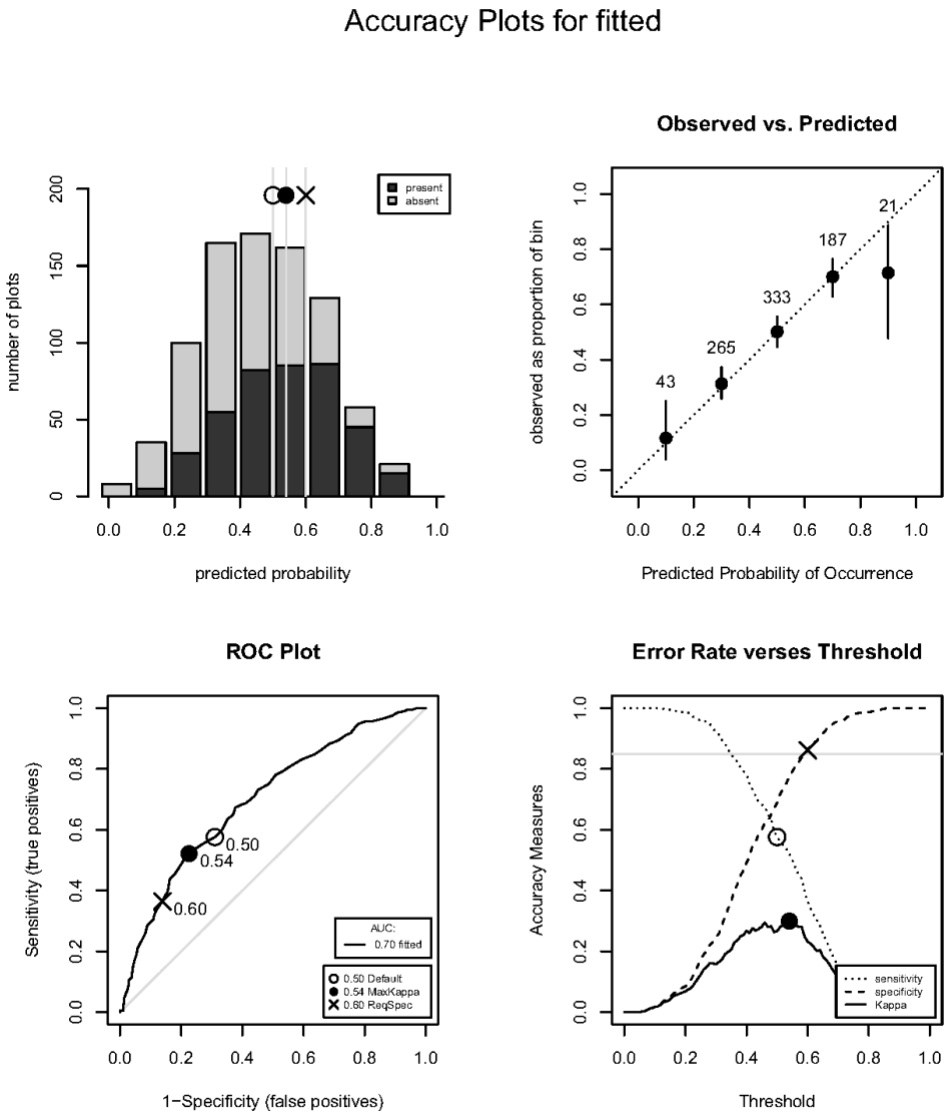


Figure S6. Model validation results for wild pig

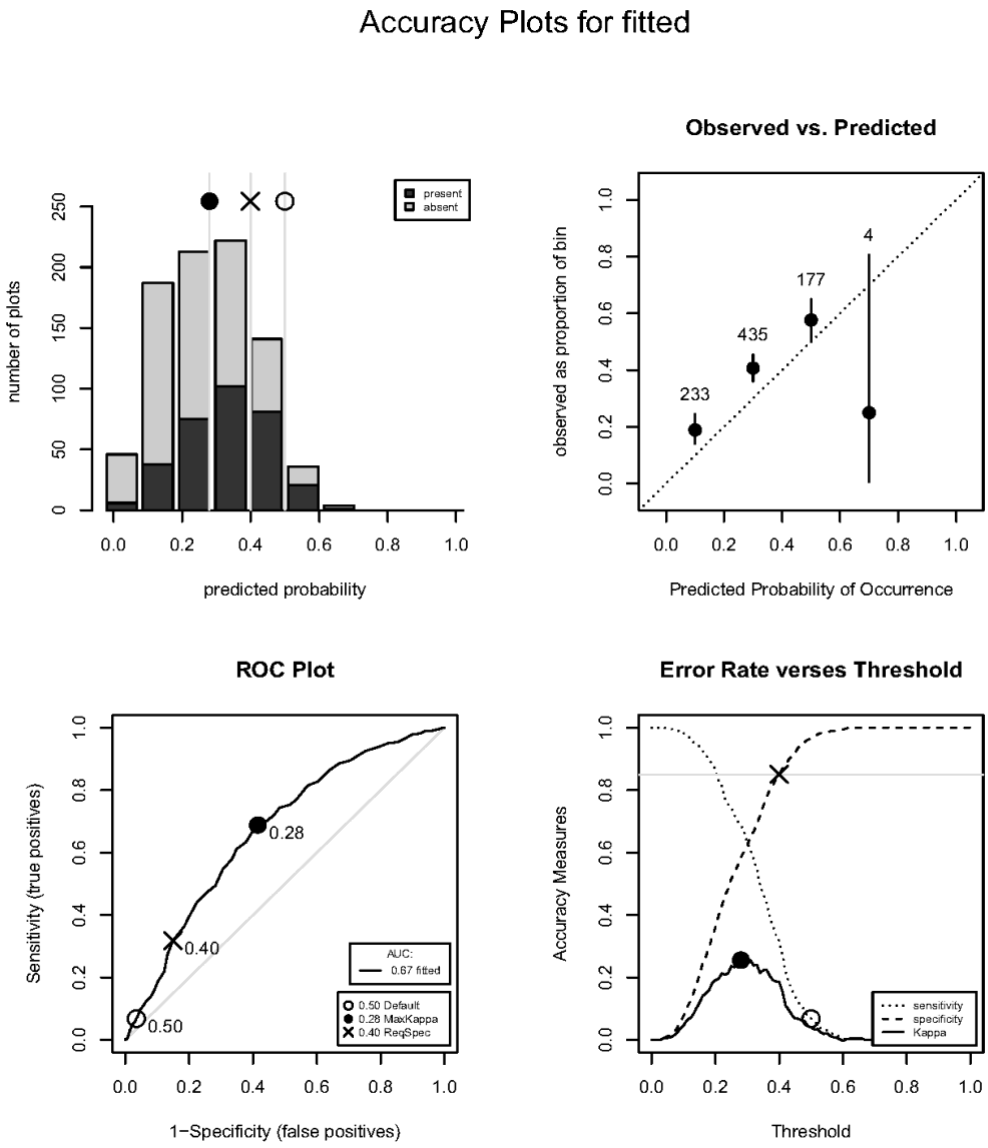
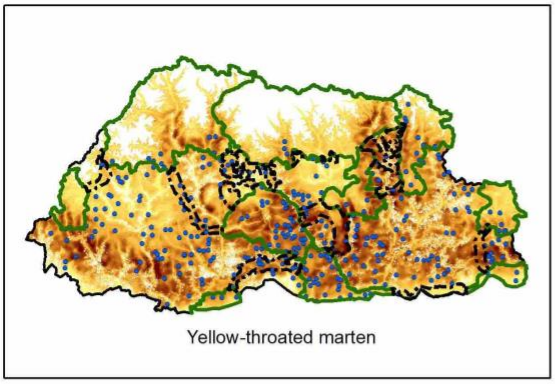
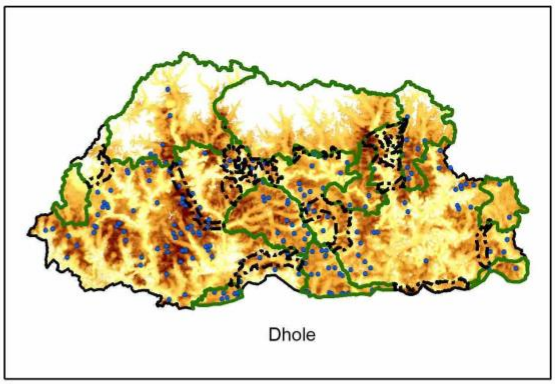


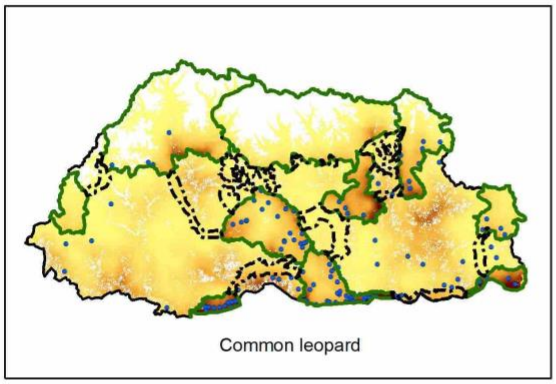
Figure S17. Model validation results for yellow-throated marten



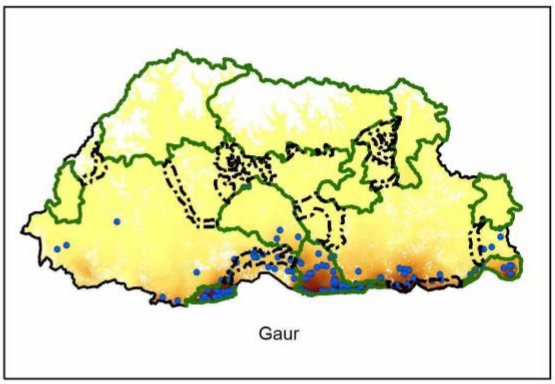
Yellow-throated marten



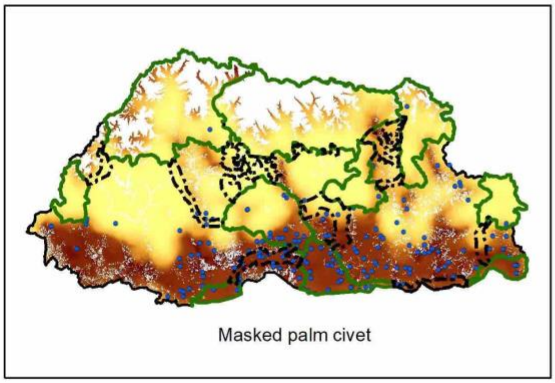
Dhole



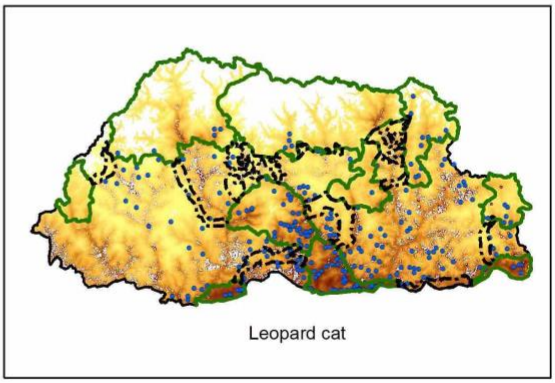
Common leopard



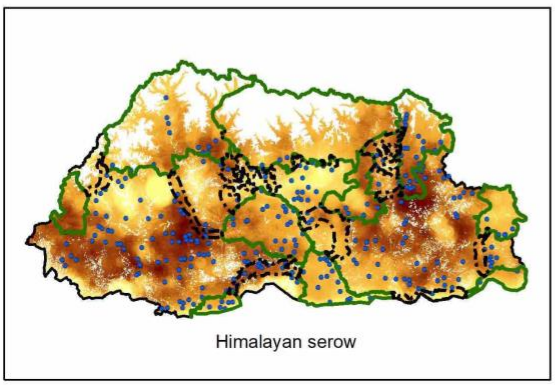
Gaur



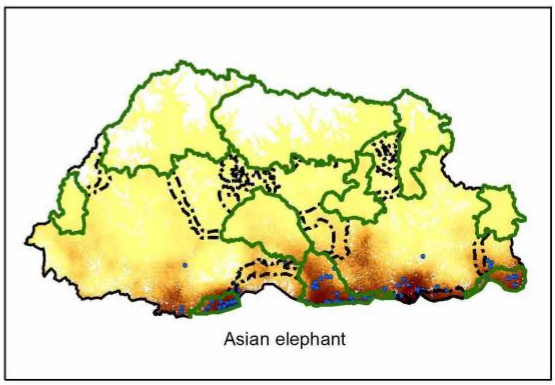
Masked palm civet



Leopard cat



Himalayan serow



Asian elephant

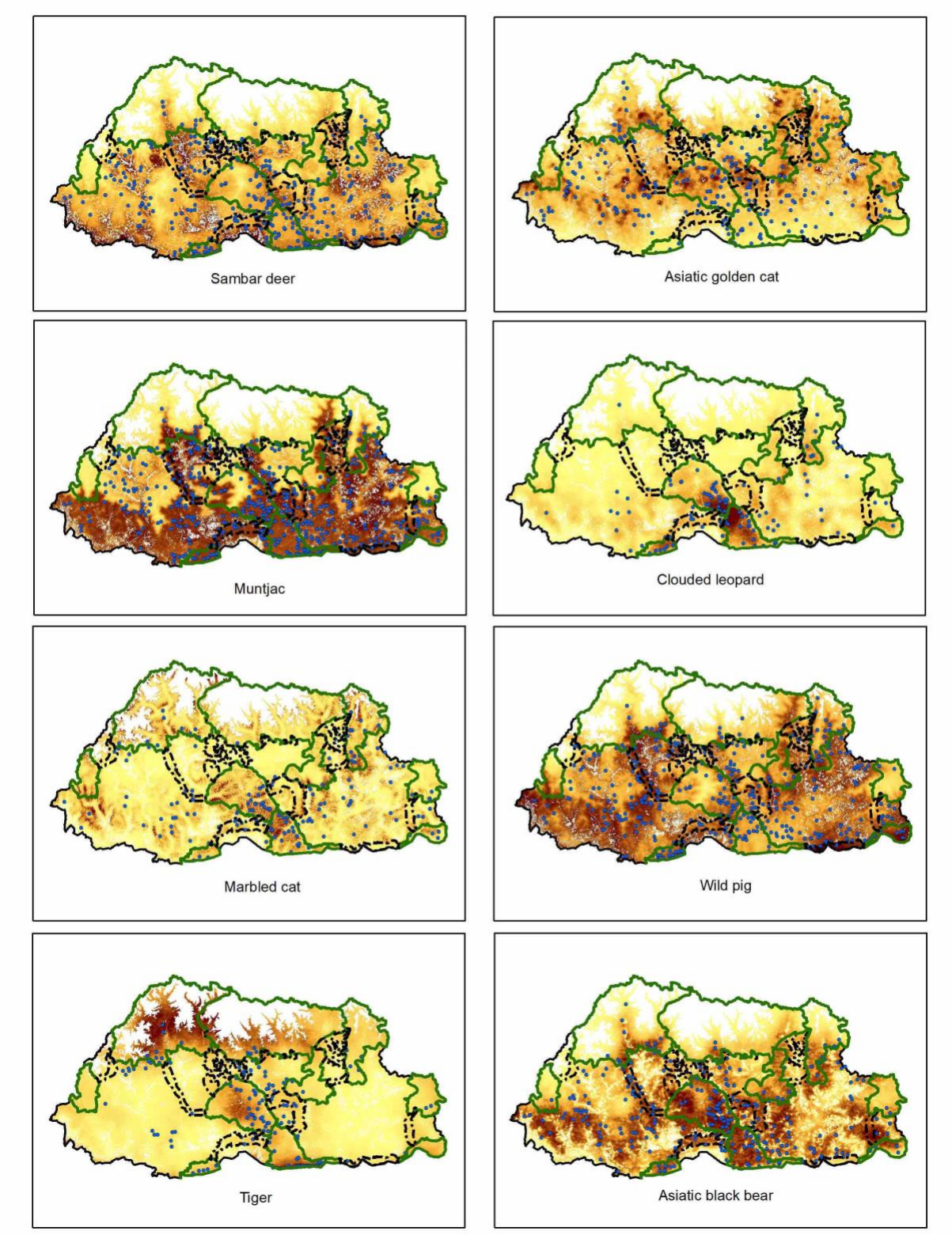


Figure S18. Predicted probabilities of habitat use for the sixteen study species. Higher probabilities represented by darker shade. Green polygons are protected areas, black, dotted-

dashed polygons are biological corridors and blue points represent species capture locations. The white patch represents areas above 4500m and human settlement

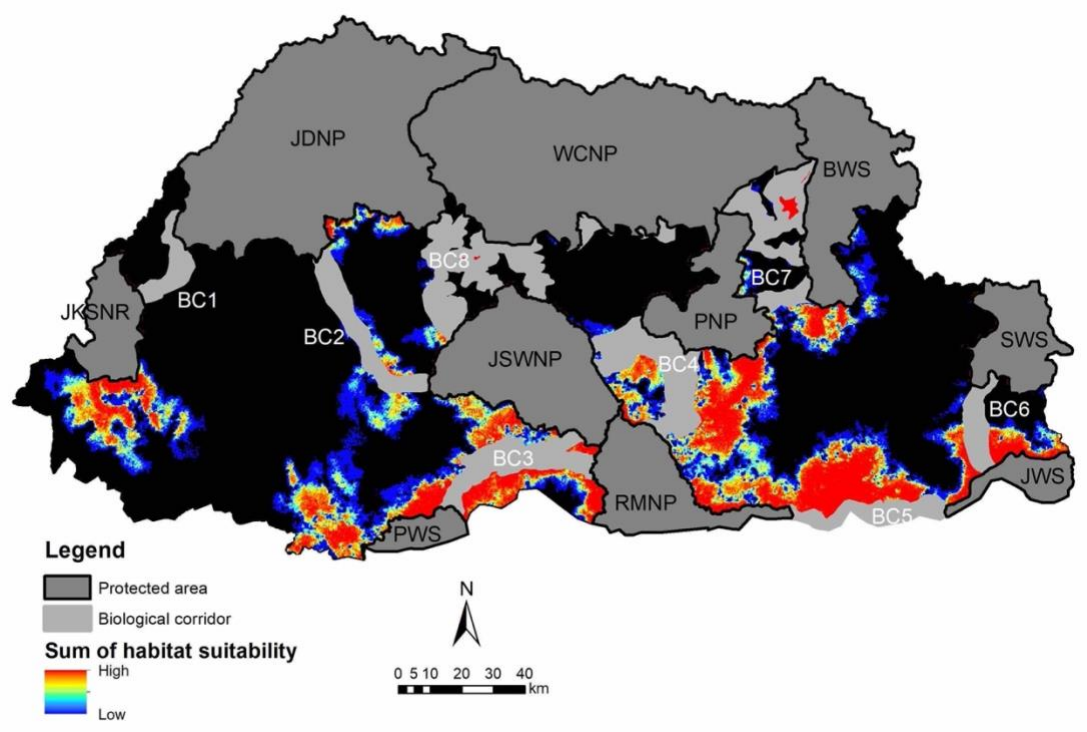
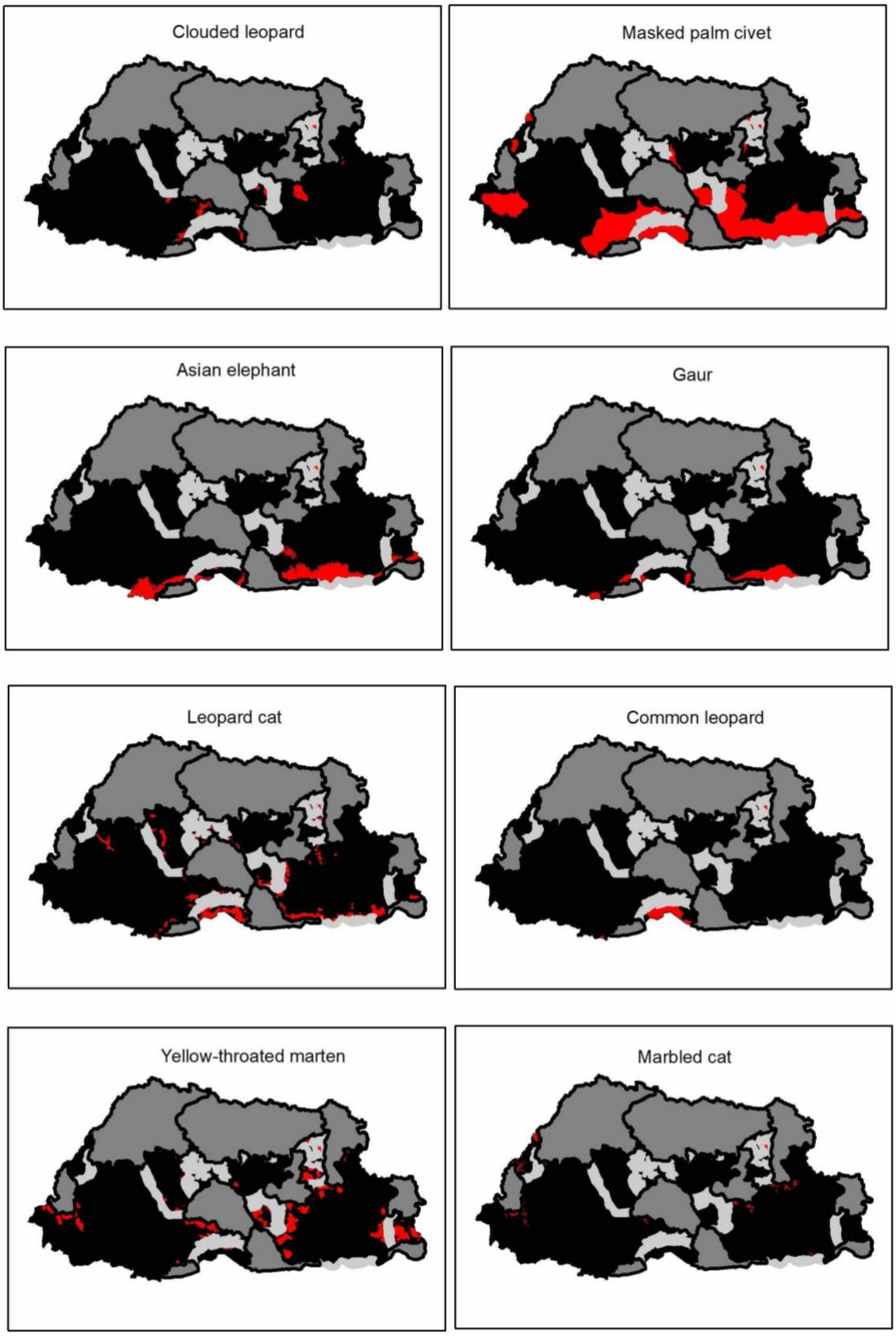


Figure S19. Sum of habitat suitability of sixteen species as an indicator of relative species richness


Clouded leopard
Masked palm civet
Asian elephant
Gaur
Leopard cat
Common leopard
Yellow-throated marten
Marbled cat

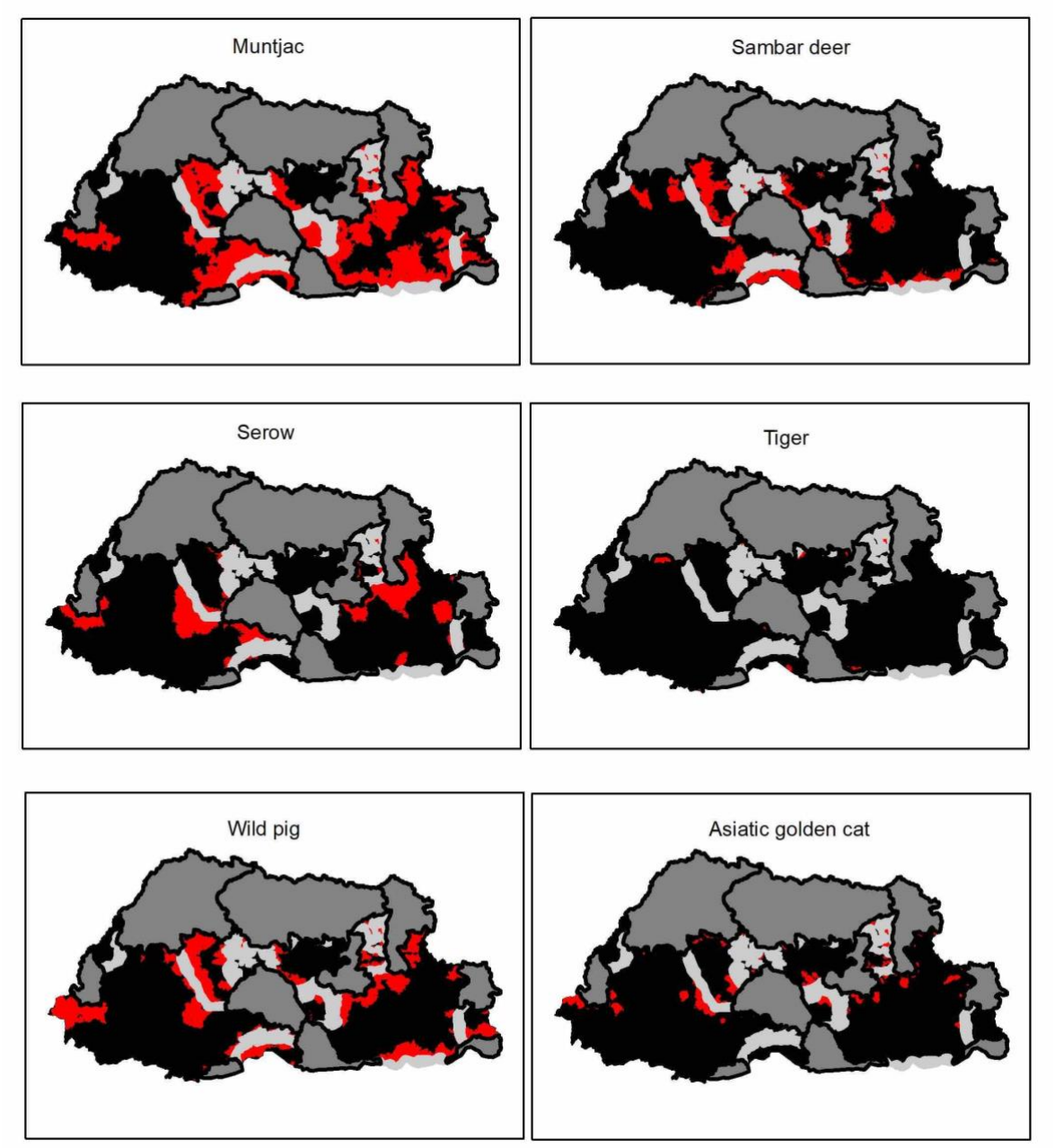


Figure S20. Optimization of priority conservation areas (red polygon) for the terrestrial mammals in Bhutan. Dark gray polygons area protected areas (national parks, wildlife sanctuaries and strict nature reserve) and light gray are biological corridors

Supplementary material for Chapter 3

Table S1 Home range and dispersal distance of the study species

Species	Home range (km^2)		Dispersal[a] (km)		Dispersal[b] (cost unit)		Mean resistance	Dispersal distance[c] (cost unit)	
	Male	Female	Male	Female	Male	Female		Male	Female
Asian elephant	165.7	238.8	514.9	618.2	514898	618163	55.3	28489309	34202969
Asiatic black bear	46.2	49.7	271.9	281.9	271882	281898	53.9	14649020	15188682
Asian golden cat	60.5	45.5	311.1	269.8	311127	269815	43.7	13602472	11796301
Clouded leopard	38.5	30.5	248.0	220.8	248032	220817	74.9	18575136	16536960
Marbled cat	*No Data*	8.6	*No Data*	117.3	*No Data*	117303	71.2	*No Data*	8351975
Leopard cat	12.4	14.0	140.9	149.7	140855	149666	37.9	5344021	5678339
Common leopard	52.6	17.0	290.0	164.9	289966	164924	70.1	20314984	11554591
Tiger	119.1	101.0	436.4	401.9	436440	401896	50.4	21992219	20251515
Sambar	18.1	9.1	170.2	120.8	170205	120797	31.4	5342722	3791829
Muntjac	0.7	0.6	33.4	30.6	33442	30620	30.0	1003609	918914
Gaur	74.3	55.5	344.8	298.0	344807	298027	69.7	24039957	20778432
Wild pig	20.2	9.6	179.6	123.8	179555	123828	27.5	4944945	3410219
Serow	*No Data*	*No Data*	*No Data*	*No Data*	*No Data*	*No Data*	47.2	*No Data*	
Dhole (pack consists of male and female)	80		357.0		356987		57.7	20591033	
Masked palm civet	2.8	1.4	66.6	46.8	66573	46819	55.71	3708797	2608275
Yellow-throated marten	10.2	7.0	127.9	105.8	127948	105754	51.79	6626422	5477022

[a] *calculated using Bowman's formula: $40 \times \sqrt{HR}$, where HR = home range (Bowman et al., 2002, Ecology)*

[b] *calculated as Dispersal (in km) × 1000 to convert to cost units*

[c] *calculated as Dispersal (in cost unit) × mean resistance*

Table S2 Priority ranking of species. Weights are assigned based on national and global conservation importance

Species	Weight	Importance	National Status[a]	IUCN Status
Tiger	16	High	Schedule I	Endangered
Asian elephant	15	High	Schedule I	Endangered
Dhole	14	High		Endangered
Common leopard	13	High	Schedule I	Near Threatened
Clouded leopard	12	High	Schedule I	Vulnerable
Gaur	11	High	Schedule I	Vulnerable
Asiatic black bear	10	Medium	Schedule I	Vulnerable
Sambar deer	9	Medium		Vulnerable
Asian golden cat	8	Medium		Near Threatened
Marbled cat	7	Medium		Near Threatened
Leopard cat	6	Medium	Schedule I	Least Concern
Serow	5	Medium	Schedule I	Vulnerable
Muntjac	4	Low		Least Concern
Masked palm civet	3	Low		Least Concern
Yellow-throated marten	2	Low		Least Concern
Wild pig	1	Low		Least Concern

[a] *As per Forest and Nature Conservation Act of Bhutan, 1995*

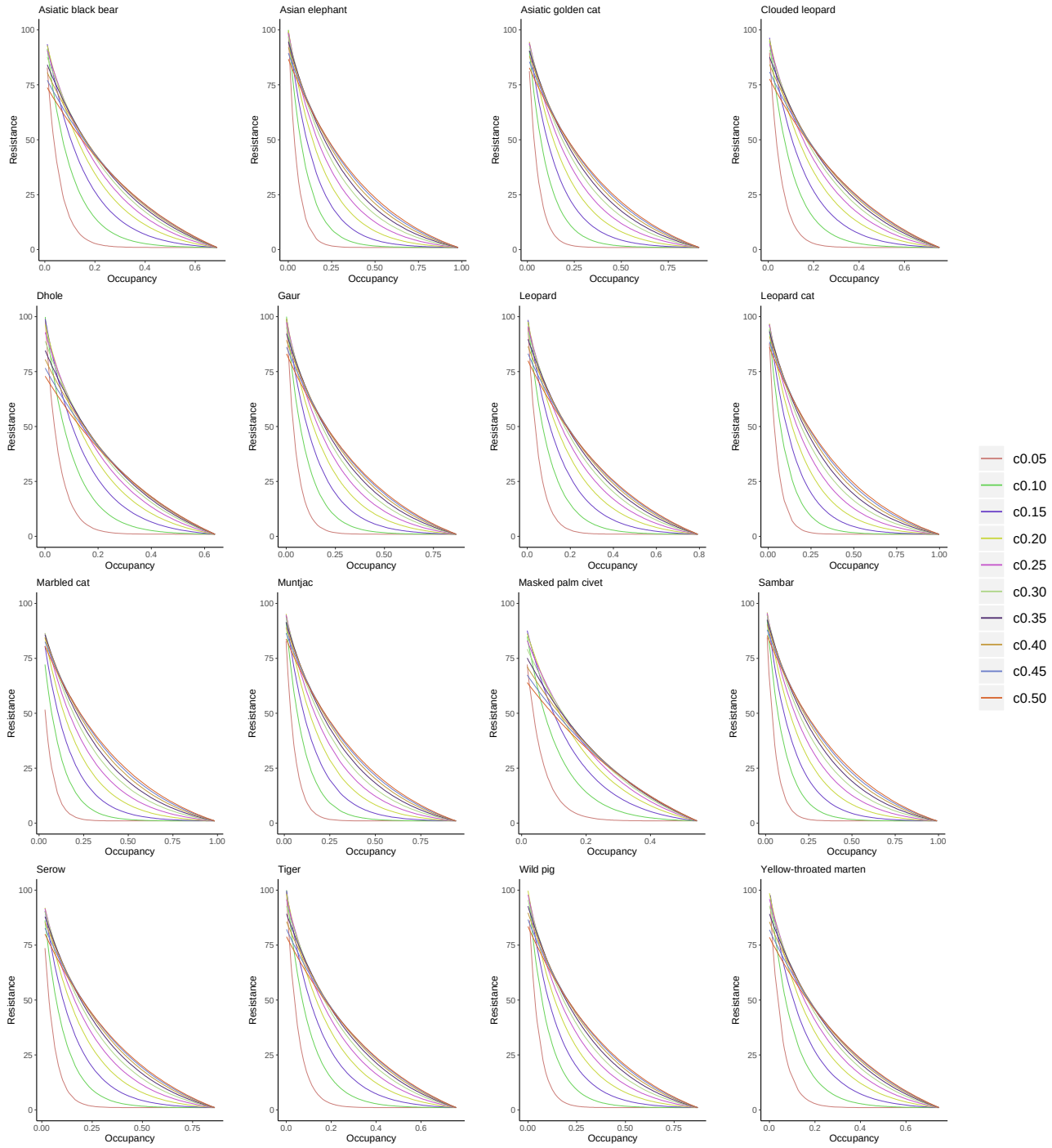
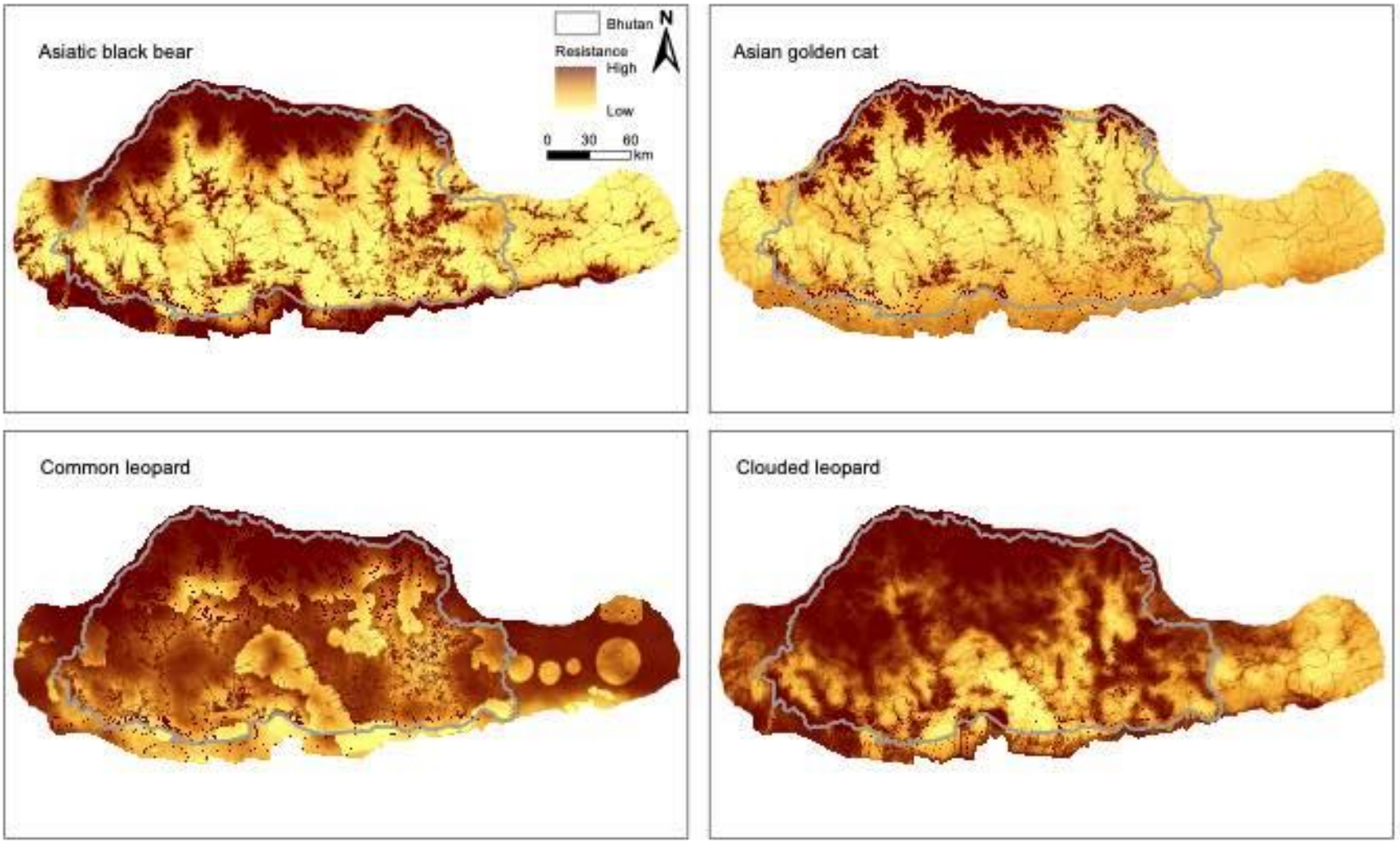
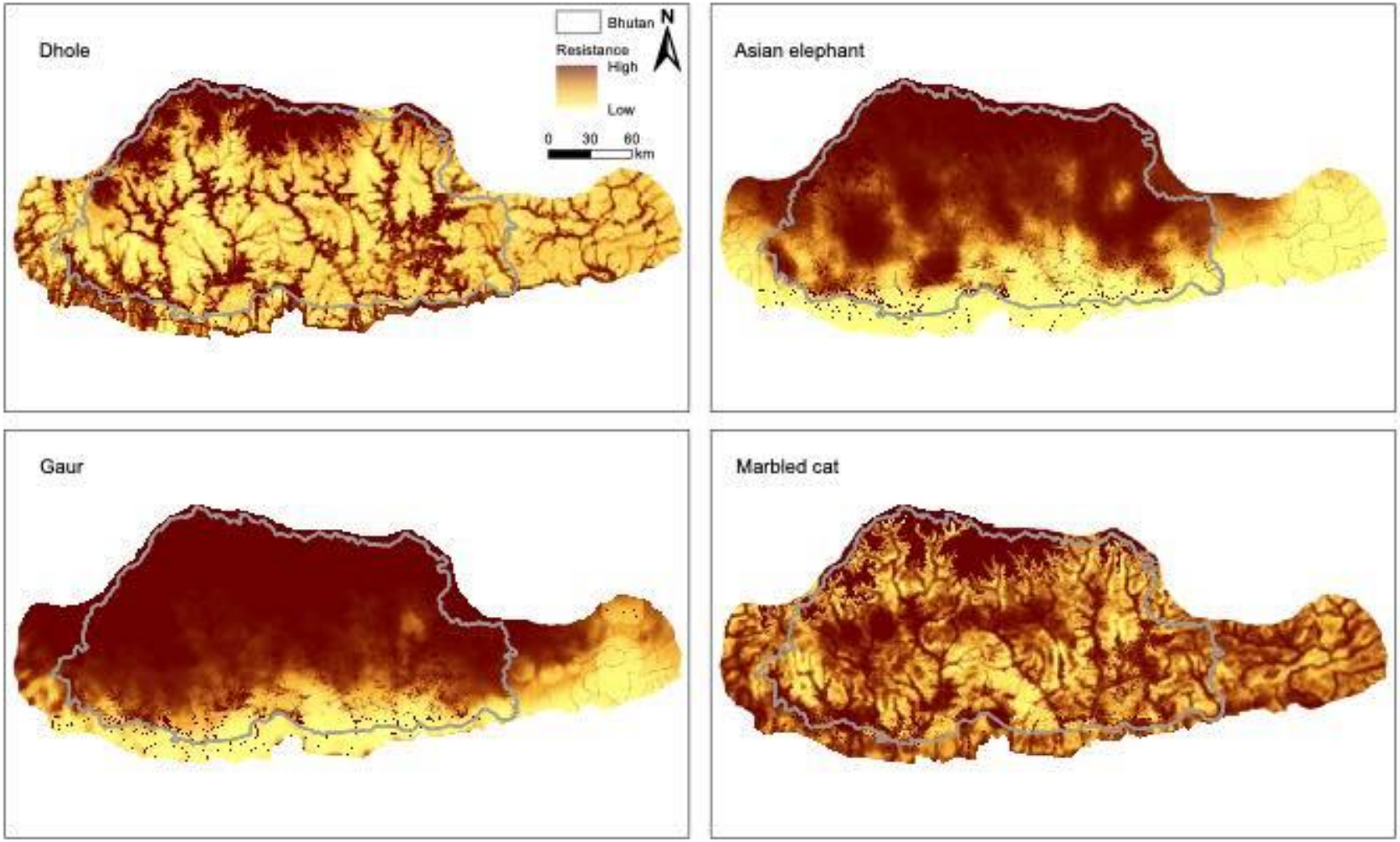
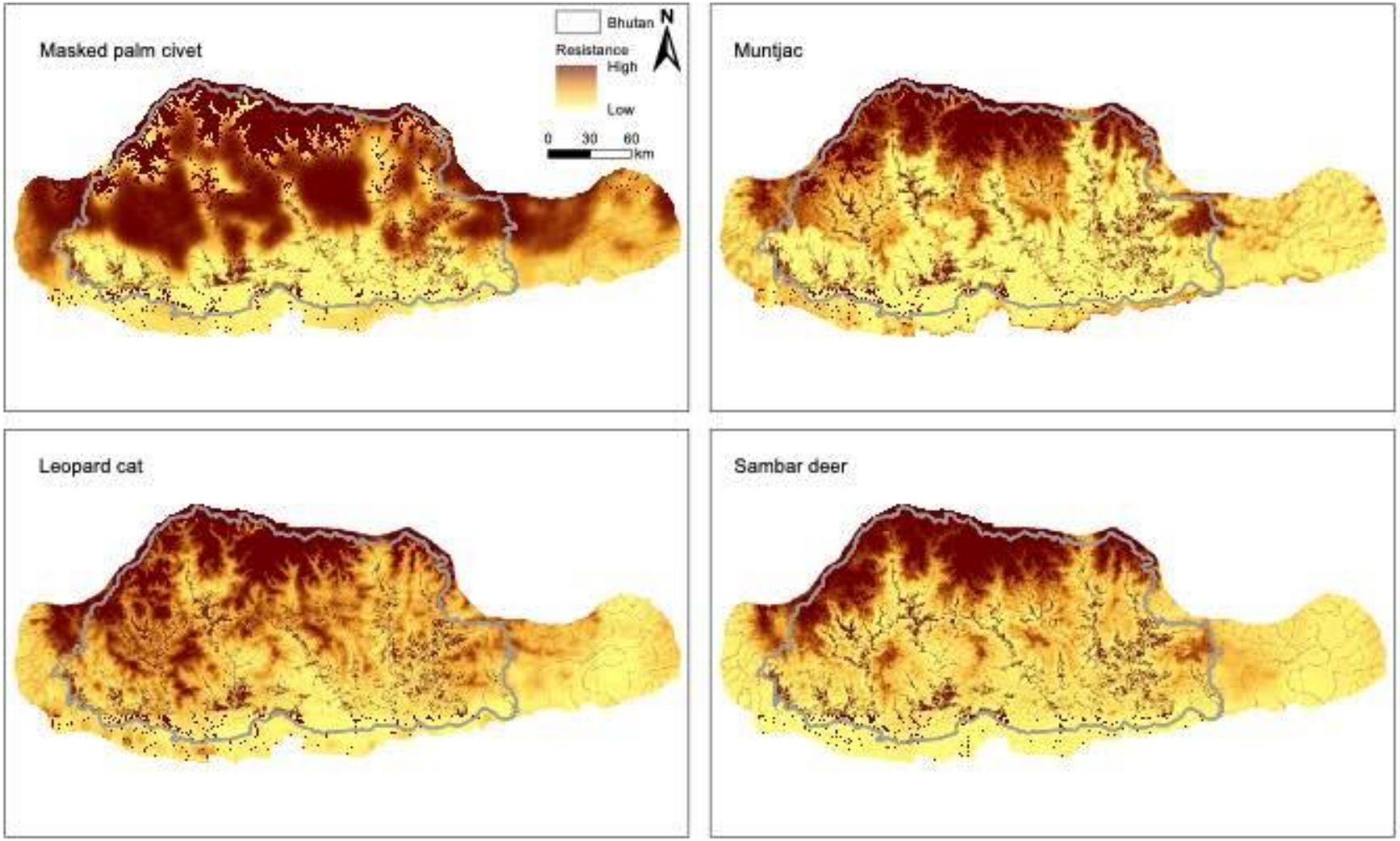


Figure S1 Transformation of habitat suitability values into resistance values. The curves are based on the transformation function, R = (exp(-1 * H/C) * 100) + Y, where R = resistance layer, H = habitat suitability layer, C = factor to determine the negative exponential relationship and Y = value used to convert minimum resistance to 1


Asiatic black bear
Bhutan
N
Resistance
High
Low
0 30 60
km
Asian golden cat
Common leopard
Clouded leopard


Dhole
Bhutan
N
Resistance
High
Low
0 30 60
km
Asian elephant
Gaur
Marbled cat


Masked palm civet
Bhutan
N
Resistance
High
Low
0 30 60
km
Muntjac
Leopard cat
Sambar deer

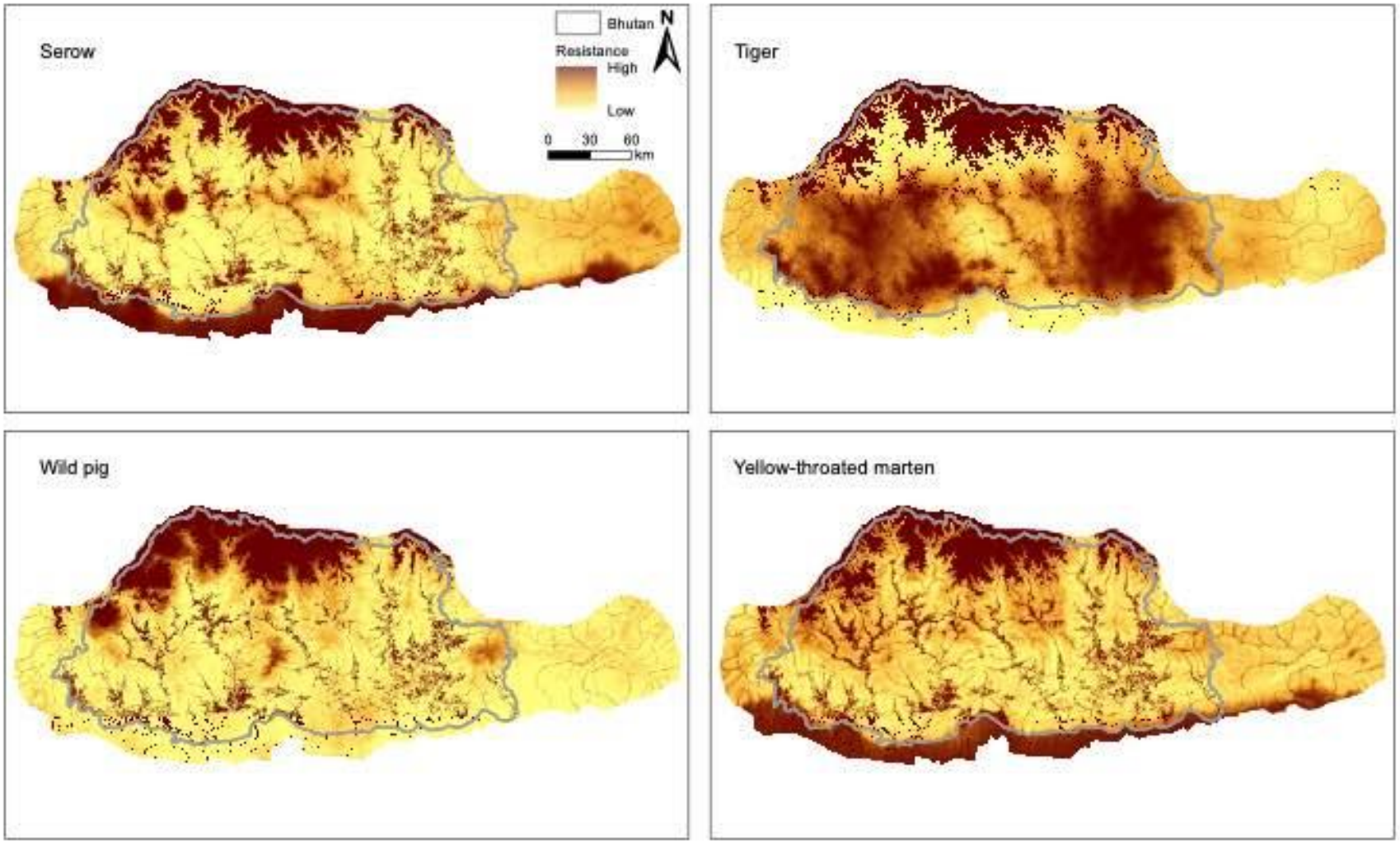
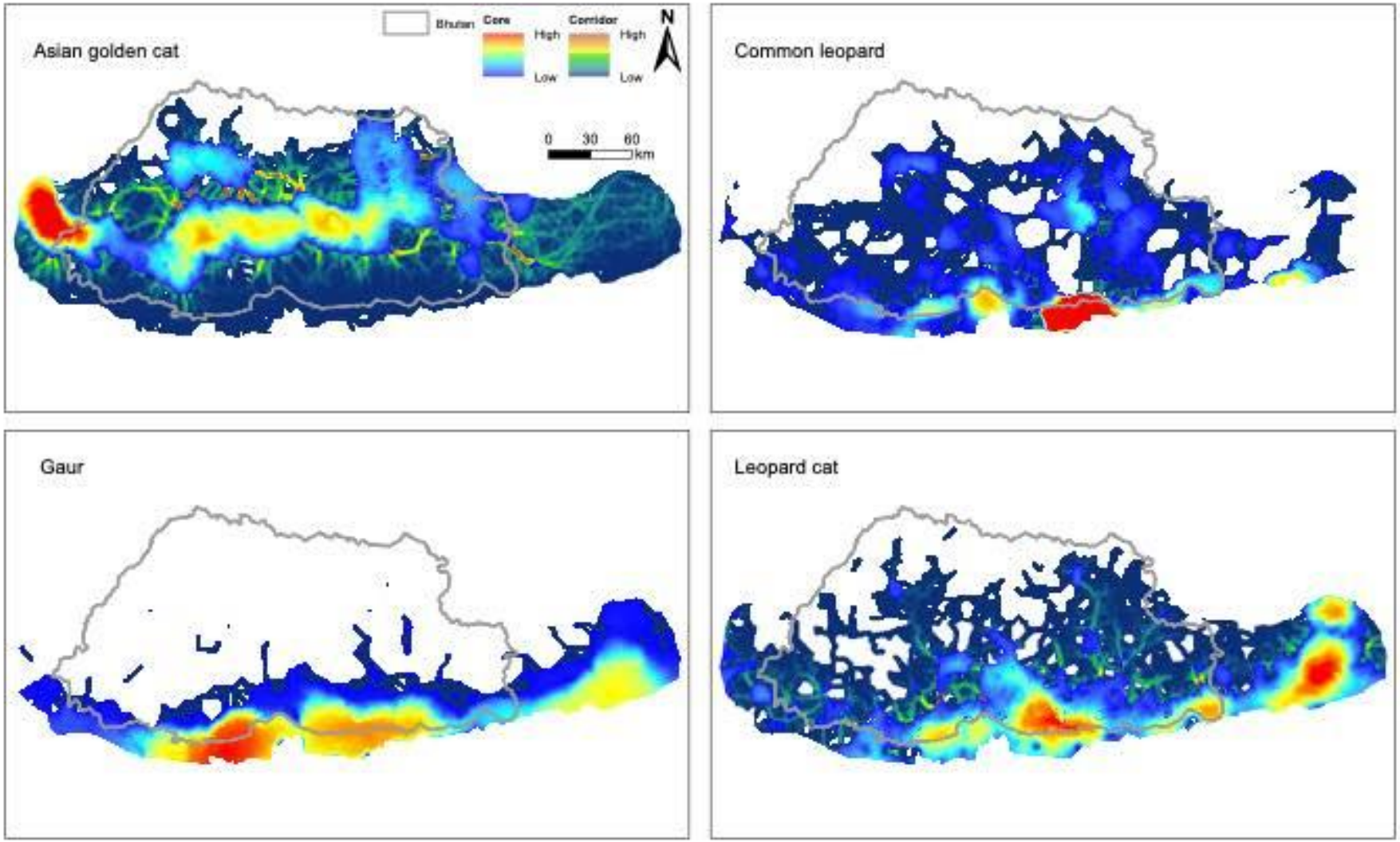
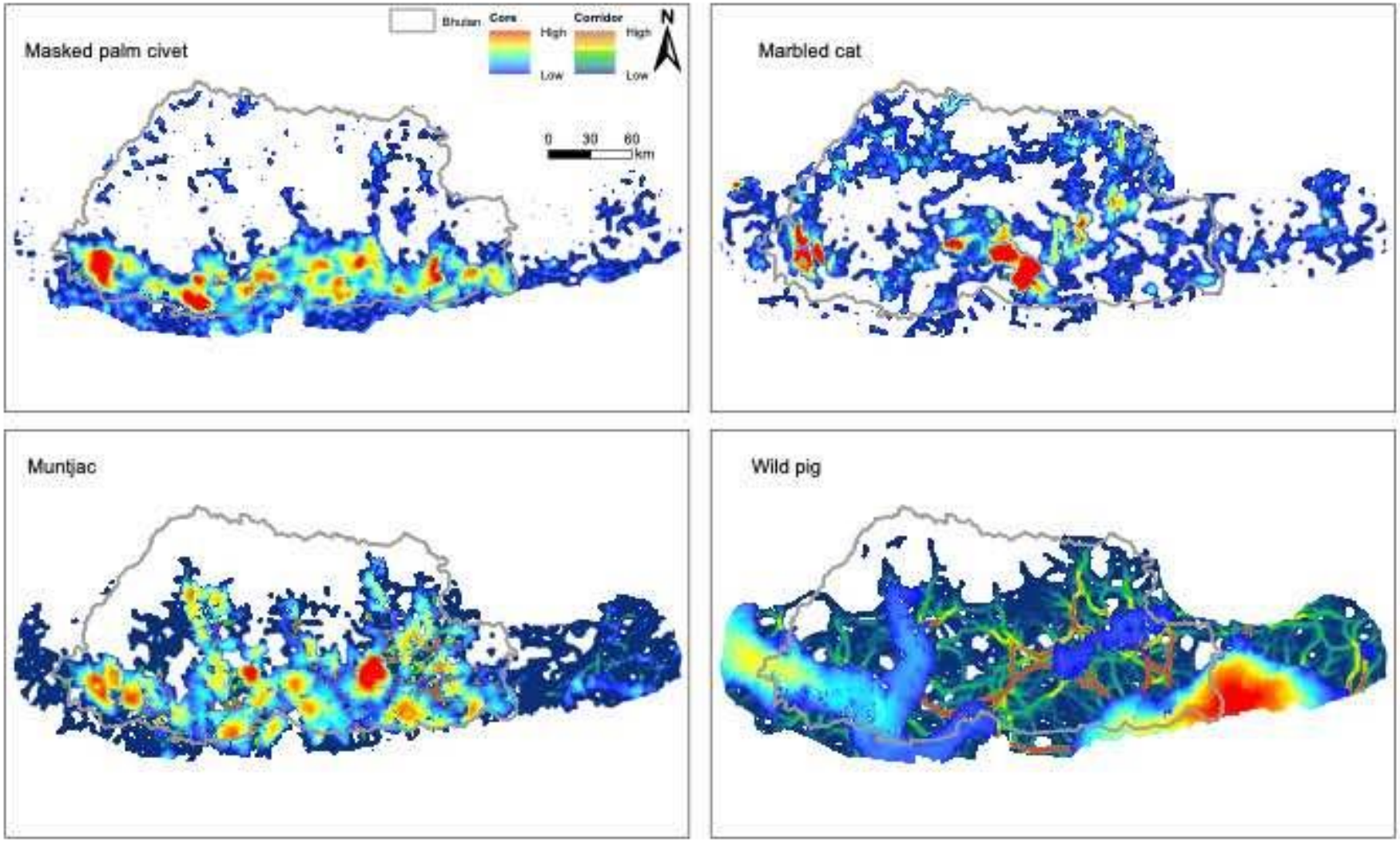


Figure S2 Resistance layers for the 16 study species.


Asian golden cat
Bhutan
Core
High
Low
Corridor
High
Low
N
0 30 60
km
Common leopard
Gaur
Leopard cat


Masked palm civet
Bhutan
Core
High
Low
Corridor
High
Low
N
0 30 60
km
Marbled cat
Muntjac
Wild pig

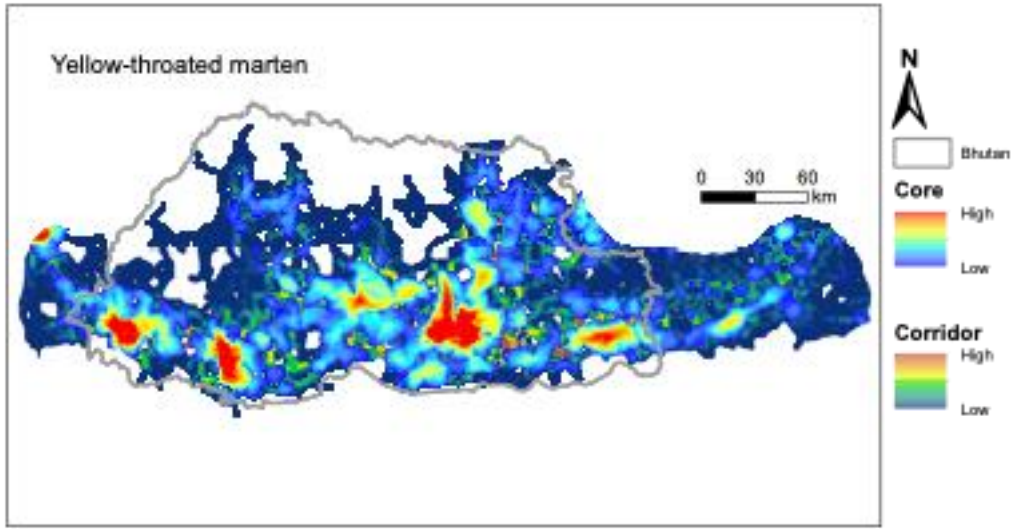


Figure S3 Predicted resistant kernel density and least-cost paths representing core area and corridor network, respectively

R script to generate resistance values for each conversion factor ('c') – see Figure S1

```
# Created by Ugyen Penjor, 27.05.2020
# Load habitat suitability (raster) layers

require(raster)

# Load habitat suitability layer
abb <- raster("abb_4500_set_clip.tif")

# Extract min and max probability values
data <- seq(from=cellStats(abb, min), to=cellStats(abb, max),
 by=.001)

# Generate random number from min, max probability values of a
 raster
random_number <- function(input){
  input <- data
  ran <- sample(input, size=101, replace=FALSE)
  ran_df <- as.data.frame(ran)
  output <- as.data.frame(ran_df[order(-ran),])
  #output <- ran_df[order(-ran),] # produces numeric - easy for
 plotting
  return(output)
}

( data2 <- random_number(data) )

hist(as.numeric(data2$`ran_df[order(-ran), ]`), breaks=101)

# Exponential function
c <- c(0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40, 0.45,
 0.50, 1, 2, 4, 8, 16, 32)

data <- as.numeric(data2$`ran_df[order(-ran), ]`)

out <- matrix(NA, length(data), length(c))

for(i in 1:length(data)){
  for(j in 1:length(c)){
```

```
    out[i,j] <- exp(-data[i]/c[j])
  }
}

out

# Function to generate Y from resistance bases
out2 <- cbind(data, as.data.frame(out))

constants <- function(x){
  x <- out2
  min_res.b <- sapply(x[, 2:17], min)
  Z <- min_res.b*100
  Y <- 1-Z
  return(Y)
}

( Y <- constants(out2) )

### OR

constants <- function(x){
  x <- out2
  min_res.b <- sapply(x[, 2:11], min)
  Z <- min_res.b*100
  Y <- 1-Z
  # Y <- as.data.frame(1-Z)
  Y <- as.data.frame(Y)
  rownames(Y) <- c("c0.05", "c0.10", "c0.15", "c0.20", "c0.25",
 "c0.30", "c0.35", "c0.40", "c0.45", "c0.50")
  return(Y)
}

( Y <- constants(out2) )


# Finally generate resistance for each factor 'c'
c <- c(0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40, 0.45,
 0.50, 1, 2, 4, 8, 16, 32)
data <- as.numeric(data2$`ran_df[order(-ran), ]`)
```

```
res_bas <- out
Ym <- as.matrix(Y)

resist <- matrix(NA, length(res_bas[,1]), length(Ym))
length(res_bas[,1])

for(i in 1:length(res_bas[,1])){
  for(j in 1:length(Ym)){
    resist[i,j] <- res_bas[i,j]*100+Ym[j]
  }

}

head(resist); class(resist)

R <- as.data.frame(resist)
Resistance <- cbind(data, R)
#write.csv(Resistance, "Resistance.csv")

### OR

for(i in 1:length(res_bas[,1])){
  for(j in 1:length(Ym)){
    resist[i,j] <- res_bas[i,j]*100+Ym[j]
    outR <- as.data.frame(cbind(data, resist))
    colnames(outR) <- c("Occupancy", "c0.05", "c0.10", "c0.15",
"c0.20", "c0.25", "c0.30", "c0.35", "c0.40", "c0.45", "c0.50",
"c1", "c2", "c4", "c8", "c16", "c32")
  }
}

head(outR); class(outR)
#write.csv(outR, "Resistance.csv")


# Plot the curves (Figure S1)
require(ggplot2; require(reshape)

outR_m <- melt(outR, id.vars="Occupancy")
```

```
q <- ggplot(data=outR_m, aes(x=Occupancy, y=value,
 colour=variable)) + geom_line()

q + ylab("Resistance") + xlab("Occupancy") +
        theme(axis.text.x=element_text(size=11),
       axis.text.y=element_text(size=11),
       axis.title.x=element_text(size=13),
       axis.title.y=element_text(size=13),
       panel.background=element_blank(),
       panel.grid.major=element_blank(),
       panel.grid.minor=element_blank(),
       axis.line=element_line(colour="black", size=0.6),
       legend.position="right"
       )
```

Supplementary material for Chapter 4

Multispecies occupancy model

The latent ecological process of a species k at site i is a Bernoulli random variable with occupancy parameter ψ, such that $z_{ik} \sim Bernolli(\psi_{ik})$. The observation process y is governed by another Bernoulli random variable conditional on species occurrence, $y_{ik}|z_{ik} \sim Bernoulli(z_{ik} * p_{ijk})$, where p_{ijk} is the probability of detection of species k at site i on occasion j. For a truly present species, $z_{ik} = 1$ and 0 otherwise and the resulting observations are fixed zeros and false detections are not allowed. Like all occupancy models (MacKenzie et al., 2002), MSOMs assume closed sites to permanent emigration or immigration for a given period. We believe that relatively short survey duration in our case respected this assumption for both groups (120 days for camera trap survey and restricting surveys for the breeding season only between October and March). We did not augment data (Dorazio et al., 2006) because our primary interest was to estimate site-level diversity (i.e., α-diversity), and not the total richness across Bhutan (i.e, γ-diversity). The site-level diversity is also known as taxonomic diversity (TD) and was used for estimating other facets of biodiversity (functional and phylogenetic diversity) (Si et al., 2018).

We modelled the probability of occupancy and detection as a function of the site and survey-specific covariates using a logistic link function: $\text{logit}(\psi_{ik}) = \beta_{0k} + \beta_{xik} \times cov_i$ for occupancy and $\text{logit}(p_{ijk}) = \alpha_{0k} + \alpha_{xijk} \times cov_{ij}$ for detectability, respectively. Parameters β_{0k} and α_{0k} are the species-specific random intercepts, β_{xik} is the slope of occupancy site-level covariate x and α_{xijk} is the slope of survey covariate x at site i on occasion j for species k. For mammals, we modelled occupancy as a function of forest cover, agriculture, settlement, distance

to road, temperature, and precipitation after omitting correlated variables and detectability as a function of the trail (whether camera traps placed on/off animal trail) and random effects of camera models to capture differences in operative capability and durability of camera models used details in (Penjor et al., 2019) adhering to the principle of parsimony. Since we did not have a time-varying survey covariate for camera trap data, our Bernoulli trials were summed to a Binomial distribution, $y_{ik} \sim Binomial(z_{ik} * p_{ik}, n_i)$, where n_i is the total number of trials (i.e., the number of active camera trap days at site i).

For birds, occupancy was modelled as a function of forest cover, built-up area, agriculture, settlement, temperature and precipitation and detectability as a function of survey date to model variability in detection probability during the breeding season and time spent at each location (duration). We added random effect of the study area in the occupancy model to accommodate the potential effect of spatial autocorrelation and geographical nuances in both groups (mammal = 20, bird = 3) though we suspect the effects of spatial autocorrelation would be small due to adequate spacing between sample locations (2.9km for camera trap and 300m for point count). We assumed dependency between logit(ψ_k) and logit(p_k) due to species abundance because more common species are expected to be widespread and easily detected. This would lead to a positive correlation between occupancy and detection probabilities. We quantified this association by adding a covariance parameter expressed as the product of correlation coefficient ρ and standard deviations of logit-scale ψ and p, $\rho\sigma_\psi\sigma_p$ (Royle and Dorazio, 2008).

In both groups, we treated parameters of each species as random drawing species-specific effects from a common distribution (Kery and Royle, 2016). For mammals, we used normal priors on intercept and slopes $\beta_k \sim Normal(\mu_{\beta_k}, \tau_{\beta_k}), \alpha_k \sim Normal(\mu_{\alpha_k}, \tau_{\alpha_k})$ of occupancy and detectability, respectively. For hyperparameters, we used normal priors on means of intercept and slope, $\mu_{\beta_k} \sim Normal(0, 0.1)$, $\mu_{\alpha_k} \sim Normal(0, 0.1)$ of occupancy and detectability, respectively and weakly informative folded Student-t priors with four degrees of freedom on standard deviations, $\sigma_{\beta_k} \sim t(0, 2.25, \nu = 4)$ with precision, $\tau_{\beta_k} = \frac{1}{\sigma^2_{\beta_k}}$ for occupancy and $\sigma_{\alpha_k} \sim t(0, 2.25, \nu = 4)$ with precision, $\tau_{\alpha_k} = \frac{1}{\sigma^2_{\alpha_k}}$ for detectability. For birds, species-specific intercepts and slopes were assigned normal priors with community-wide means and precisions, $\beta_k \sim Normal(\mu_{\beta_k}, \tau_{\beta_k})$, $\alpha_k \sim Normal(\mu_{\alpha_k}, \tau_{\alpha_k})$ for ecological and observation processes, respectively. We specified weakly informative half-Cauchy distribution with $\sigma = 2.25$ on hyperparameter means, $\mu_{\beta_k} \sim Normal(0, \tau_{\mu_{\beta_k}})$ where precision, $\tau_{\mu_{\beta_k}} = \frac{1}{\sigma^2_{\mu_{\beta_k}}}$ with $\sigma^2_{\mu_{\beta_k}} \sim half\text{-}Cauchy(2.25^2)$ for occupancy and $\mu_{\alpha_k} \sim Normal(0, \tau_{\mu_{\alpha_k}})$ where, $\tau_{\mu_{\alpha_k}} = \frac{1}{\sigma^2_{\mu_{\alpha_k}}}$ with $\sigma^2_{\mu_{\alpha_k}} \sim half\text{-}Cauchy(2.25^2)$ for detectability. We used weakly informative priors and implemented models in program JAGS (Plummer, 2003) to run Monte Carlo Markov Chain (MCMC) simulations called through R 4. (R Core Team, 2021) using the package jagsUI (Kellner, 2019). The use of weakly informative proper priors provides a small amount of information based on data and model but less than the actual knowledge without influencing the posteriors (Gelman et al., 2013, Banner et al., 2020). Three parallel chains of 50000 iterations each were run discarding 10000 during burn-in and adaptation and thinning by 50 to obtain posterior estimates. Visual inspection of trace plots revealed adequate chain convergence further supported by Gelman-Rubin

statistics $\hat{R}$ below 1.1 for all parameters (Gelman et al., 2013). All covariates were standardised to zero mean and one standard deviation. We assessed model fit by comparing observed data to the predicted values through the Freeman-Tukey discrepancy test (Kéry and Royle, 2016) and lack-of-fit ratio $\hat{C}$ (ratio of the posterior distribution of simulated and observed data with *ca.* 1 for a good fit). We computed the Posterior predictive Bayesian p value which ranges between 0 and 1. Models with poot fit will have values on the extremes while the good fit will have around the centre.

Additionally, we also evaluated the 'detectability' of diversity measures (q_{TD}, q_{FD}, q_{PD}) as the ratio of naively observed metric to its corresponding detection-corrected metric (e.g., detectability of TD was calculated as $q_{TD} = \frac{TD_{observed}}{TD_{estimated}}$) (Jarzyna and Jetz, 2016).

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Supplementary Results

Across the survey, we recorded 45 mammal species in 17 families and 336 bird species in 66 families at 849 and 679 sites, respectively. The overall mean occupancy across the community was low in both groups [ψ_{mammal} = 0.047 (0.02 – 0.09); ψ_{bird} = 0.03 (0.019 – 0.035)]. However, overall community detection probability was higher for birds than mammals [p_{bird} = 0.193 (0.025 – 0.247); p_{mammal} = 0.016 (0.011 – 0.022)]. Community occupancy showed strong negative association with agriculture [β_{agri} = -0.073 (-0.132 – -0.017)], temperature [β_{temp} = -

0.24 (-0.407 – -0.066)] and precipitation [β_{prec} = -0.063 (-0.132 – -0.003)] but weak positive association with forest [β_{forest} = 0.024 (-0.082 – 0.13)], distance to settlement [β_{set} = 0.019 (-0.051 – 0.085)] and distance to road [β_{road} = 0.045 (-0.041 – 0.129)] for mammals. For bird communities, the overall occupancy was strongly and negatively associated with agriculture [β_{agri} = -0.302 (-0.426 – -0.181)], built-up area [β_{built} = -0.2 (-0.291 – -0.12)] and temperature [β_{temp} = -0.563 (-0.776 – -0.36)] but strongly and positively with precipitation [β_{prec} = 0.258 (0.016 – 0.505)]. A weak negative association was observed between community occupancy and forest [β_{forest} = -0.086 (-0.204 – 0.031)] and a weak positive association with distance to settlement [β_{set} = 0.001 (-0.047 – 0.076)]. However, individual response in both mammal and bird communities was highly variable.

Detectability in mammals was higher in camera traps closer to trails [α_{trail}= 0.311 (0.074 – 0.535)] and varied for different camera models [α_{cam} = 0.066 (-0.339 – 0.45). Detectability of birds was high during the start of the survey [α_{date} = 0.257 (0.163 – 0.35)] and declined towards the end [α_{date^2} = -1.794 (-2.06 – - 1.528]. The time spent at point location by an observer did not contribute to the detectability of birds [α_{dur} = -0.776 (-0.991 – -0.571)].

Across survey sites, the detectability of diversity was significantly low for FD and PD compared with TD (Fig. S5). qPD was marginally lower than qFD in birds but marginally higher in mammals. qTD for both groups increased with agriculture but decreased with elevation. The settlement did not have a notable effect on both groups. qFD and qPD showed a significant negative relationship with agriculture in birds than mammals, only marginal effects with

settlement in both groups and opposing effects with elevation (decreasing in a mammal, weakly increasing in birds).

Please refer to Figure 1 in Supplementary Chapter 1

Figure S1 Map of Bhutan's location in south Asia (inset). Camera trap locations are shown in coloured dots (blue indicating stations in the north block and green indicating stations in the south block)

Please refer to Figure 1 in Supplementary Chapter 2

Figure S2 Map of Bhutan showing study sites and transects with point count locations. The insets show the plot design

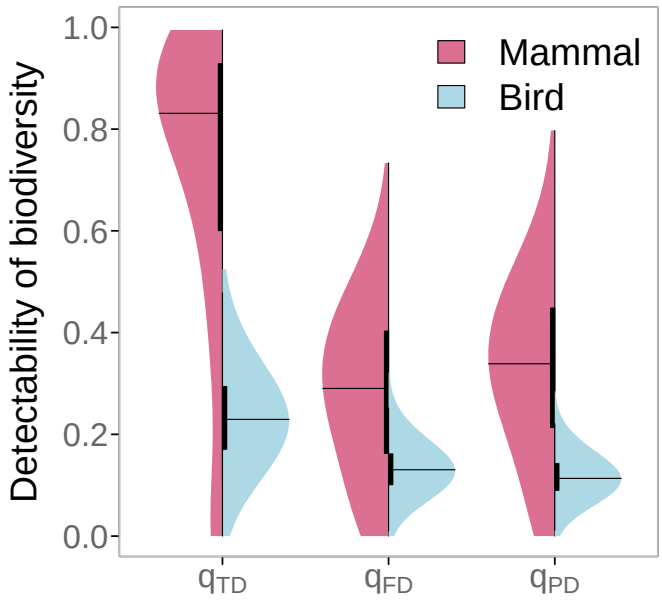


Figure S3 Detectability of diversity for mammal and bird community. Box plots and interquartile ranges are indicated by black vertical lines and median estimates are indicated by black horizontal lines. q_{TD} = detectability of taxonomic diversity, q_{FD} = detectability of functional diversity, q_{PD} = detectability of phylogenetic diversity

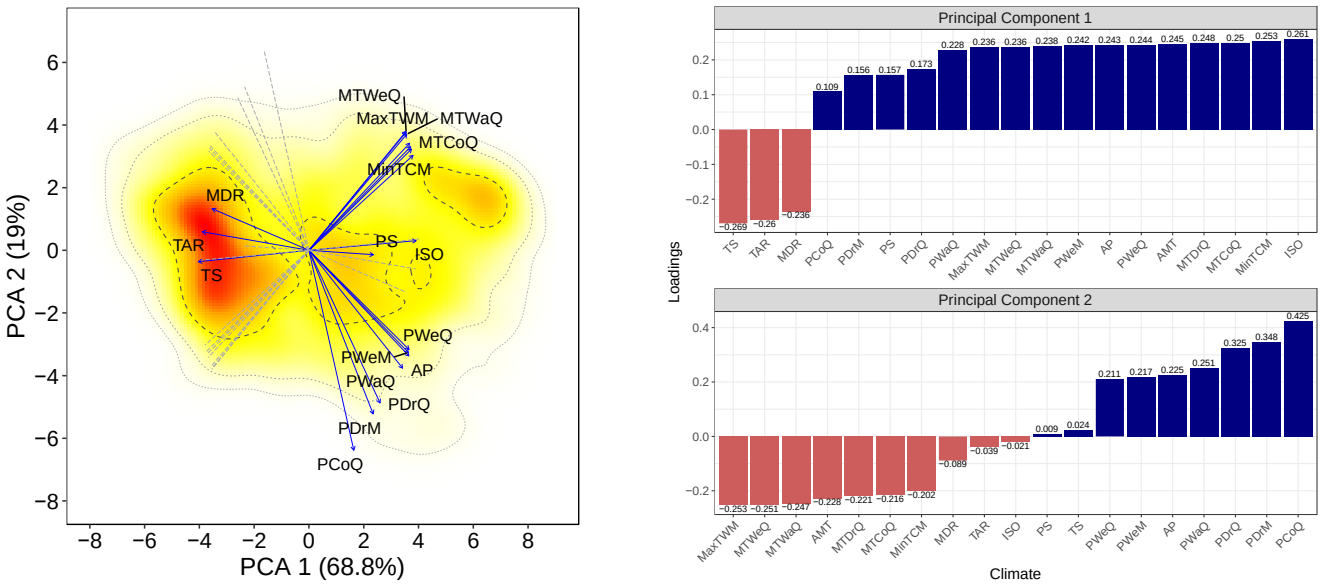


Figure S4 Principal component dimensions (left) and trait loadings (right) based on 19 bioclimatic variables for mammals (red bars indicate negative eigenvalues and blue shows positive values)

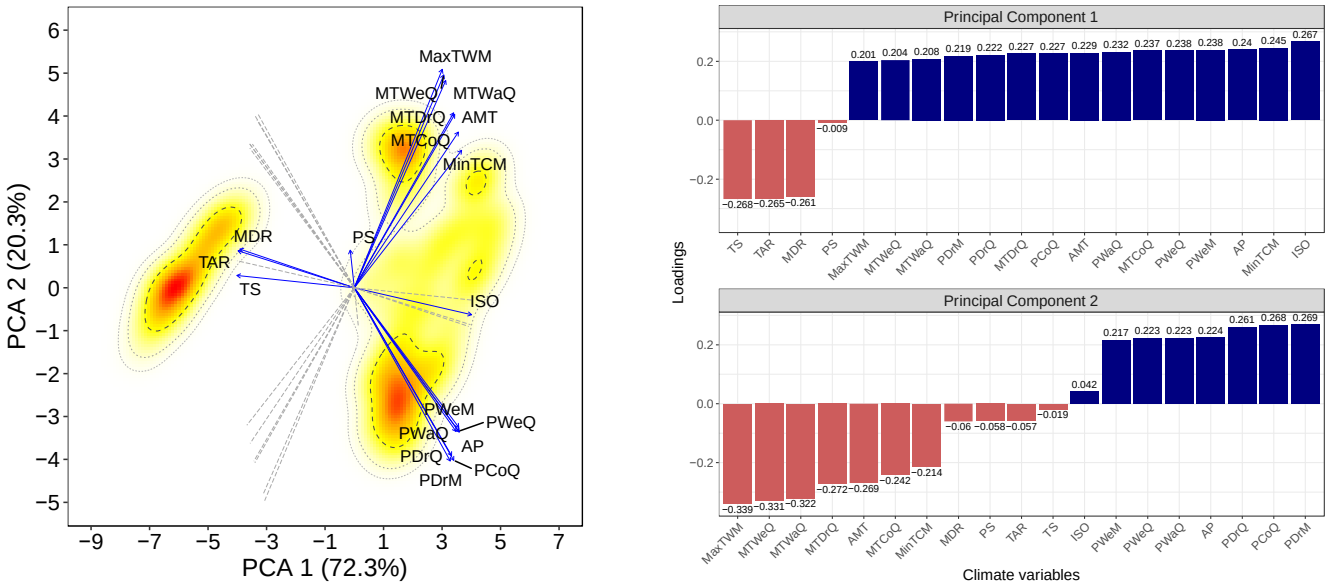


Figure S5 Principal component dimensions (left) and trait loadings (right) based on 19 bioclimatic variables for birds (red bars indicate negative eigenvalues and blue shows positive values)

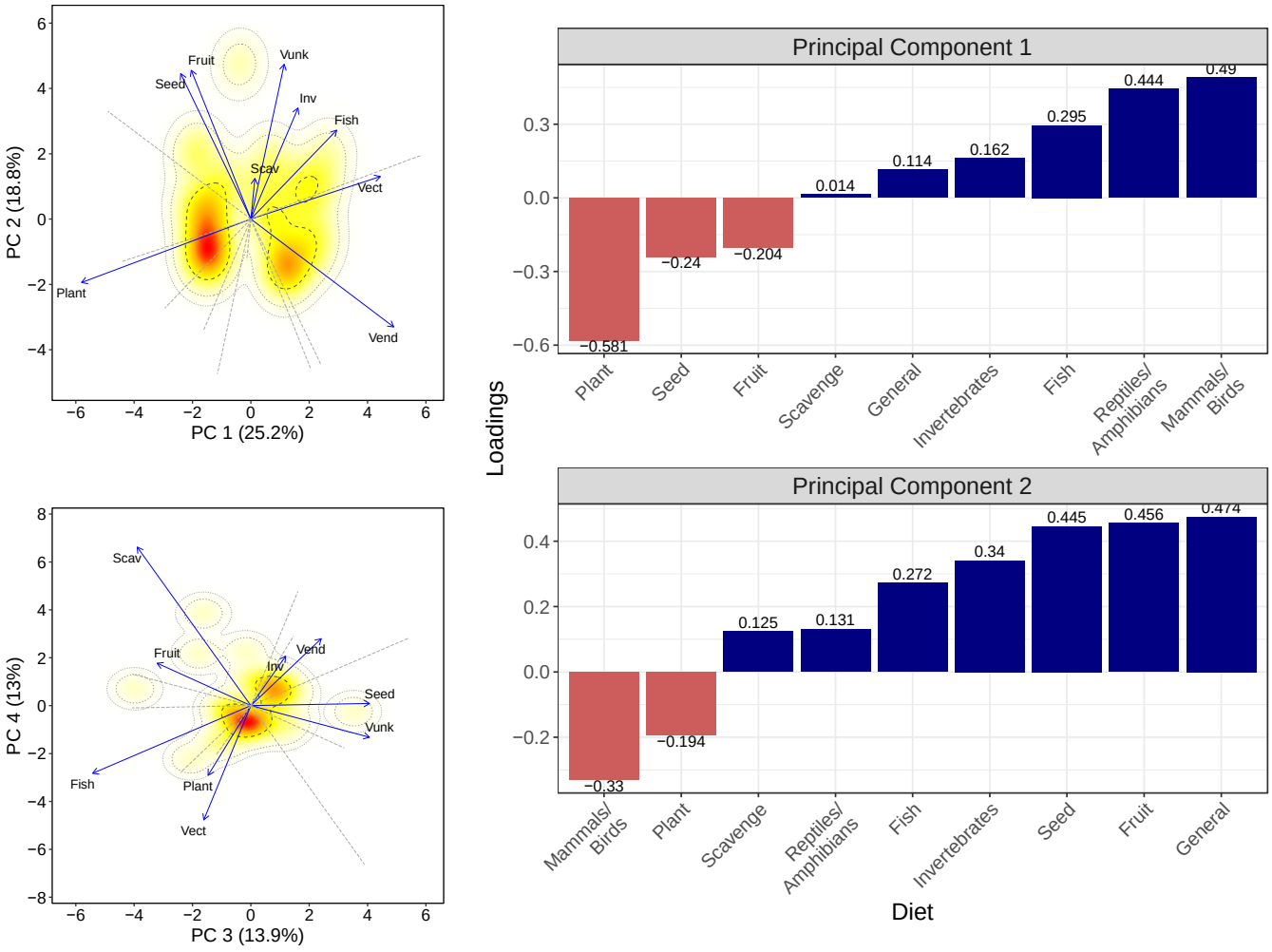


Figure S6 Principal component dimensions (left) and trait loadings (right) based on 9 diet variables for mammals (red bars indicate negative eigenvalues and blue shows positive values)

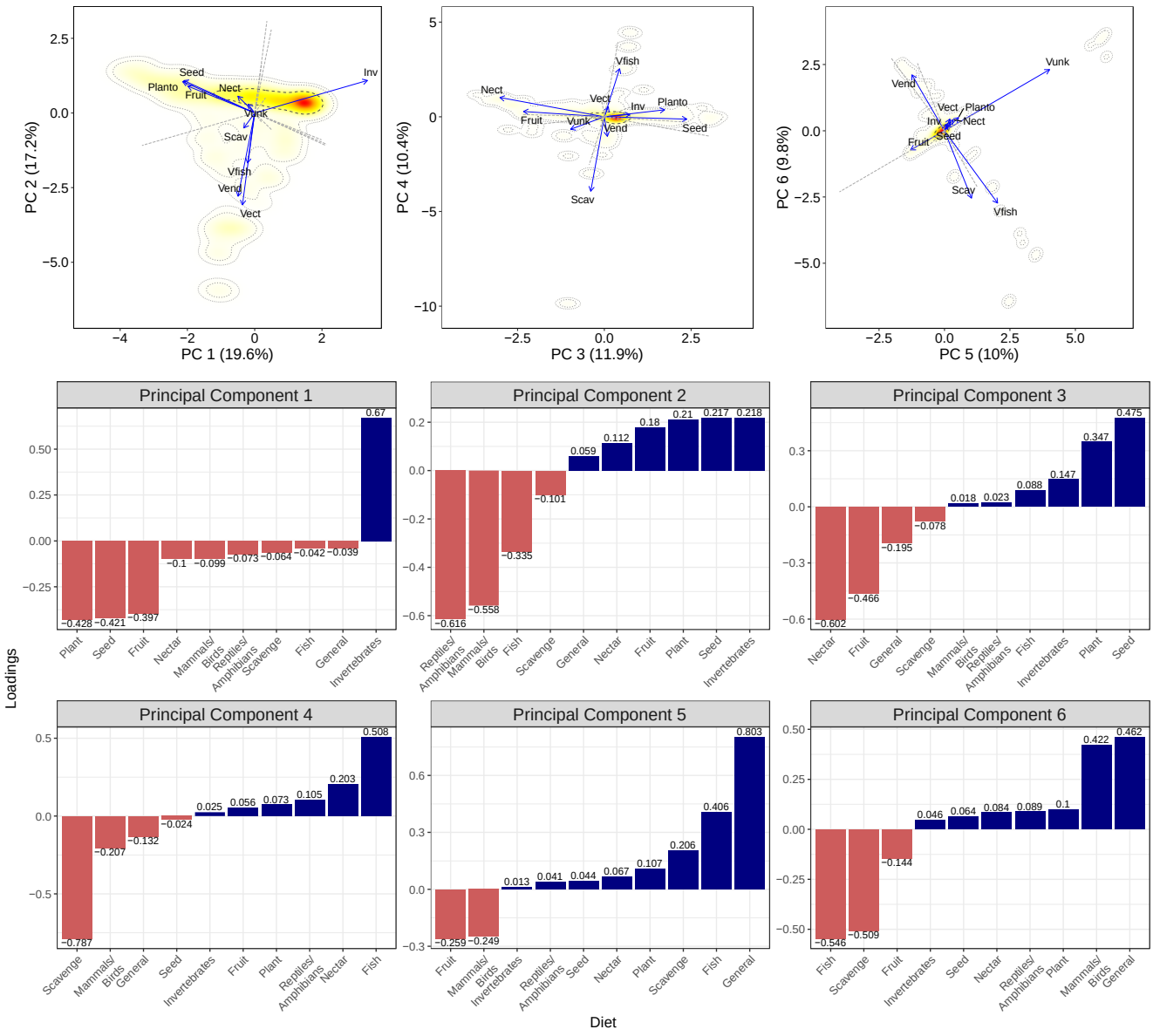


Figure S7 Principal component dimensions (left) and trait loadings (right) based on 10 diet variables for birds (red bars indicate negative eigenvalues and blue shows positive values)

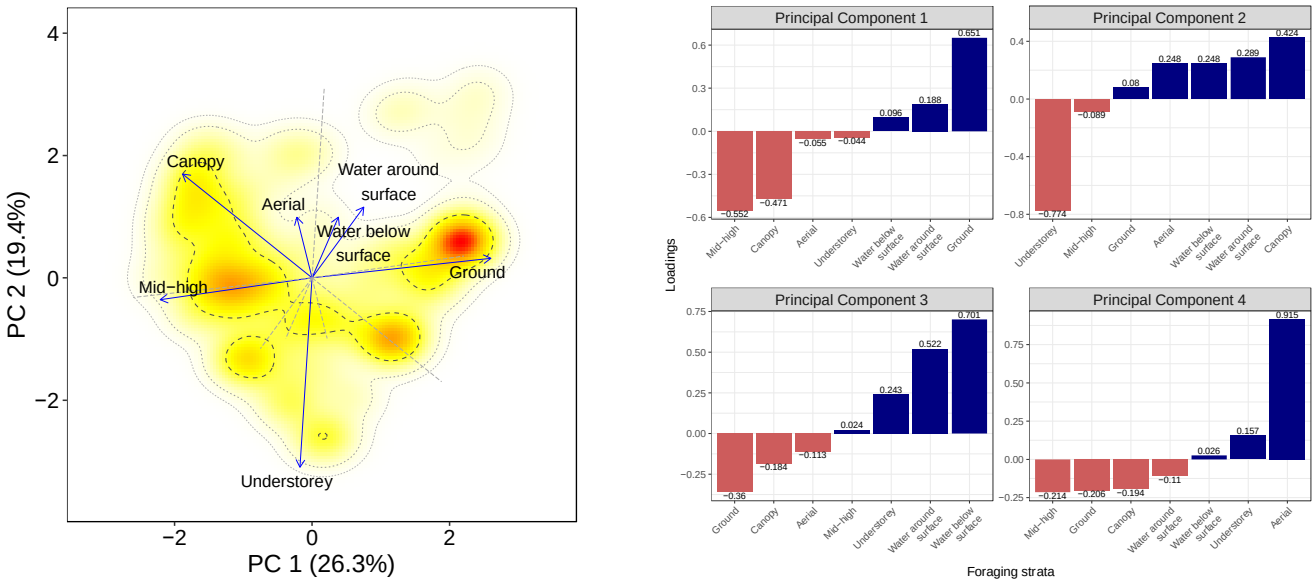


Figure S8 Principal component dimensions (left) and trait loadings (right) based on 7 foraging strata for birds (red bars indicate negative eigenvalues and blue shows positive values)

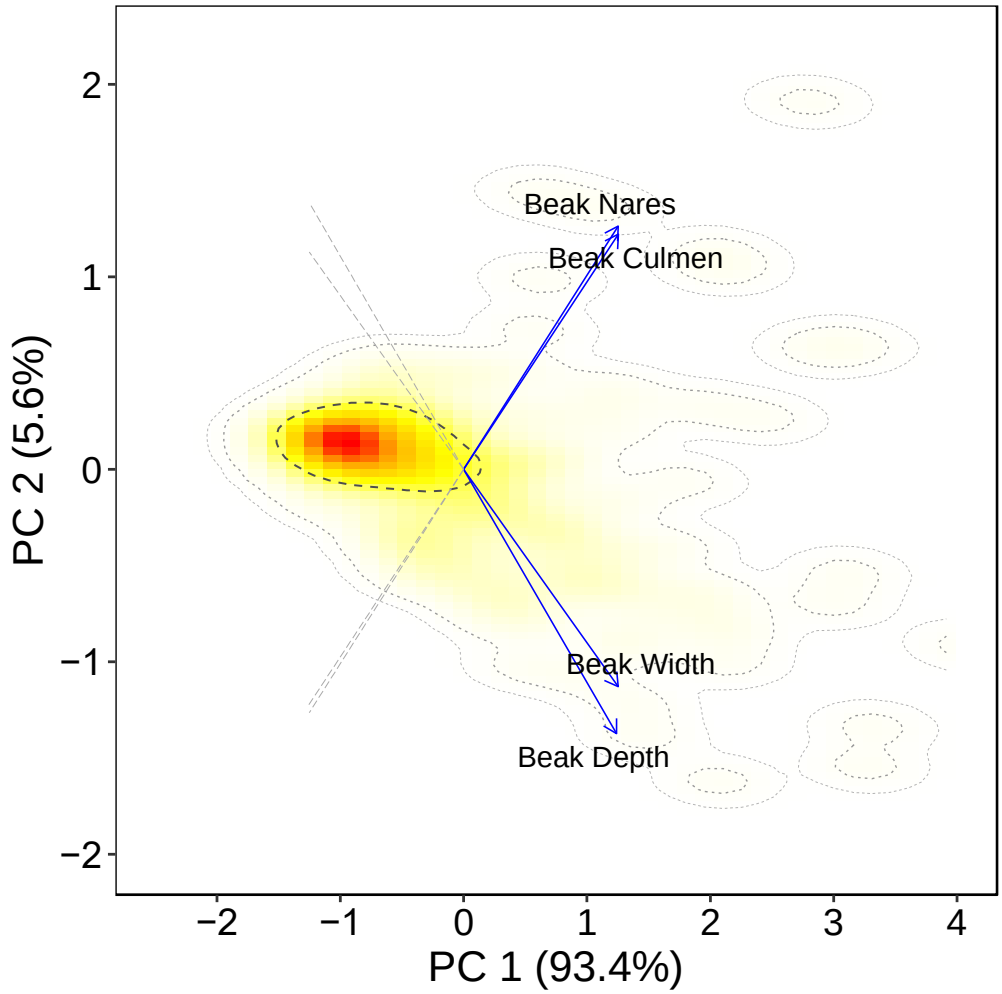


Figure S9 Principal component dimensions based on four beak morphology for birds (red bars indicate negative eigenvalues and blue shows positive values)

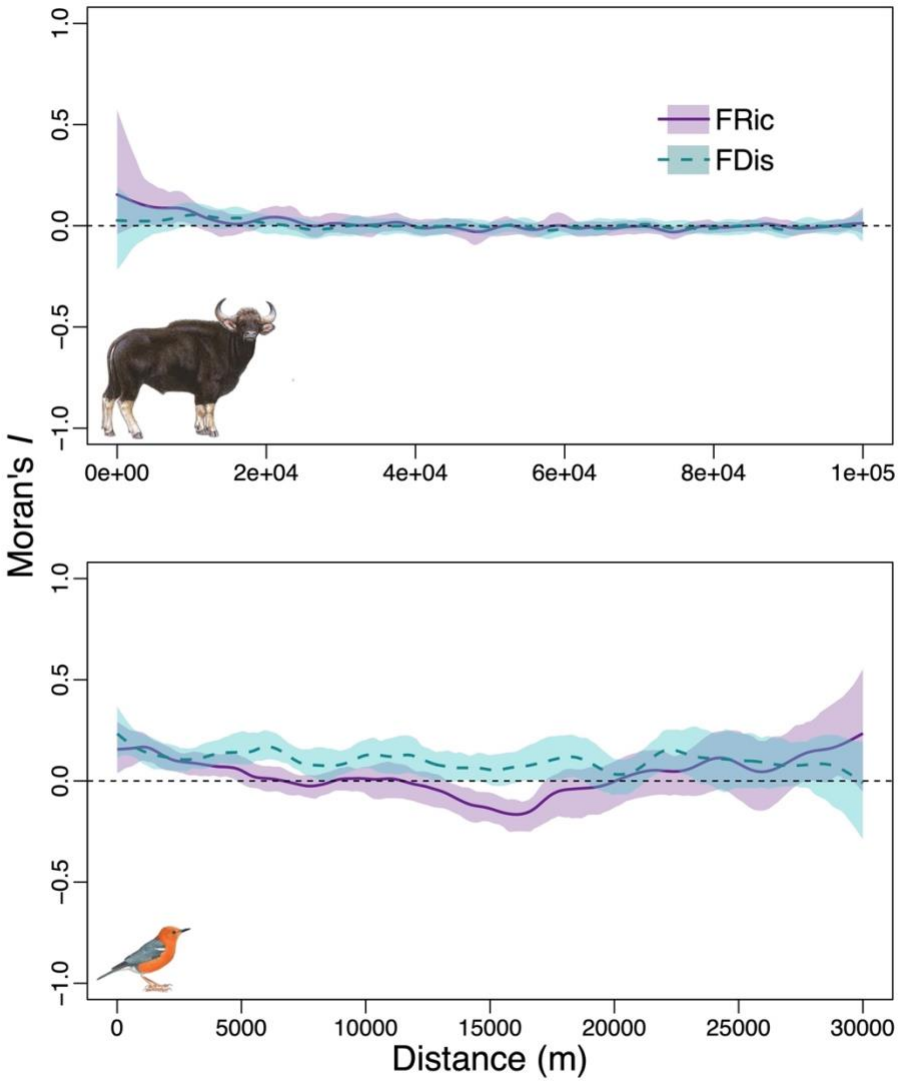


Figure S10 Spline correlograms of spatial autocorrelation for FD metrics across the study sites (camera stations) for mammals (top) and birds (bottom) using Moran's I test. Solid and dashed lines indicate mean, and shaded areas indicate 95% confidence intervals

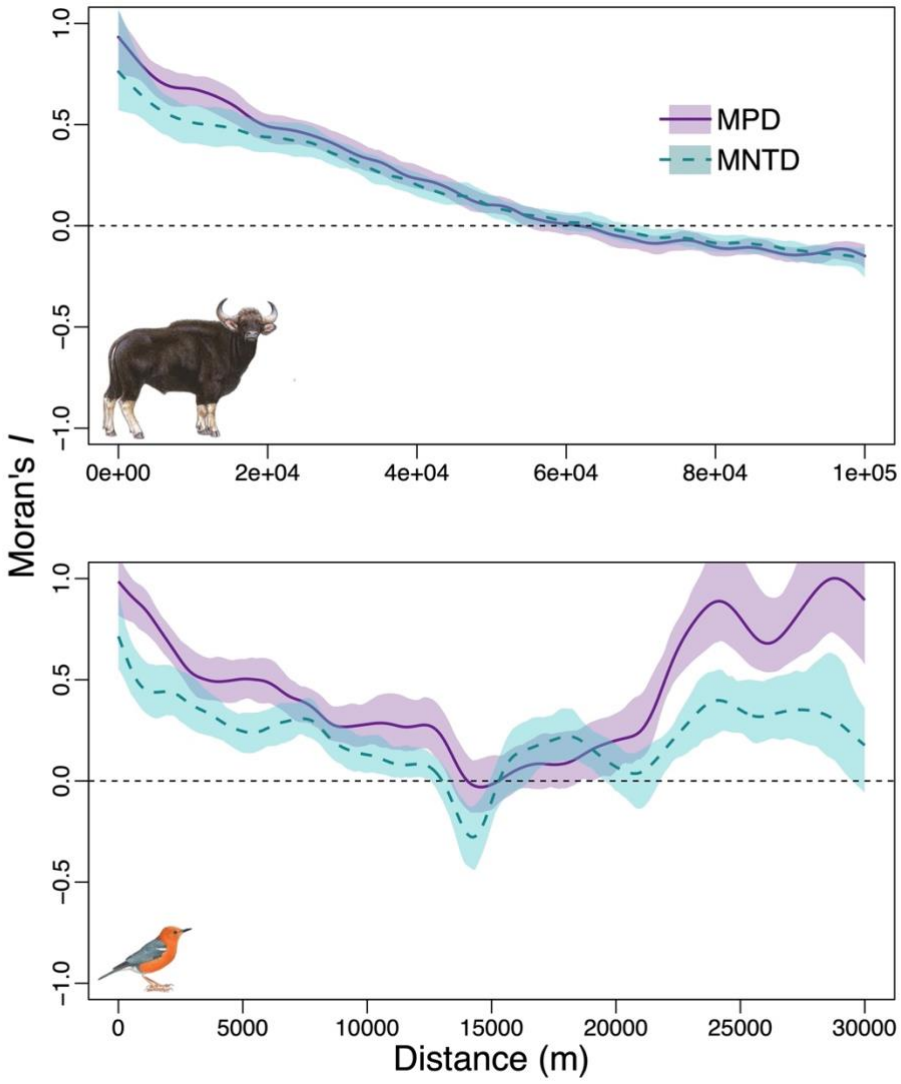


Figure S11 Spline correlograms of spatial autocorrelation for PD metrics across the study sites (camera stations) for mammals (top) and birds (bottom) using Moran's I test. Solid and dashed lines indicate mean, and shaded areas indicate 95% confidence intervals

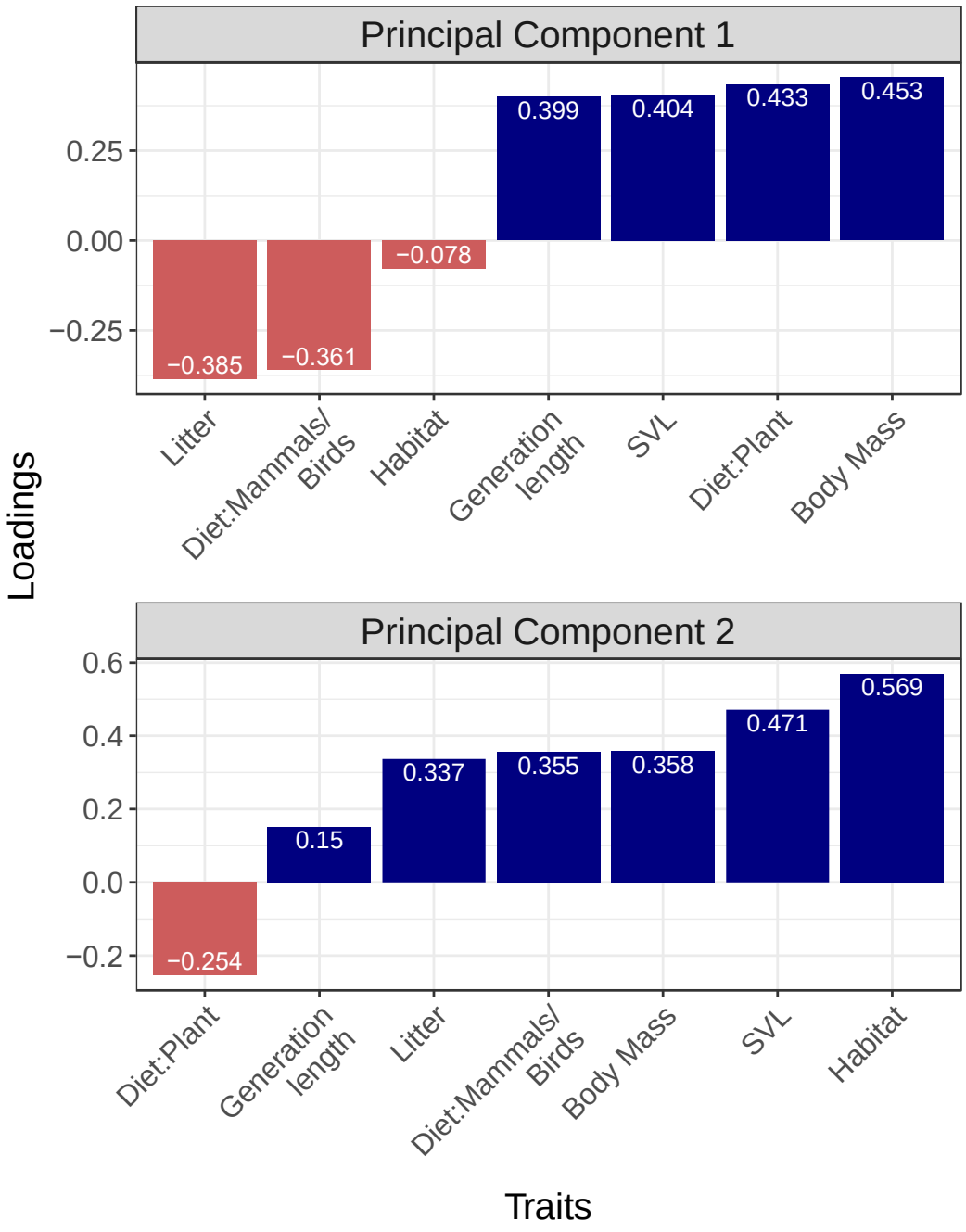


Figure S12 Trait loadings (right) based on 7 morphological and ecological traits for mammals (red bars indicate negative eigenvalues and blue shows positive values) presented along the two axes

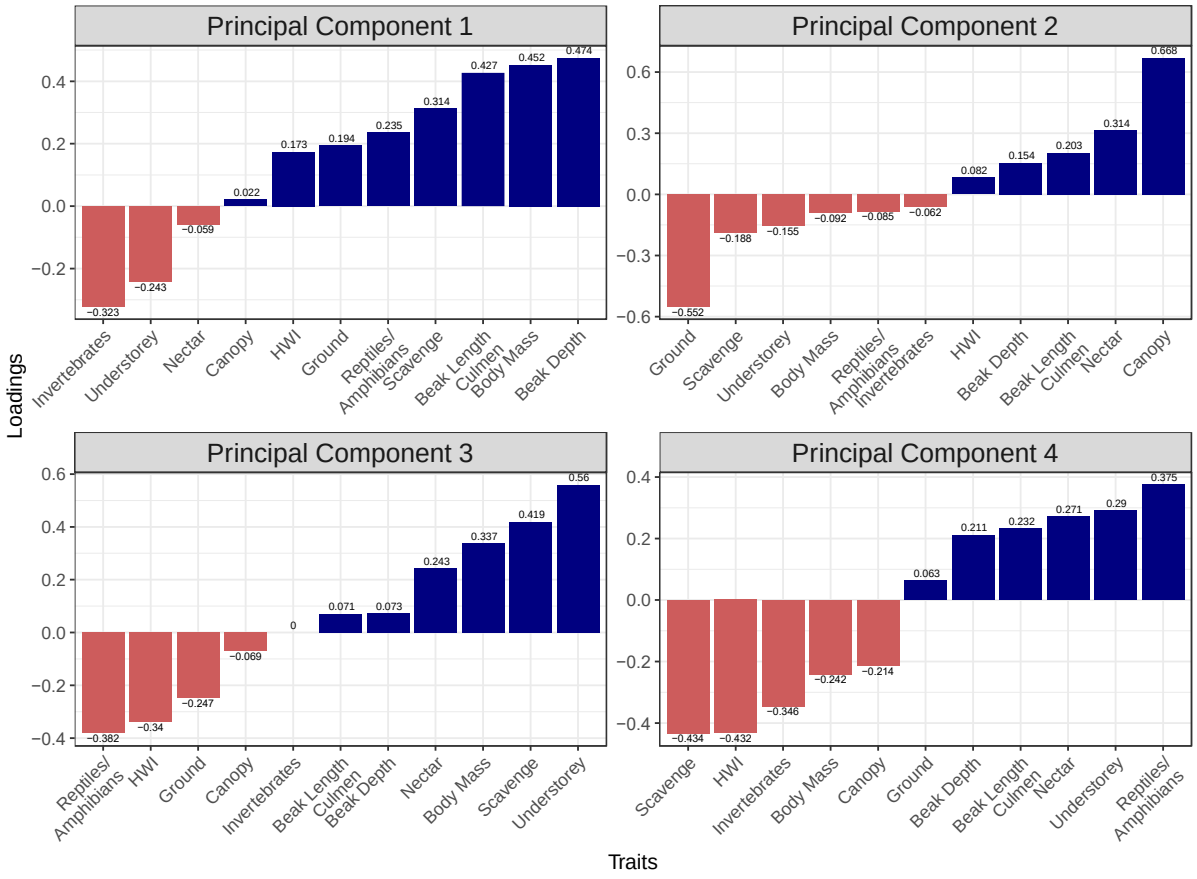


Figure S13 Trait loadings (right) based on 11 morphological and ecological traits for birds (red bars indicate negative eigenvalues and blue shows positive values) represented along the four axes

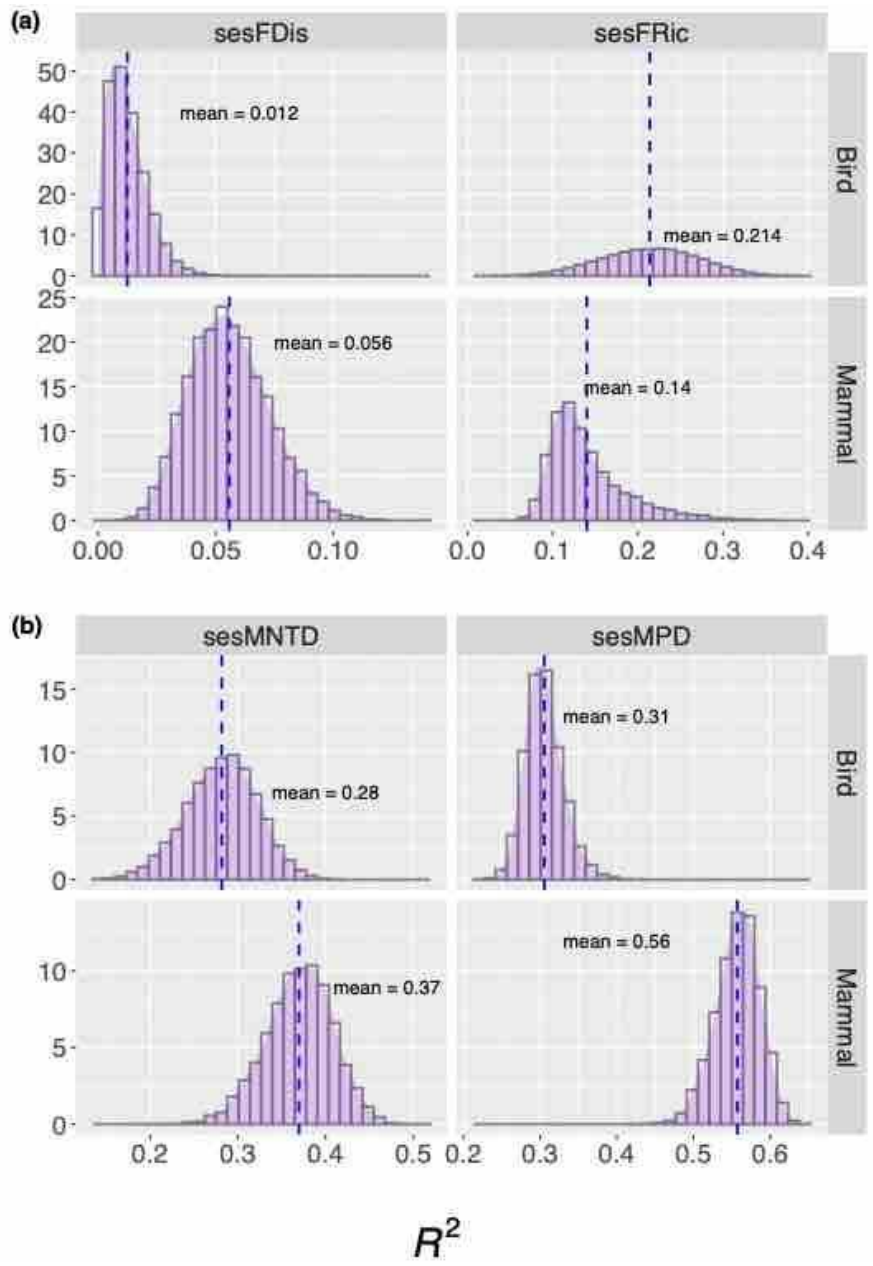


Figure S14 Posterior distributions of Bayesian R^2 for the linear mixed-effect models of diversity metrics. Vertical lines indicate posterior means

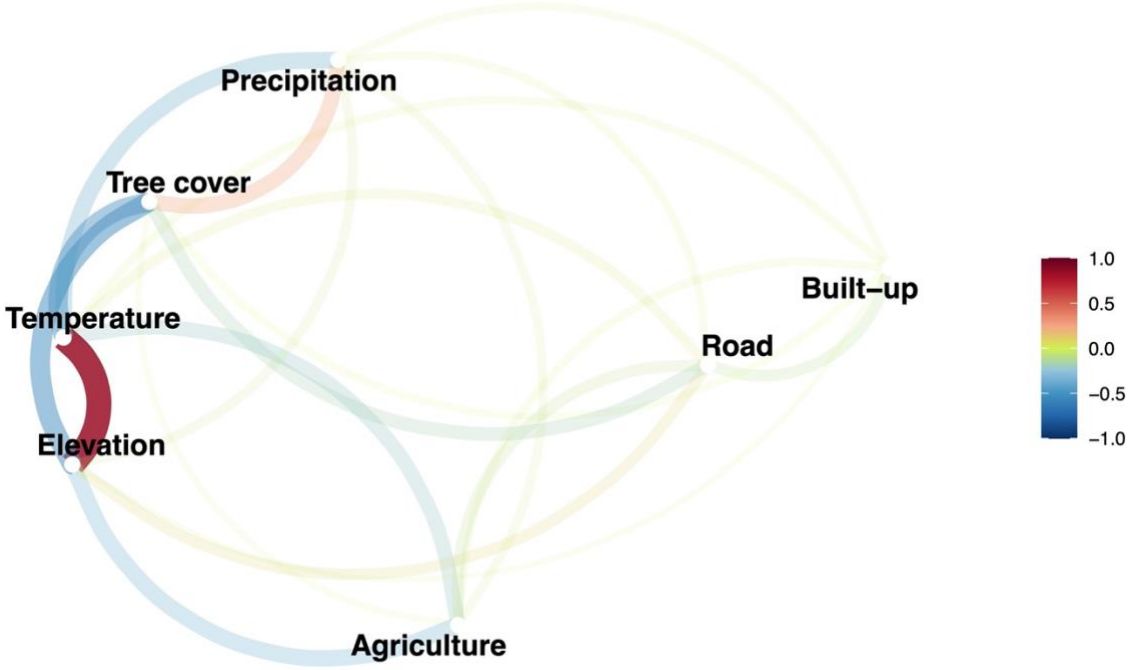


Figure S15 Correlation among variables used in regression models for mammals FD and PD

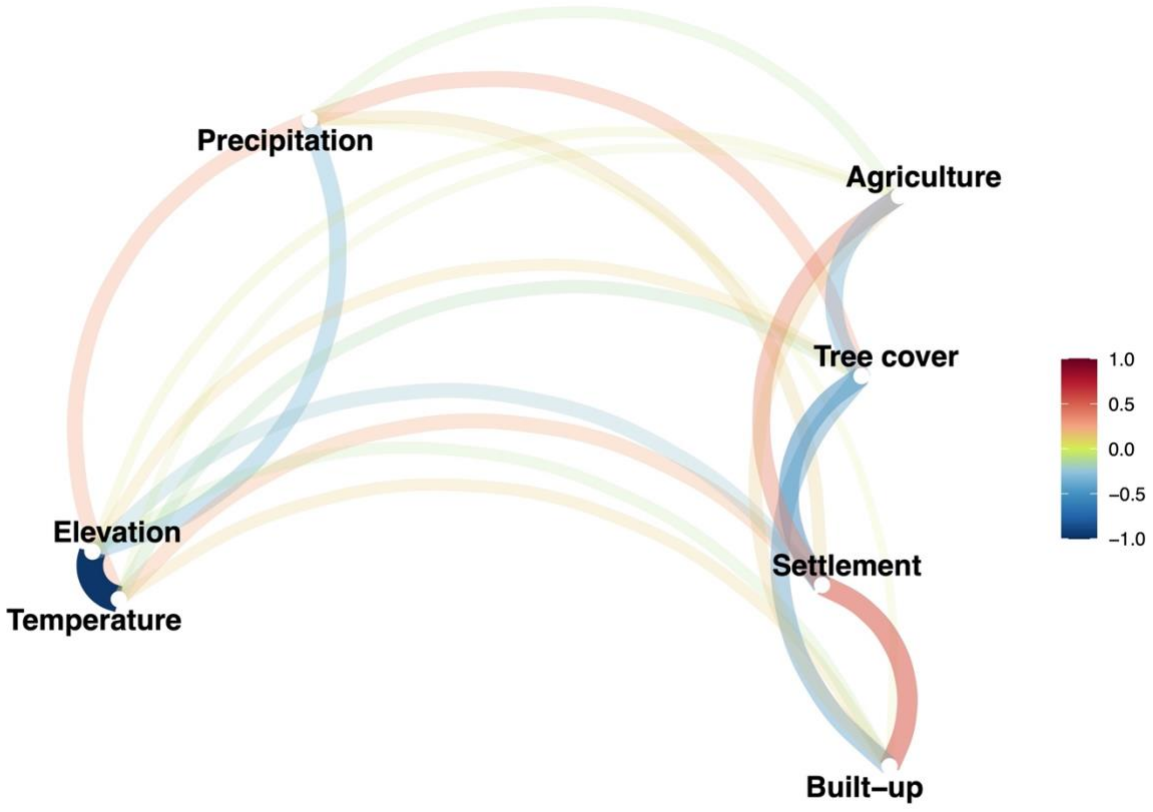


Figure S16 Correlation among variables used in regression models for birds FD and PD

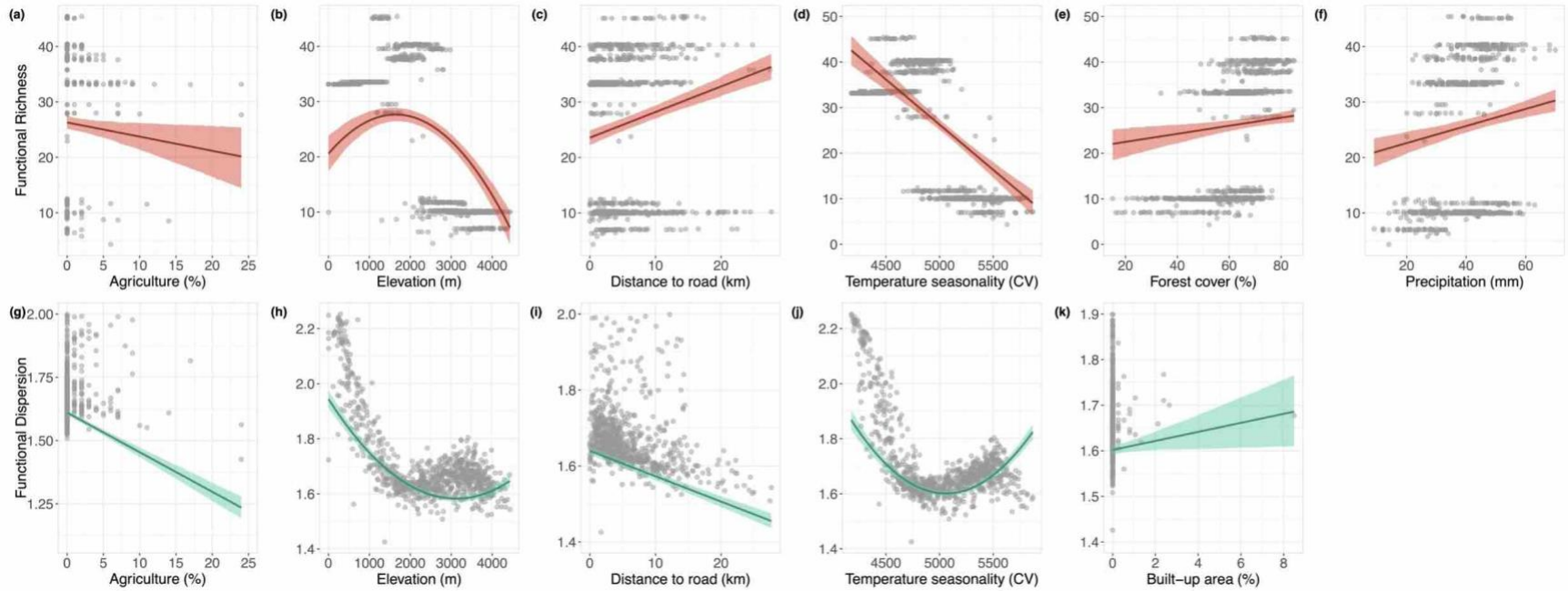


Figure S17 Relationship between FD (represented by FRic and FDis without accounting for species richness) and land use and climate variables for mammals. Predictions were made from the top model. Solid lines indicate mean, and polygons represent 95% credible intervals

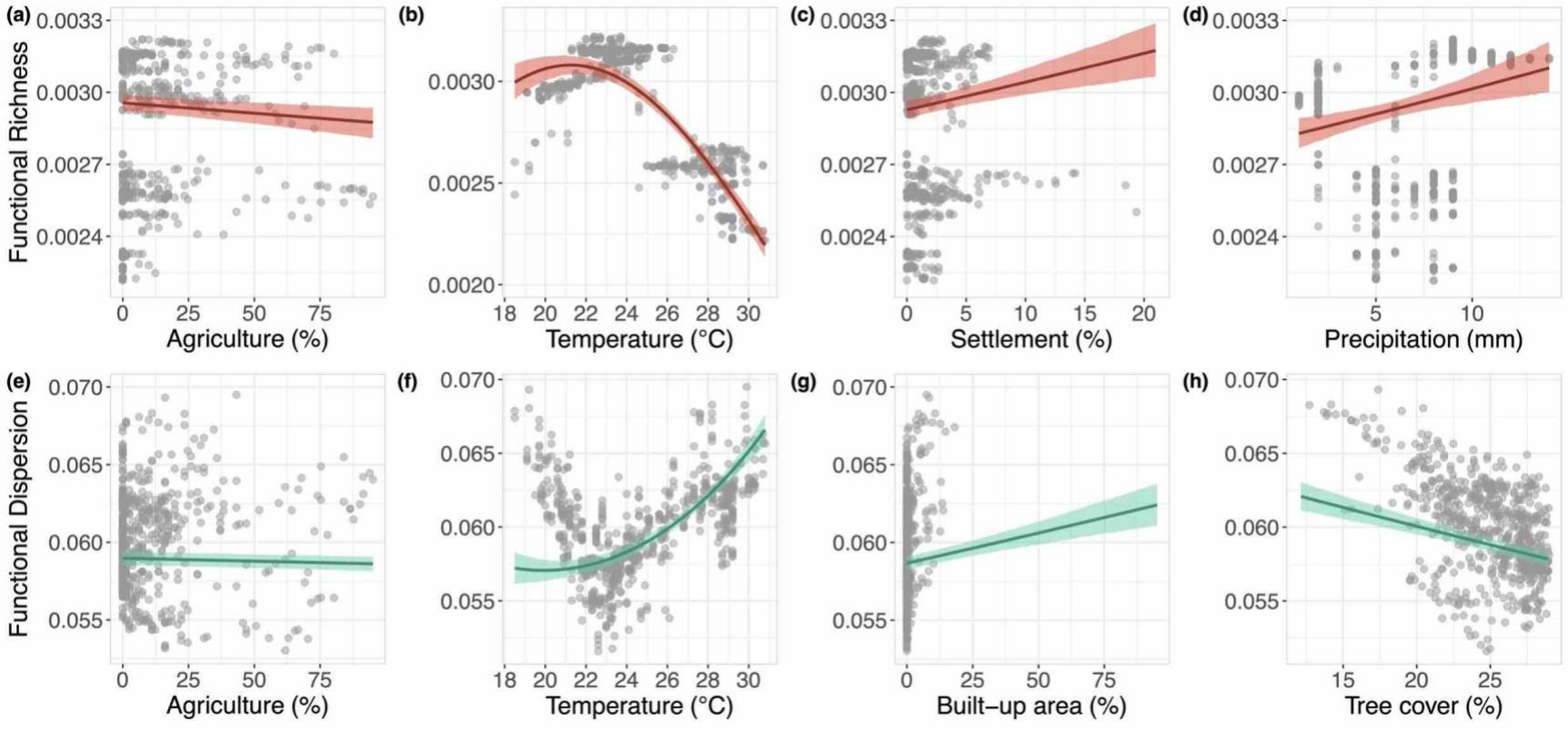


Figure S18 Relationship between PD (represented by FRic and FDis without accounting for species richness) and land use and climate variables for birds. Predictions were made from the top model. Solid lines indicate mean, and polygons represent 95% credible intervals

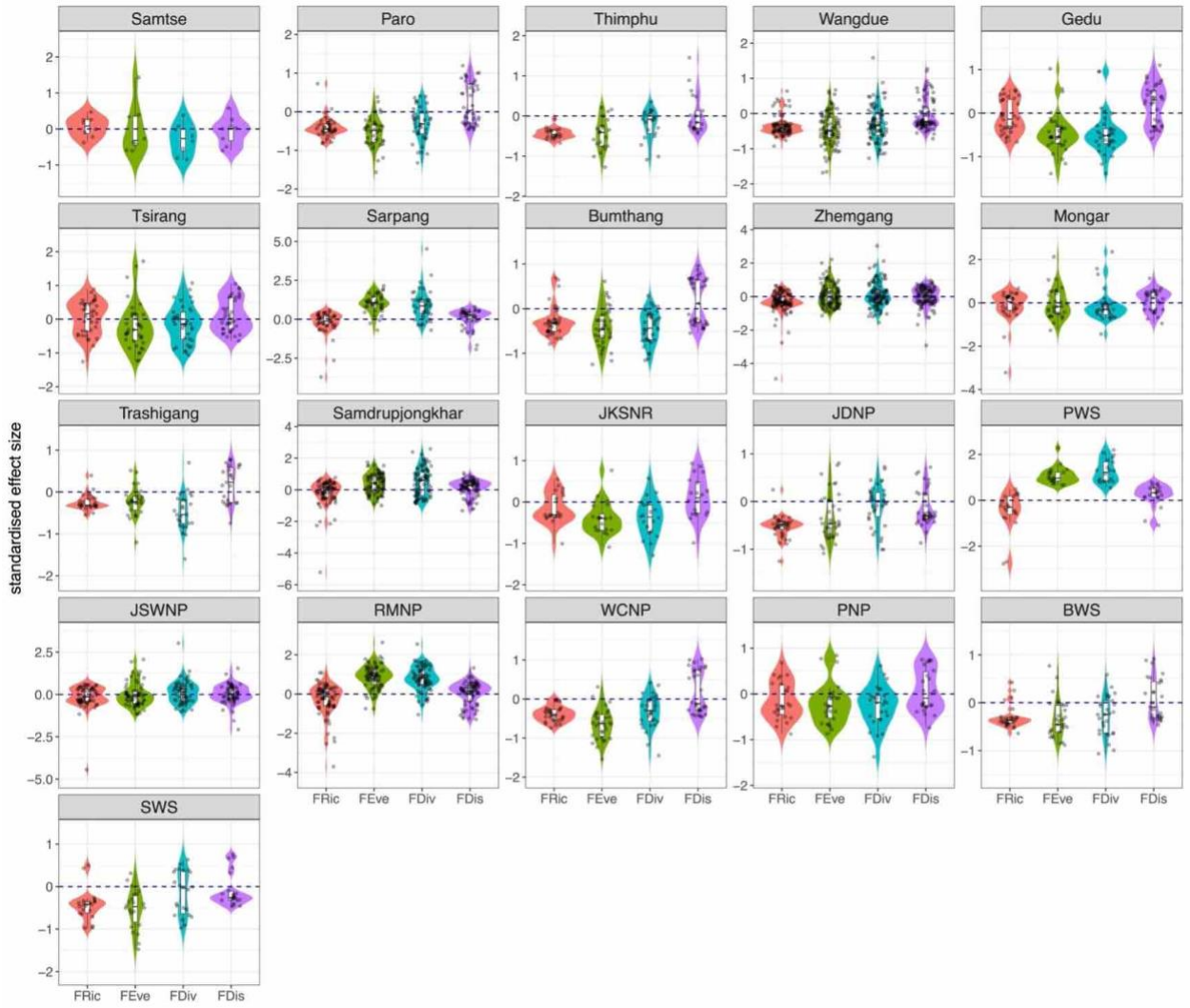


Figure S19 Functional Diversity of mammals (measured using functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis)) across 21 study areas in Bhutan. Boxplots complement density plots with means indicated by white dots and medians by horizontal bars

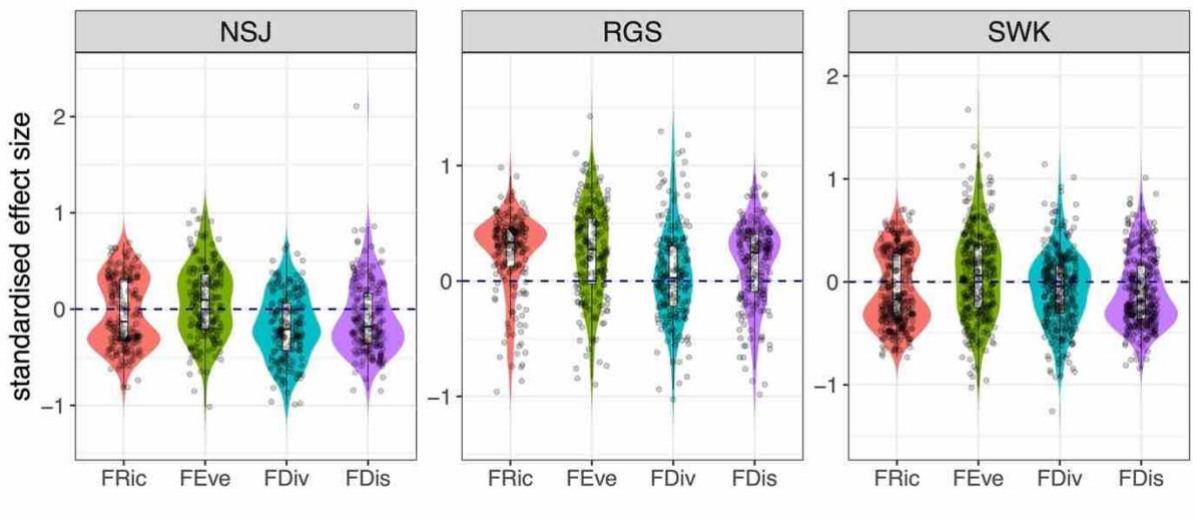


Figure S20 Functional Diversity of birds (measured using functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis)) across three study areas in Bhutan. Boxplots complement density plots with means indicated by white dots and medians by horizontal bars

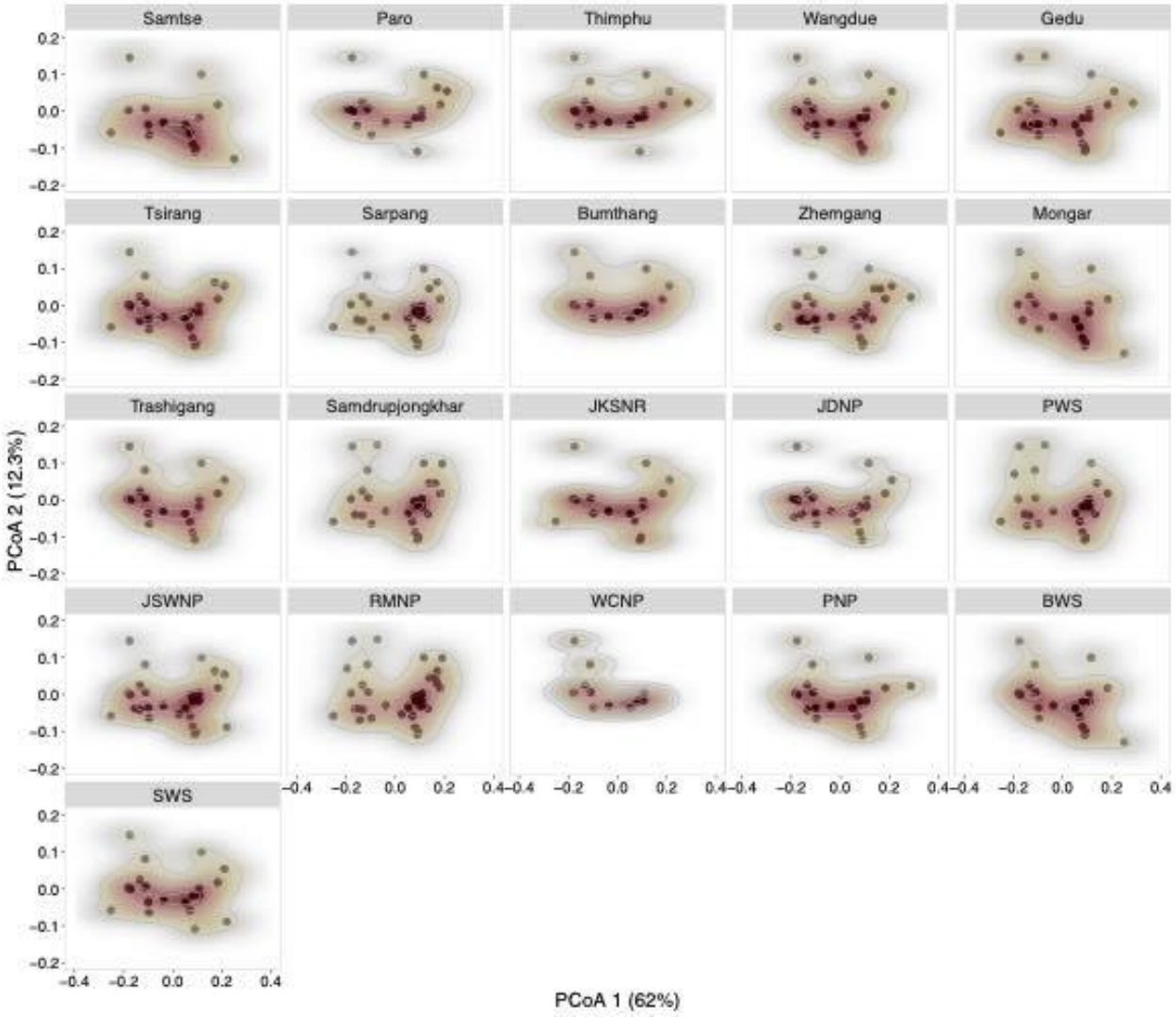


Figure S21 Functional trait space of mammal communities across 21 study areas in Bhutan visualised on principal coordinate analysis (PCoA) 1 and 2 (accounting for about 74% of the trait variance). Each point represents a species, and fill colour represents their density in functional space

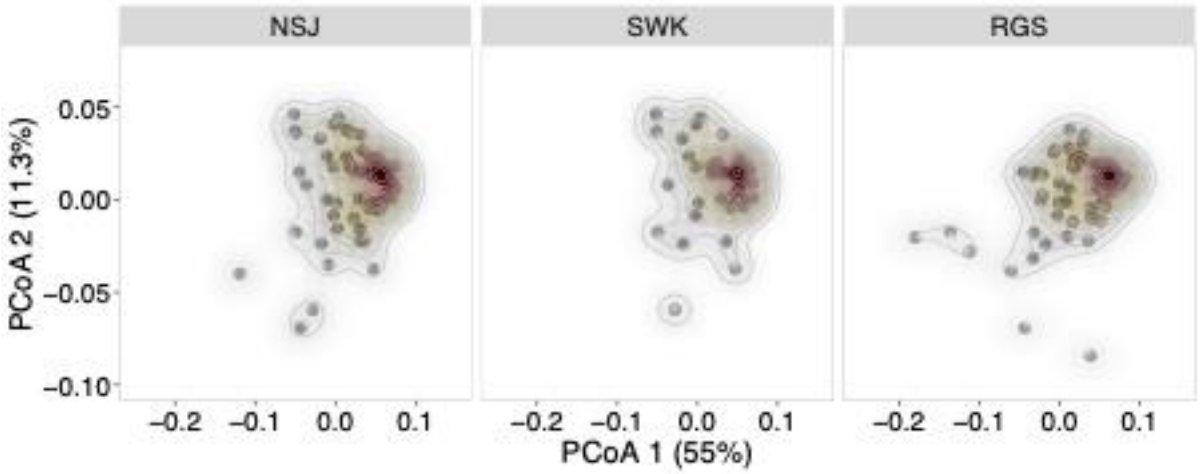
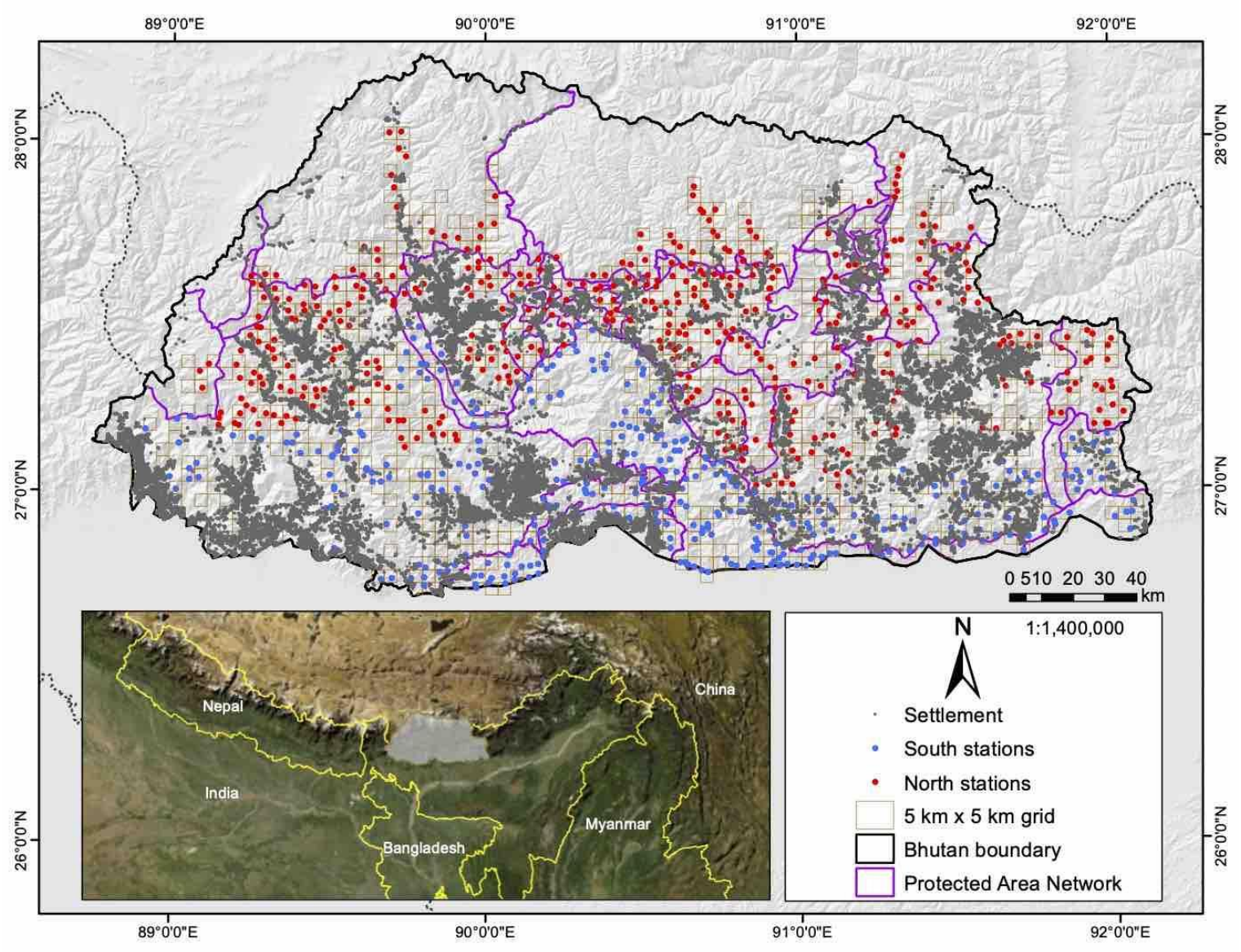


Figure S22 Functional trait space of bird communities across three study areas in Bhutan visualised on principal coordinate analysis (PCoA) 1 and 2 (accounting for about 66% of the trait variance). Each point represents a species, and fill colour represents their density in functional space

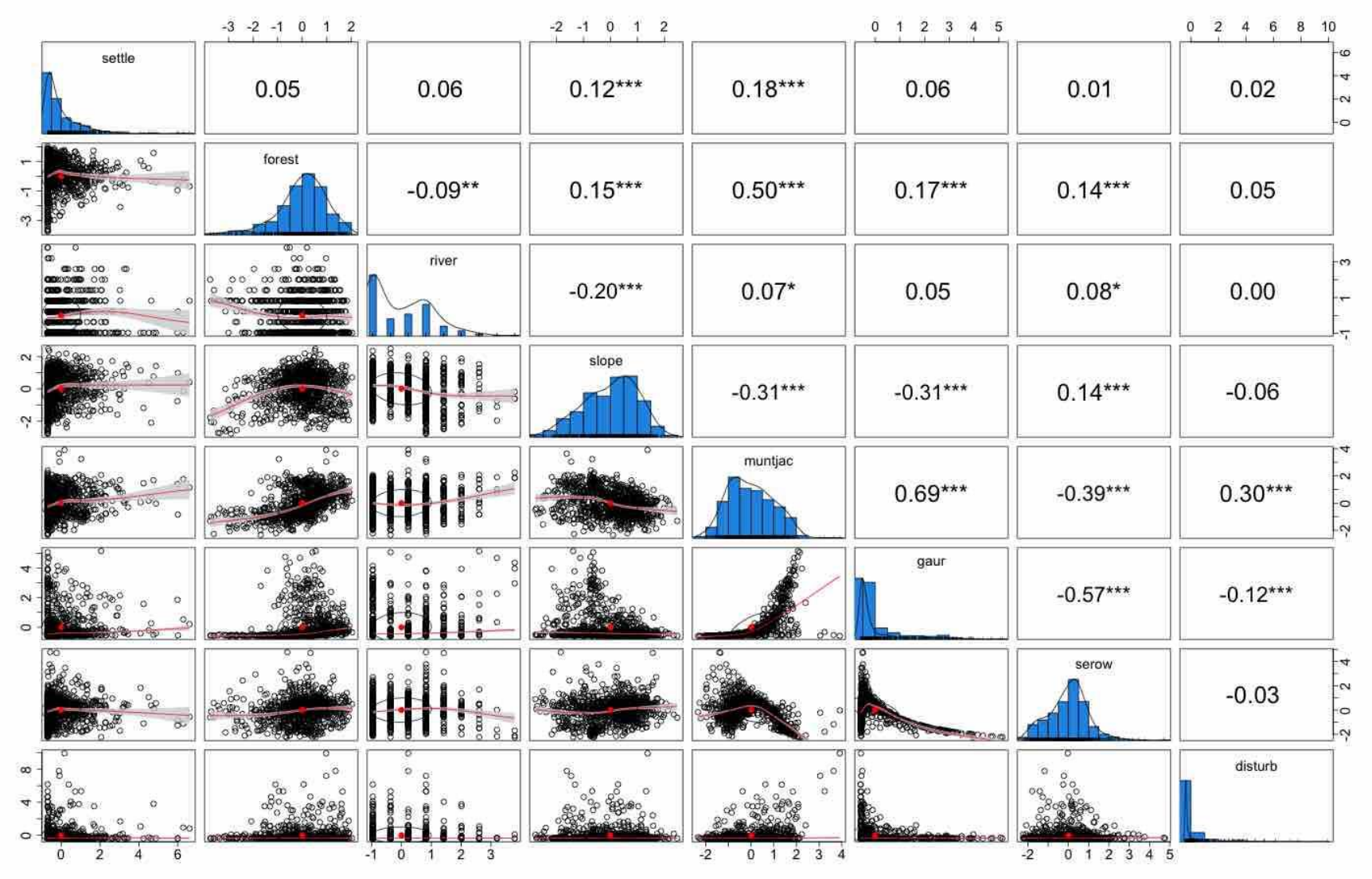
Supplementary material for Chapter 5



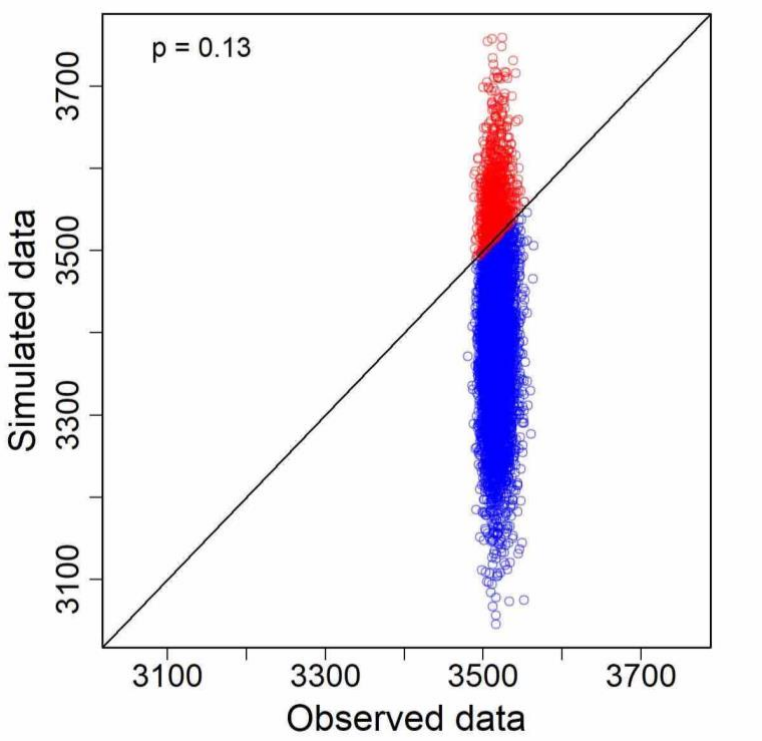
Appendix S1 Study area with camera trap locations. Inset shows the location of Bhutan in continental south Asia

Appendix S2 Table showing mean, and range of landscape variables used in the analysis

Landscape covariate	**Mean**	**Range**
Settlement density (percentage of land under settlement)	2.02	0 – 21.19
Disturbance (daily detection rates of livestock and humans at camera trap site)	49.19	0 – 1360
Forest cover (percentage of land under forest)	59.03	13.31 – 83.78
River density (percentage of land under river)	1.6	0 – 8
Slope	127.07	-821.66 – 971.51
Gaur (abundance at a site)	1.48	0 – 14.33
Muntjac (abundance at a site)	6.94	5.59 – 9.51
Serow (abundance at a site)	3.16	1.18 – 7.36
Effort (number of active camera trap days)	83.3	1 – 156



Appendix S3 Correlation plot of the landscape variables used in the multispecies interaction model



Appendix S4 Posterior predictive check of the top model. Red and blue points show the simulated and observed data, respectively. The model adequately fitted the data (Bayesian p-value = 0.13). The poor fit model has these points on either side of the diagonal line and p-value < 0.05 or > 0.95

Appendix S5 Marginal occupancy parameter estimates of tiger

Parameter	Mean	2.5%	97.5%
Intercept	**-2.498**	**-4.620**	**-0.944**
Settlement	0.252	-0.682	1.277
Disturbance	0.420	-2.274	2.671
Forest	**0.780**	**0.256**	**1.369**
River	0.460	0.109	0.858
Slope	-0.096	-0.587	0.324
Gaur	-0.813	-3.320	1.141
Muntjac	-0.086	-1.944	2.082
Serow	-0.496	-1.890	0.841

Bold *indicates a significant effect*

Appendix S6 Marginal occupancy parameter estimates of leopard

Parameter	Mean	2.5%	97.5%
Intercept	**-1.098**	**-2.302**	**-0.059**
Settlement	-0.161	-1.037	0.477
Disturbance	0.087	-2.100	2.249
Forest	0.119	-0.318	0.553
River	**0.407**	**0.110**	**0.740**
Slope	**0.370**	**0.040**	**0.709**
Gaur	-0.600	-1.957	0.639
Muntjac	0.501	-0.832	1,829
Serow	**-1.257**	**-2.539**	**-0.101**

Bold *indicates a significant effect*

Appendix S7 Marginal occupancy parameter estimates of dhole

Parameter	Mean	2.5%	97.5%
Intercept	-0.512	-1.709	0.796
Settlement	**-1.529**	**-2.832**	**-0.456**
Disturbance	0.404	-2.059	2.943
Forest	-0.472	-1.274	0.221
River	**-0.593**	**-1.082**	**-0.153**
Slope	**0.641**	**0.088**	**1.332**
Gaur	-1.496	-3.520	0.175
Muntjac	0.561	-0.915	2.053
Serow	0.324	-0.732	1.448

Bold *indicates a significant effect*

Appendix S8 Conditional occupancy parameter estimates of tiger-leopard pair

Parameter	**Mean**	**2.5%**	**97.5%**
Intercept	0.464	-0.830	1.819
Settlement	**-1.621**	**-3.164**	**-0.258**
Disturbance	1.244	-1.234	3.862
Gaur	**2.296**	**0.306**	**4.562**
Muntjac	-1.130	-2.516	0.226
Serow	0.695	-0.210	1.717

Bold *indicates a significant effect*

Appendix S9 Conditional occupancy parameter estimates of tiger-dhole pair

Parameter	Mean	2.5%	97.5%
Intercept	**2.735**	**0.917**	**5.179**
Settlement	0.050	-1.323	1.576
Disturbance	1.142	-1.542	4.044
Gaur	0.579	-1.237	2.465
Muntjac	-0.776	-2.759	0.959
Serow	-0.132	-1.620	1.342

Bold *indicates a significant effect*

Appendix S10 Conditional occupancy parameter estimates of leopard-dhole pair

Parameter	Mean	2.5%	97.5%
Intercept	0.955	-0.621	2.658
Settlement	**2.047**	**0.795**	**3.669**
Disturbance	-0.096	-3.186	2.851
Gaur	1.724	-0.360	3.880
Muntjac	-0.386	-2.213	1.380
Serow	1.036	-0.501	2.585

Bold *indicates a significant effect*

Appendix S11 Parameter estimates of detection probability of tiger

Parameter	Mean	2.5%	97.5%
Intercept	**-3.236**	**-3.912**	**-2.617**
Trail	**1.663**	**1.044**	**2.336**
Effort	**0.488**	**0.281**	**0.689**
Disturbance	**-0.725**	**-1.062**	**-0.384**

Bold *indicates a significant effect*

Appendix S12 Parameter estimates of detection probability of leopard

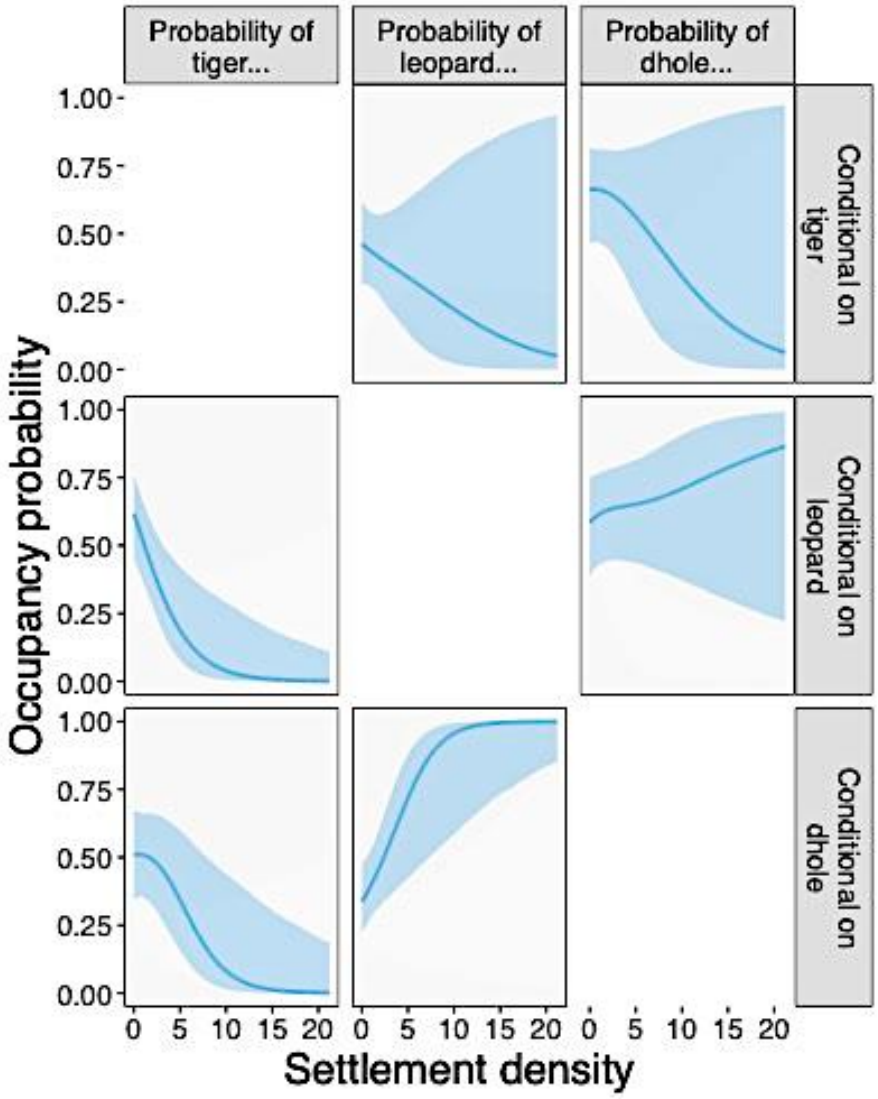
Parameter	Mean	2.5%	97.5%
Intercept	**-2.479**	**-2.992**	**-1.959**
Trail	**1.310**	**0.785**	**1.823**
Effort	**0.510**	**0.341**	**0.679**
Disturbance	**-0.280**	**-0.446**	**-0.123**

Bold *indicates a significant effect*

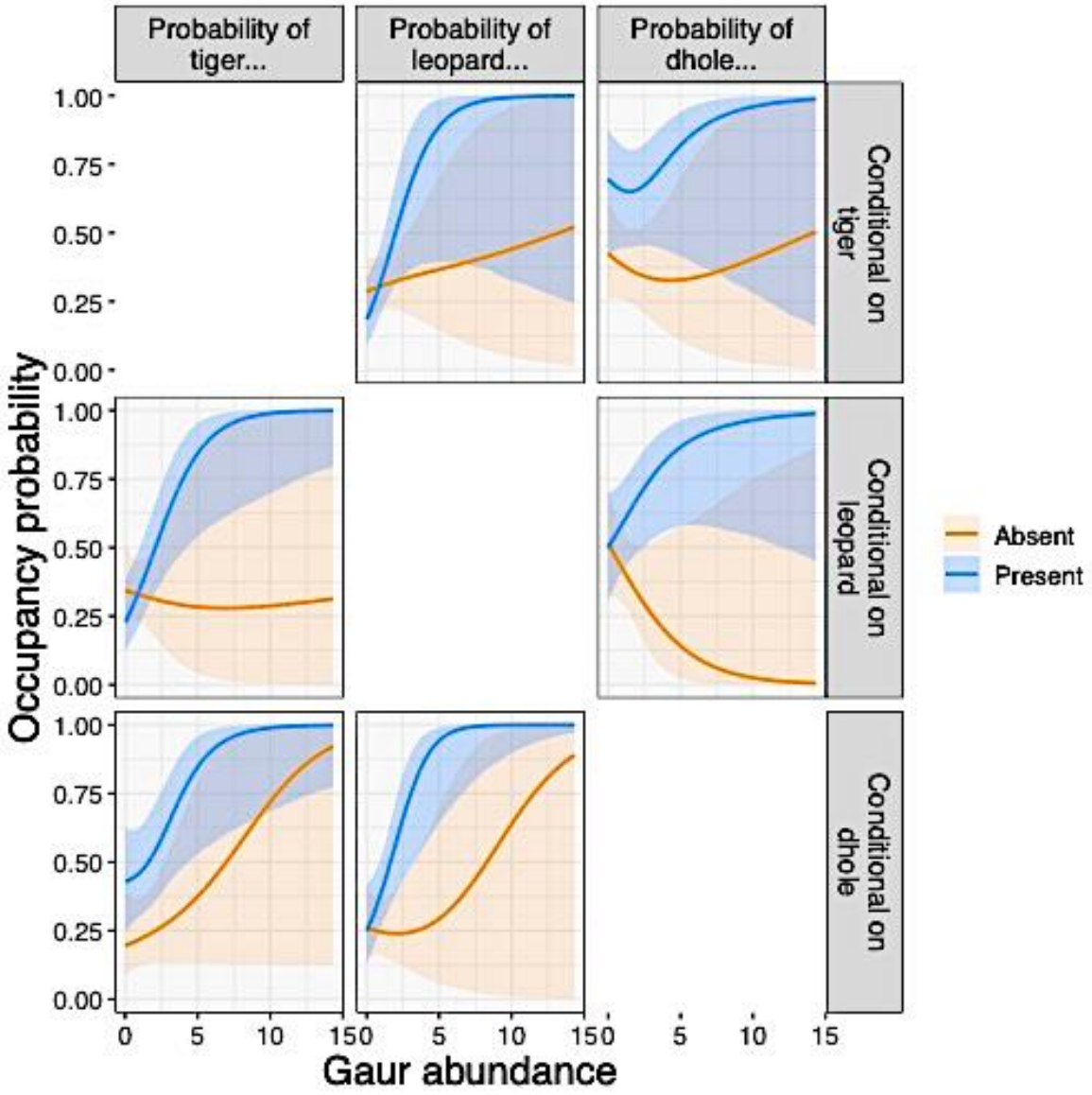
Appendix S13 Parameter estimates of detection probability of dhole

Parameter	Mean	2.5%	97.5%
Intercept	**-3.288**	**-3.792**	**-2.803**
Trail	**1.415**	**0.934**	**1.935**
Effort	**0.732**	**0.579**	**0.885**
Disturbance	-0.039	-0.162	0.075

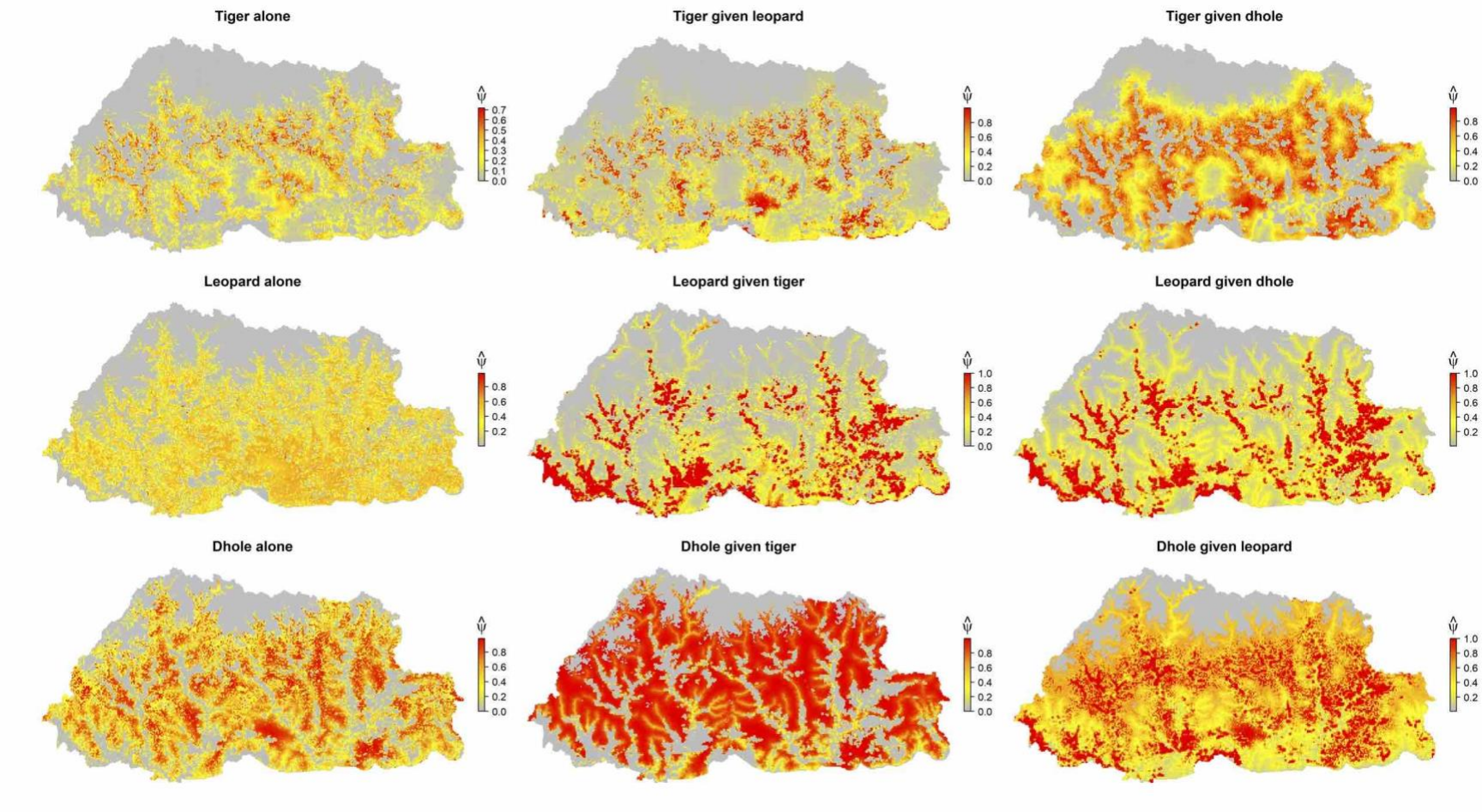
Bold *indicates a significant effect*



Appendix S14 Occupancy probability of tiger, leopard and dhole conditional on the presence and absence of each of the other species along a human settlement density gradient around each camera trap. The probability of the species in each column is conditional on the presence and absence of the species in each row. The posterior means are represented by lines and 95% credible intervals by shaded ribbons



Appendix S15 Occupancy probability of tiger, leopard and dhole conditional on the presence and absence of each of the other species as a function of gaur abundance. The probability of the species in each column is conditional on the presence and absence of the species in each row. The posterior means are represented by lines and 95% credible intervals by shaded ribbons



Appendix S16 Spatial prediction of occupancy probability. Marginal occupancy probability (left), conditional occupancy probability (centre and right)

Supplementary material for Supplementary Chapter 1

Table S1. Details of the camera trap survey in Bhutan during the year 2014 and 2015. Divisions are areas outside protected areas (national parks and wildlife sanctuaries)

Study area	Block	Year	Number of stations	Total trap days	Mean trap days (SD)
Jigme Khesar Strict Nature Reserve	North	2014-15	20	1701	85(37.2)
Paro Division	North	2014-15	40	2775	69.4(31.7)
Jigme Dorji National Park	North	2014-15	38	1997	52.5(31.1)
Thimphu Division	North	2014-15	21	1825	86.9(48.1)
Wangdue Division	North	2014-15	81	5393	66.6(40.1)
Wangchuck Centenniel National Park	North	2014-15	31	1091	35.2(24.5)
Bumthang Division	North	2014-15	37	3914	105.8(36.8)
Mongar Division	North	2014-15	30	1931	64.4(24.5)
Phrumsengla National Park	North	2014-15	26	1873	72(40.6)
Bumdelling Wildlife Sanctuary	North	2014-15	29	3369	116.2(45.8)
Trashigang Division	North	2014-15	25	2419	96.8(30.3)
Sakteng Wildlife Sanctuary	North	2014-15	22	1908	86.7(53.7)
Samtse Division	South	2014	8	762	95.2(25.2)
Gedu Division	South	2014	34	2655	78.1(38.0)
Tsirang Division	South	2014	37	4020	108.6(38.1)
Phipsoo Wildlife Sanctuary	South	2014	20	2353	117.6(20.2)
Sarpang Division	South	2014	39	3807	97.6(24.3)
Jigme Singye Wangchuck National Park	South	2014	58	6264	108(23.1)
Royal Manas National Park	South	2014	73	7728	105.9(27.4)
Zhengang Division	South	2014	102	8637	84.7(33.0)
Samdrupjongkhar Division	South	2014	78	6837	87.6(33.8)
			849	73259	

Table S2. Coefficient estimates and uncertainties of the overall response of mammal assemblage in Bhutan to land use and climate variables (1960-1990). Bold figures indicate that the 95% CRIs do not overlap zero

Parameters ($\widehat{\beta}$)	**mean**	**SD**	**2.50%**	**97.50%**
Intercept (ψ)	**-2.727**	**0.295**	**-3.310**	**-2.155**
Agriculture	**-0.102**	**0.028**	**-0.161**	**-0.051**
Distance to road	**0.105**	**0.037**	**0.036**	**0.181**
Distance to settlement	0.025	0.058	-0.087	0.143
Forest cover	**0.206**	**0.086**	**0.035**	**0.373**
Precipitation	**-0.248**	**0.077**	**-0.407**	**-0.105**
Temperature	**-0.259**	**0.088**	**-0.434**	**-0.089**
Intercept (p)	**-4.196**	**0.186**	**-4.581**	**-3.846**
Camera model (HCO)*	0.000	0.000	0.000	0.000
Camera model (Bushnell)	**0.194**	**0.026**	**0.142**	**0.245**
Camera model (Cuddeback)	-0.041	0.021	-0.083	0.001
Camera model (Reconyx)	**0.211**	**0.023**	**0.166**	**0.257**
Camera model (Uway)	**-0.110**	**0.021**	**-0.152**	**-0.068**
Trail	**0.323**	**0.115**	**0.094**	**0.547**

** values for this camera model are zero because it was taken as a reference camera model and takes the value of the intercept (see BUGS model code)*

Table S3. The list of 45 terrestrial mammal species used in the multi-species occupancy model. The common names are alphabetically ordered. The order of Latin names corresponds to the common names and are abbreviated for the first three letters of Genus and Species names

Sl. No.	Common name	Scientific name	Abbreviation	IUCN Red List	
1	Asian elephant	*Elephas maximus*	ELEMAX	Endangered	EN
2	Asiatic black bear	*Ursus thibetanus laniger*	URSTHI	Vulnerable	VU
3	Asiatic brush-tailed porcupine	*Atherurus macrourus*	ATHMAC	Least Concern	LC
4	Asiatic golden cat	*Catopuma timminckii*	CATTIM	Near Threatened	NT
5	Asiatic wild water buffalo	*Bubalus arnee*	BUBARN	Endangered	EN
6	Assamese macaque	*Macaca assamensis*	MACASS	Near Threatened	NT
7	Bengal tiger	*Panthera tigris tigris*	PANTIG	Endangered	EN
8	Bhutan takin	*Budorcas taxicolor whitei*	BUDTAX	Vulnerable	VU
9	Binturong	*Arctictis binturong*	ARCBIN	Vulnerable	VU
10	Bharal/Bluesheep	*Pseudois nayaur*	PSENAY	Least Concern	LC
11	Capped langur	*Trachypithecus pileatus*	TRAPIL	Vulnerable	VU
12	Clouded leopard	*Neofelis nebulosa*	NEONEB	Vulnerable	VU
13	Common leopard	*Panthera pardus*	PANPAR	Vulnerable	VU
14	Common palm civet	*Paradoxurus hermaphroditus*	PARHER	Least Concern	LC
15	Crab-eating mongoose	*Herpestes urva*	HERURV	Least Concern	LC
16	Dhole	*Cuon alpinus*	CUOALP	Endangered	EN
17	Gaur	*Bos gaurus*	BOSGAU	Vulnerable	VU
18	Golden jackal	*Canis aureus*	CANAUR	Least Concern	LC
19	Golden langur	*Trachypithecus geei*	TRAGEE	Endangered	EN
20	Himalayan goral	*Naemorhedus goral*	NAEGOR	Near Threatened	NT
21	Himalayan musk deer	*Moschus leucogaster*	MOSLEU	Endangered	EN
22	Himalayan serow	*Capricornis thar*	CAPTHA	Near Threatened	NT
23	Indian hare	*Lepus nigricollis*	LEPNIG	Least Concern	LC
24	Indian muntjac	*Muntiacus muntjak*	MUNMUN	Least Concern	LC
25	Jungle cat	*Felis chaus*	FELCHA	Least Concern	LC
26	Large Indian civet	*Viverra zibetha*	VIVZIB	Least Concern	LC
27	Leopard cat	*Prionailurus bengalensis*	PRIBEN	Least Concern	LC
28	Malayan porcupine	*Hystrix brachyura*	HYSBRA	Least Concern	LC
29	Marbled cat	*Pardofelis marmorata*	PARMAR	Near Threatened	NT
30	Masked palm civet	*Paguma larvata*	PAGLAR	Least Concern	LC
31	Mountain weasel	*Mustela altaica*	MUSALT	Near Threatened	NT
32	Pangolin	*Manis spp.*	MANISS	Endangered	EN
33	Red fox	*Vulpes vulpes*	VULVUL	Least Concern	LC
34	Red panda	*Ailurus fulgens*	AILFUL	Endangered	EN
35	Rhesus macaque	*Macaca mulatta*	MACMUL	Least Concern	LC

36	Sambar	*Rusa unicolor*	RUSUNI	Vulnerable	VU
37	Siberian weasel	*Mustela sibirica*	MUSSIB	Least Concern	LC
38	Small-tooth ferret badger	*Melogale moschata*	MELMOS	Least Concern	LC
39	Small Indian civet	*Viverricula indica*	VIVIND	Least Concern	LC
40	Small Indian mongoose	*Herpestes auropunctatus*	HERAUR	Least Concern	LC
41	Spotted linsang	*Prionodon pardicolor*	PRIPAR	Least Concern	LC
42	Tarai Gray langur	*Semnopithecus hector*	SEMHEC	Least Concern	LC
43	Wild pig	*Sus scrofa*	SUSSCR	Least Concern	LC
44	Yellow-bellied weasel	*Mustela kathiah*	MUSKAT	Least Concern	LC
45	Yellow-throated marten	*Martes flavigula*	MARFLA	Least Concern	LC

Table S4. Posterior summary results of the number of sites occupied by each species (left), occupancy (centre) and detection (right) probabilities. The uncertainties of the point estimates (mean) are shown as standard deviations (SD) and 95% CRIs (2.50%, 97.50%)

Scientific name	Number of sites occupied					Occupancy probability (ψ)				Detection probability (p)			
	observed	Estimated mean	SD	2.50%	97.50%	mean	SD	2.50%	97.50%	mean	SD	2.50%	97.50%
Elephas maximus	81	83.88	1.73	81.00	88.00	0.06	0.01	0.04	0.08	0.061	0.007	0.049	0.074
Atherurus macrourus	36	40.10	2.47	36.00	46.00	0.04	0.01	0.02	0.06	0.025	0.012	0.008	0.056
Catopuma timminckii	260	336.00	10.71	316.00	358.00	0.39	0.02	0.35	0.44	0.019	0.002	0.015	0.023
Bubalus arnee	5	5.66	0.91	5.00	8.00	0.01	0.00	0.00	0.01	0.031	0.018	0.009	0.076
Macaca assamensis	132	177.35	9.29	161.00	197.00	0.20	0.02	0.16	0.24	0.018	0.003	0.012	0.025
Panthera tigris tigris	151	244.36	14.70	218.00	275.00	0.28	0.03	0.23	0.33	0.005	0.001	0.003	0.008
Budorcas taxicolor whitei	3	3.81	1.17	3.00	7.00	0.00	0.00	0.00	0.01	0.035	0.018	0.010	0.081
Arctictis binturong	4	27.84	30.74	5.00	109.00	0.03	0.03	0.00	0.11	0.004	0.003	0.001	0.013
Pseudois nayaur	1	6.27	9.50	1.00	31.00	0.01	0.01	0.00	0.03	0.008	0.009	0.001	0.031
Trachypithecus pileatus	11	21.56	7.85	12.00	42.00	0.02	0.01	0.01	0.04	0.009	0.004	0.003	0.020
Neofelis nebulosa	114	203.74	17.32	173.00	241.00	0.20	0.03	0.15	0.26	0.005	0.002	0.003	0.009
Panthera pardus	197	274.98	12.24	252.00	300.00	0.32	0.02	0.28	0.37	0.009	0.002	0.006	0.013
Paradoxurus hermaphroditus	49	52.33	1.94	49.00	57.00	0.05	0.01	0.03	0.07	0.048	0.008	0.035	0.065
Herpestes urva	45	57.63	4.63	50.00	68.00	0.04	0.01	0.03	0.06	0.020	0.005	0.012	0.030
Cuon alpinus	210	348.11	17.78	315.00	385.00	0.42	0.03	0.36	0.48	0.004	0.001	0.003	0.006
Bos gaurus	107	114.71	2.90	110.00	121.00	0.11	0.01	0.09	0.14	0.048	0.005	0.038	0.059
Trachypithecus geei	11	19.17	5.26	12.00	32.00	0.02	0.01	0.01	0.04	0.009	0.006	0.002	0.024
Semnopithecus hector	9	22.69	10.80	11.00	51.00	0.02	0.01	0.01	0.05	0.007	0.005	0.002	0.020
Ursus thibetanus laniger	292	395.51	13.32	371.00	423.00	0.45	0.03	0.40	0.50	0.013	0.002	0.010	0.017
Hystrix brachyura	182	199.29	4.38	191.00	208.00	0.22	0.02	0.19	0.26	0.038	0.005	0.030	0.048
Naemorhedus goral	127	161.26	7.50	148.00	177.00	0.19	0.02	0.16	0.23	0.018	0.003	0.012	0.025
Moschus leucogaster	34	48.19	5.25	39.00	60.00	0.04	0.01	0.03	0.06	0.013	0.005	0.006	0.024
Paguma larvata	166	193.05	5.98	182.00	206.00	0.19	0.02	0.15	0.23	0.025	0.004	0.018	0.033
Capricornis thar	287	349.63	9.07	333.00	368.00	0.43	0.02	0.38	0.47	0.026	0.003	0.021	0.031
Martes flavigula	324	403.80	10.52	384.00	425.00	0.47	0.02	0.43	0.52	0.015	0.002	0.012	0.020
Lepus nigricollis	6	6.56	0.82	6.00	9.00	0.01	0.00	0.00	0.01	0.026	0.011	0.010	0.051

Canis aureus	1	8.17	13.18	1.00	40.00	0.01	0.01	0.00	0.04	0.006	0.006	0.001	0.021
Felis chaus	9	34.45	20.25	13.00	89.00	0.03	0.02	0.01	0.09	0.004	0.003	0.001	0.012
Viverra zibetha	40	44.75	2.48	41.00	50.00	0.04	0.01	0.03	0.06	0.026	0.006	0.015	0.040
Prionailurus bengalensis	264	320.40	9.22	303.00	339.00	0.37	0.02	0.33	0.42	0.015	0.003	0.011	0.020
Pardofelis marmorata	162	181.54	4.75	173.00	191.00	0.19	0.02	0.15	0.22	0.040	0.006	0.029	0.051
Mustela altaica	4	7.69	3.46	4.00	17.00	0.01	0.00	0.00	0.02	0.024	0.011	0.008	0.052
Muntiacus muntjak	494	508.55	3.14	503.00	515.00	0.62	0.02	0.58	0.66	0.122	0.004	0.114	0.130
Manis spp.	7	15.76	8.58	8.00	37.00	0.02	0.01	0.01	0.04	0.012	0.007	0.003	0.030
Vulpes vulpes	40	45.94	2.64	42.00	52.00	0.03	0.01	0.02	0.05	0.052	0.010	0.034	0.072
Ailurus fulgens	51	73.93	6.69	62.00	88.00	0.08	0.01	0.05	0.10	0.009	0.003	0.005	0.017
Macaca mulatta	13	19.84	4.17	14.00	30.00	0.02	0.01	0.01	0.04	0.011	0.005	0.004	0.023
Rusa unicolor	348	365.97	3.97	359.00	374.00	0.43	0.02	0.39	0.47	0.070	0.004	0.063	0.078
Mustela sibirica	5	10.86	5.36	5.00	24.00	0.01	0.01	0.00	0.03	0.011	0.006	0.003	0.027
Melogale moschata	7	11.77	4.02	7.00	22.00	0.01	0.01	0.00	0.03	0.012	0.006	0.004	0.027
Viverricula indica	11	20.62	6.27	13.00	36.00	0.02	0.01	0.01	0.04	0.009	0.005	0.003	0.020
Herpestes auropuntatus	2	8.75	10.15	2.00	35.00	0.01	0.01	0.00	0.03	0.008	0.006	0.001	0.024
Prionodon pardicolor	26	73.35	23.89	42.00	133.00	0.08	0.03	0.04	0.15	0.005	0.003	0.002	0.011
Sus scrofa	401	421.46	4.03	414.00	430.00	0.46	0.02	0.42	0.50	0.079	0.004	0.072	0.086
Mustela kathiah	4	15.11	14.19	4.00	51.00	0.02	0.02	0.00	0.06	0.007	0.005	0.001	0.020

Table S5. Summary results for 45 mammal species in the climate models (1960-1990). The table shows slope estimates (mean) for climate variables for each species with standard deviations (SD) and 95% CRIs (2.50%, 97.50%). Bold figures indicate 95% CRIs exclude zero

Scientific name	Precipitation				Temperature			
	mean	SD	2.50%	97.50%	mean	SD	2.50%	97.50%
Elephas maximus	**-0.73**	**0.20**	**-1.14**	**-0.36**	0.10	0.32	-0.52	0.73
Atherurus macrourus	-0.31	0.19	-0.70	0.05	**-0.60**	**0.30**	**-1.21**	**-0.03**
Catopuma timminckii	0.13	0.10	-0.07	0.34	**-0.26**	**0.12**	**-0.49**	**-0.02**
Bubalus arnee	-0.26	0.27	-0.82	0.25	-0.12	0.35	-0.82	0.57
Macaca assamensis	0.10	0.12	-0.13	0.33	**-0.34**	**0.15**	**-0.65**	**-0.05**
Panthera tigris tigris	**0.48**	**0.13**	**0.22**	**0.74**	**0.34**	**0.15**	**0.05**	**0.65**
Budorcas taxicolor whitei	-0.05	0.35	-0.73	0.65	-0.13	0.36	-0.85	0.57
Arctictis binturong	-0.30	0.31	-0.93	0.29	-0.15	0.37	-0.88	0.59
Pseudois nayaur	-0.20	0.35	-0.91	0.48	-0.06	0.39	-0.81	0.72
Trachypithecus pileatus	**-0.50**	**0.27**	**-1.07**	**-0.01**	-0.48	0.34	-1.18	0.16
Neofelis nebulosa	-0.19	0.15	-0.49	0.09	-0.18	0.19	-0.57	0.19
Panthera pardus	**0.37**	**0.12**	**0.14**	**0.62**	0.01	0.13	-0.26	0.27
Paradoxurus hermaphroditus	**-0.60**	**0.22**	**-1.06**	**-0.19**	-0.53	0.33	-1.21	0.09
Herpestes urva	**-0.48**	**0.24**	**-0.97**	**-0.01**	0.14	0.36	-0.54	0.88
Cuon alpinus	0.03	0.12	-0.19	0.27	-0.11	0.14	-0.38	0.17
Bos gaurus	-0.29	0.15	-0.58	0.00	0.33	0.21	-0.08	0.75
Trachypithecus geei	-0.29	0.25	-0.81	0.18	-0.29	0.34	-0.97	0.36
Semnopithecus hector	-0.07	0.30	-0.67	0.51	-0.24	0.31	-0.86	0.36
Ursus thibetanus laniger	-0.11	0.11	-0.32	0.11	-0.24	0.13	-0.49	0.02
Hystrix brachyura	0.09	0.11	-0.12	0.30	**-0.29**	**0.14**	**-0.56**	**-0.01**
Naemorhedus goral	-0.12	0.13	-0.38	0.13	**-0.56**	**0.15**	**-0.86**	**-0.27**
Moschus leucogaster	-0.50	0.31	-1.18	0.06	-0.45	0.26	-0.98	0.05
Paguma larvata	**-0.48**	**0.13**	**-0.73**	**-0.24**	**-1.06**	**0.22**	**-1.50**	**-0.65**
Capricornis thar	**-0.28**	**0.10**	**-0.48**	**-0.08**	**-0.54**	**0.12**	**-0.78**	**-0.31**
Martes flavigula	**-0.23**	**0.10**	**-0.44**	**-0.03**	**-0.57**	**0.13**	**-0.82**	**-0.32**
Lepus nigricollis	-0.14	0.26	-0.67	0.36	-0.05	0.35	-0.74	0.66
Canis aureus	-0.19	0.32	-0.83	0.44	-0.20	0.39	-0.97	0.58
Felis chaus	0.04	0.24	-0.43	0.51	0.18	0.30	-0.40	0.77
Viverra zibetha	**-0.58**	**0.21**	**-1.01**	**-0.19**	-0.16	0.29	-0.73	0.39
Prionailurus bengalensis	0.15	0.11	-0.06	0.37	0.19	0.13	-0.07	0.44
Pardofelis marmorata	-0.01	0.12	-0.24	0.22	**-0.47**	**0.14**	**-0.76**	**-0.19**
Mustela altaica	-0.46	0.35	-1.21	0.18	-0.44	0.35	-1.16	0.22
Muntiacus muntjak	**-0.25**	**0.10**	**-0.44**	**-0.06**	**-0.56**	**0.12**	**-0.78**	**-0.33**
Manis spp.	-0.48	0.29	-1.08	0.05	-0.40	0.35	-1.13	0.28
Vulpes vulpes	**-0.82**	**0.35**	**-1.56**	**-0.21**	**-0.66**	**0.29**	**-1.26**	**-0.13**
Ailurus fulgens	**-0.53**	**0.24**	**-1.03**	**-0.09**	**-0.63**	**0.22**	**-1.07**	**-0.21**
Macaca mulatta	-0.42	0.24	-0.91	0.03	0.24	0.30	-0.35	0.83
Rusa unicolor	-0.06	0.09	-0.24	0.12	-0.15	0.11	-0.36	0.07
Mustela sibirica	-0.35	0.34	-1.06	0.29	-0.47	0.36	-1.21	0.22
Melogale moschata	-0.36	0.27	-0.91	0.15	-0.04	0.36	-0.74	0.67
Viverricula indica	-0.16	0.26	-0.67	0.35	-0.09	0.35	-0.78	0.61
Herpestes auropuntatus	-0.36	0.32	-1.02	0.24	-0.24	0.38	-1.00	0.50

Prionodon pardicolor	**-0.91**	**0.29**	**-1.53**	**-0.37**	**-0.96**	**0.32**	**-1.64**	**-0.37**
Sus scrofa	**-0.21**	**0.09**	**-0.39**	**-0.03**	**-0.23**	**0.11**	**-0.43**	**-0.02**
Mustela kathiah	-0.29	0.33	-0.97	0.31	-0.24	0.34	-0.92	0.42

Table S6. Summary results for 45 mammal species in the land-use model. The table shows slope estimates (mean) for different land-use variables for each species with standard deviations (SD) and 95% CRIs (2.50%, 97.50%). Bold figures indicate 95% CRIs exclude zero

Scientific name	Agriculture				Road				Settlement				Forest			
	mean	SD	2.50%	97.50%	mean	SD	2.50%	97.50%	mean	SD	2.50%	97.50%	mean	SD	2.50%	97.50%
Elephas maximus	**-0.13**	**0.04**	**-0.21**	**-0.05**	0.15	0.11	-0.07	0.38	**0.53**	**0.15**	**0.24**	**0.84**	**0.51**	**0.17**	**0.18**	**0.86**
Atherurus macrourus	**-0.30**	**0.10**	**-0.51**	**-0.13**	0.08	0.11	-0.14	0.30	-0.26	0.15	-0.56	0.04	**0.79**	**0.24**	**0.33**	**1.27**
Catopuma timminckii	-0.01	0.05	-0.10	0.08	-0.06	0.08	-0.22	0.10	-0.01	0.09	-0.18	0.17	0.03	0.09	-0.15	0.20
Bubalus arnee	-0.18	0.11	-0.43	0.02	0.10	0.14	-0.18	0.38	0.35	0.28	-0.15	0.94	0.26	0.34	-0.39	0.95
Macaca assamensis	-0.01	0.04	-0.10	0.08	0.16	0.09	-0.01	0.35	-0.09	0.10	-0.29	0.11	**0.34**	**0.12**	**0.11**	**0.57**
Panthera tigris tigris	0.00	0.05	-0.11	0.10	-0.03	0.10	-0.23	0.15	**0.33**	**0.11**	**0.11**	**0.55**	0.13	0.11	-0.08	0.35
Budorcas taxicolor whitei	-0.14	0.12	-0.39	0.07	0.13	0.14	-0.14	0.43	-0.04	0.26	-0.56	0.48	-0.56	0.34	-1.23	0.11
Arctictis binturong	-0.11	0.11	-0.34	0.10	0.15	0.14	-0.11	0.47	-0.04	0.26	-0.56	0.49	0.44	0.40	-0.33	1.26
Pseudois nayaur	-0.13	0.12	-0.38	0.09	0.12	0.14	-0.15	0.42	-0.12	0.29	-0.71	0.44	-0.41	0.41	-1.22	0.39
Trachypithecus pileatus	0.03	0.07	-0.10	0.17	0.17	0.14	-0.08	0.46	-0.29	0.22	-0.73	0.13	0.39	0.32	-0.21	1.04
Neofelis nebulosa	-0.05	0.06	-0.18	0.07	0.20	0.11	0.00	0.43	0.02	0.12	-0.22	0.26	**1.01**	**0.17**	**0.70**	**1.35**
Panthera pardus	0.00	0.05	-0.08	0.10	0.08	0.08	-0.08	0.25	-0.04	0.09	-0.23	0.14	0.09	0.10	-0.11	0.29
Paradoxurus hermaphroditus	**-0.24**	**0.06**	**-0.37**	**-0.13**	0.15	0.12	-0.06	0.40	0.22	0.15	-0.07	0.52	**0.47**	**0.20**	**0.09**	**0.88**
Herpestes urva	**-0.27**	**0.07**	**-0.41**	**-0.15**	0.01	0.12	-0.24	0.24	**0.63**	**0.19**	**0.27**	**1.02**	0.18	0.21	-0.23	0.61
Cuon alpinus	-0.07	0.06	-0.18	0.03	0.09	0.09	-0.08	0.27	0.15	0.10	-0.05	0.35	0.04	0.11	-0.17	0.24
Bos gaurus	**-0.19**	**0.04**	**-0.28**	**-0.11**	**0.23**	**0.11**	**0.03**	**0.46**	0.23	0.12	0.00	0.48	**0.55**	**0.15**	**0.27**	**0.86**
Trachypithecus geei	-0.17	0.11	-0.41	0.04	0.13	0.13	-0.13	0.40	-0.01	0.22	-0.43	0.43	0.39	0.29	-0.18	0.98
Semnopithecus hector	-0.15	0.12	-0.41	0.07	0.04	0.13	-0.23	0.29	-0.20	0.23	-0.65	0.24	-0.49	0.27	-1.04	0.03
Ursus thibetanus laniger	0.05	0.05	-0.04	0.15	0.09	0.08	-0.07	0.25	0.08	0.09	-0.11	0.26	**0.59**	**0.10**	**0.39**	**0.80**
Hystrix brachyura	-0.04	0.04	-0.13	0.03	0.11	0.08	-0.04	0.28	-0.14	0.09	-0.32	0.04	**0.61**	**0.11**	**0.40**	**0.83**
Naemorhedus goral	-0.08	0.07	-0.23	0.05	0.14	0.09	-0.04	0.32	-0.09	0.10	-0.29	0.11	0.09	0.11	-0.11	0.30
Moschus leucogaster	-0.14	0.12	-0.39	0.09	-0.05	0.12	-0.30	0.16	-0.04	0.16	-0.36	0.29	-0.56	0.16	-0.88	-0.25
Paguma larvata	**-0.15**	**0.05**	**-0.25**	**-0.06**	0.15	0.09	-0.01	0.33	-0.36	0.10	-0.56	-0.16	**1.04**	**0.14**	**0.77**	**1.32**
Capricornis thar	-0.09	0.05	-0.19	0.00	0.13	0.08	-0.02	0.29	0.00	0.09	-0.17	0.16	0.07	0.09	-0.10	0.24
Martes flavigula	0.01	0.04	-0.08	0.08	0.05	0.08	-0.10	0.20	-0.11	0.09	-0.28	0.06	**0.28**	**0.09**	**0.11**	**0.45**
Lepus nigricollis	-0.17	0.10	-0.38	0.00	0.14	0.14	-0.12	0.43	0.44	0.28	-0.06	1.02	0.17	0.34	-0.48	0.86
Canis aureus	-0.15	0.12	-0.39	0.07	0.10	0.14	-0.18	0.40	0.13	0.29	-0.43	0.74	0.00	0.43	-0.84	0.85

Felis chaus	-0.11	0.10	-0.31	0.08	0.13	0.14	-0.13	0.43	0.45	0.26	-0.03	1.00	-0.03	0.31	-0.63	0.59
Viverra zibetha	**-0.18**	**0.06**	**-0.31**	**-0.07**	0.04	0.11	-0.19	0.27	0.20	0.16	-0.11	0.52	**0.51**	**0.22**	**0.09**	**0.95**
Prionailurus bengalensis	-0.04	0.04	-0.11	0.03	0.14	0.08	-0.02	0.29	-0.08	0.09	-0.25	0.09	**0.49**	**0.10**	**0.31**	**0.69**
Pardofelis marmorata	0.05	0.04	-0.04	0.13	**0.30**	**0.11**	**0.11**	**0.52**	-0.17	0.10	-0.36	0.02	**0.58**	**0.11**	**0.37**	**0.80**
Mustela altaica	-0.13	0.12	-0.38	0.09	0.15	0.14	-0.11	0.47	0.15	0.27	-0.36	0.69	-0.20	0.32	-0.83	0.44
Muntiacus muntjak	-0.04	0.04	-0.12	0.04	0.03	0.07	-0.12	0.18	-0.14	0.08	-0.31	0.02	**0.64**	**0.09**	**0.48**	**0.81**
Manis spp.	-0.19	0.11	-0.42	0.00	0.12	0.13	-0.14	0.40	-0.18	0.24	-0.66	0.28	0.31	0.35	-0.34	1.02
Vulpes vulpes	-0.16	0.12	-0.41	0.06	0.10	0.11	-0.12	0.33	-0.12	0.16	-0.43	0.20	-0.91	0.16	-1.22	-0.61
Ailurus fulgens	-0.13	0.11	-0.37	0.06	**0.23**	**0.13**	**0.01**	**0.50**	0.05	0.14	-0.23	0.34	-0.44	0.14	-0.72	-0.17
Macaca mulatta	0.00	0.06	-0.13	0.12	0.02	0.13	-0.26	0.26	0.13	0.21	-0.28	0.56	0.16	0.27	-0.36	0.71
Rusa unicolor	-0.04	0.03	-0.10	0.03	0.02	0.07	-0.13	0.15	-0.13	0.08	-0.29	0.02	**0.45**	**0.08**	**0.29**	**0.62**
Mustela sibirica	-0.14	0.12	-0.40	0.08	0.11	0.14	-0.16	0.39	-0.29	0.26	-0.82	0.19	-0.19	0.33	-0.82	0.47
Melogale moschata	**-0.19**	**0.10**	**-0.40**	**-0.02**	0.09	0.13	-0.17	0.36	-0.02	0.24	-0.49	0.45	-0.01	0.34	-0.65	0.66
Viverricula indica	**-0.19**	**0.09**	**-0.38**	**-0.03**	0.16	0.14	-0.10	0.46	0.38	0.24	-0.06	0.89	0.18	0.32	-0.42	0.82
Herpestes auropunctatus	-0.06	0.10	-0.26	0.14	0.10	0.14	-0.18	0.38	-0.26	0.29	-0.85	0.28	0.18	0.42	-0.63	1.03
Prionodon pardicolor	-0.17	0.11	-0.41	0.03	0.13	0.12	-0.10	0.39	-0.25	0.18	-0.62	0.11	**0.64**	**0.26**	**0.16**	**1.17**
Sus scrofa	**0.16**	**0.05**	**0.07**	**0.27**	-0.06	0.08	-0.22	0.08	-0.06	0.08	-0.21	0.10	**0.46**	**0.08**	**0.30**	**0.62**
Mustela kathiah	-0.14	0.12	-0.39	0.08	0.15	0.14	-0.11	0.47	0.21	0.27	-0.30	0.77	-0.04	0.34	-0.71	0.65

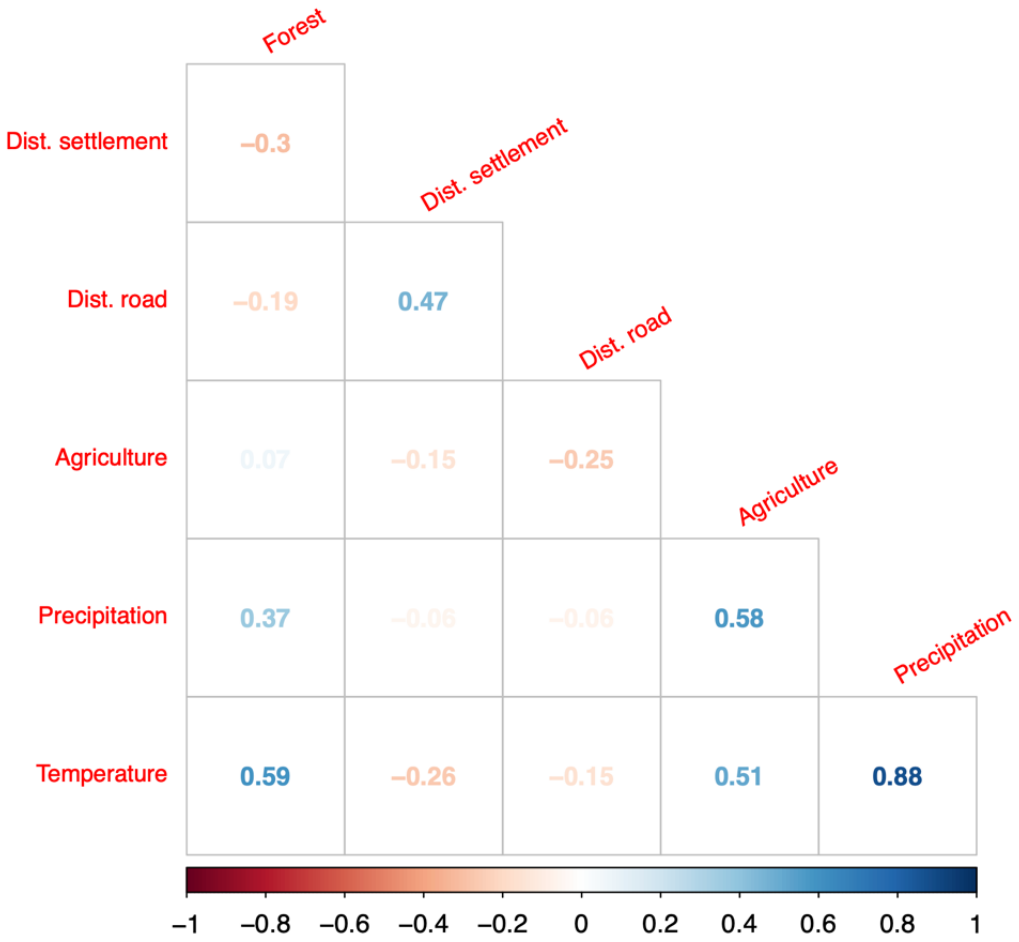


Figure S1. Pearson's correlation coefficient of the land use (agriculture, distance to settlement, distance to road and forest cover) and climate (temperature and precipitation) variables

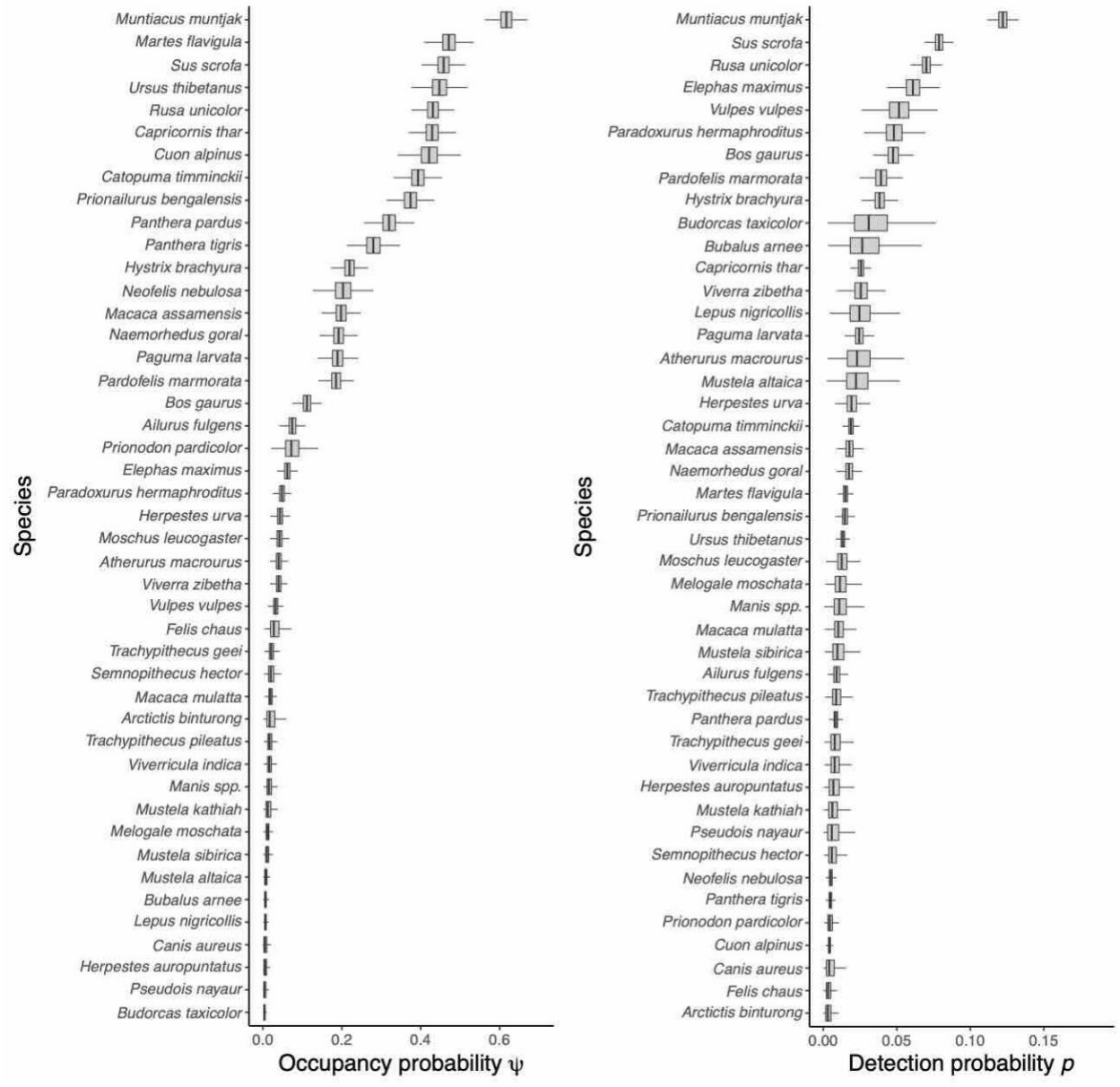


Figure S2. Posterior occupancy and detection probabilities under multi-species occupancy model for each observed species. The box plots (horizontally arranged) can be interpreted as any standard box plot where the black centre line of the box represents the median probability, black line on either side of the box as the interquartile range and the whiskers as the last data points within the median ± 1.5x the interquartile range. The values of the mean probabilities are given in Table S6

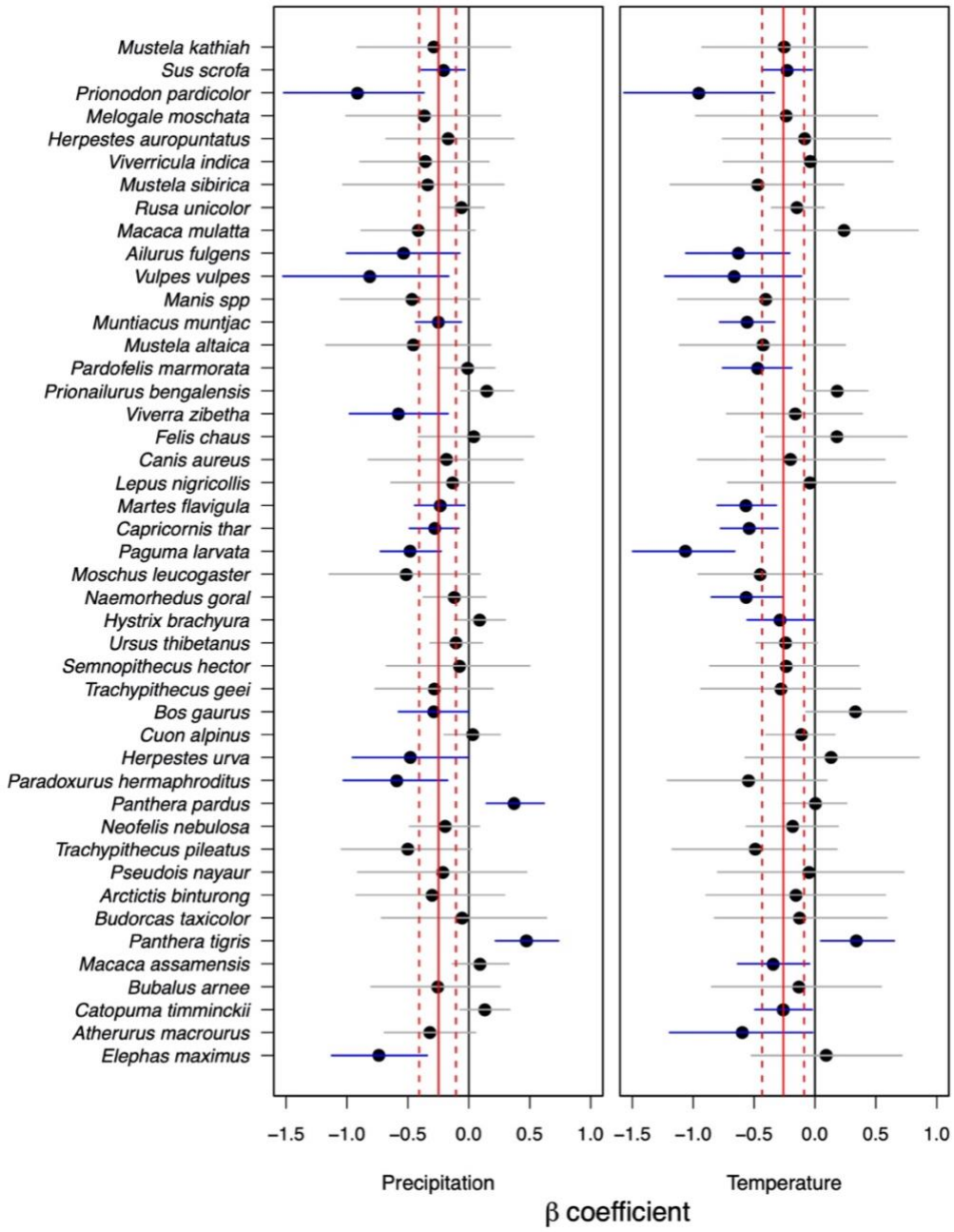


Figure S3. The overall mammal community response (red solid and dash lines) and individual species response (black full circles and gray lines) to climate variables (precipitation and temperature)

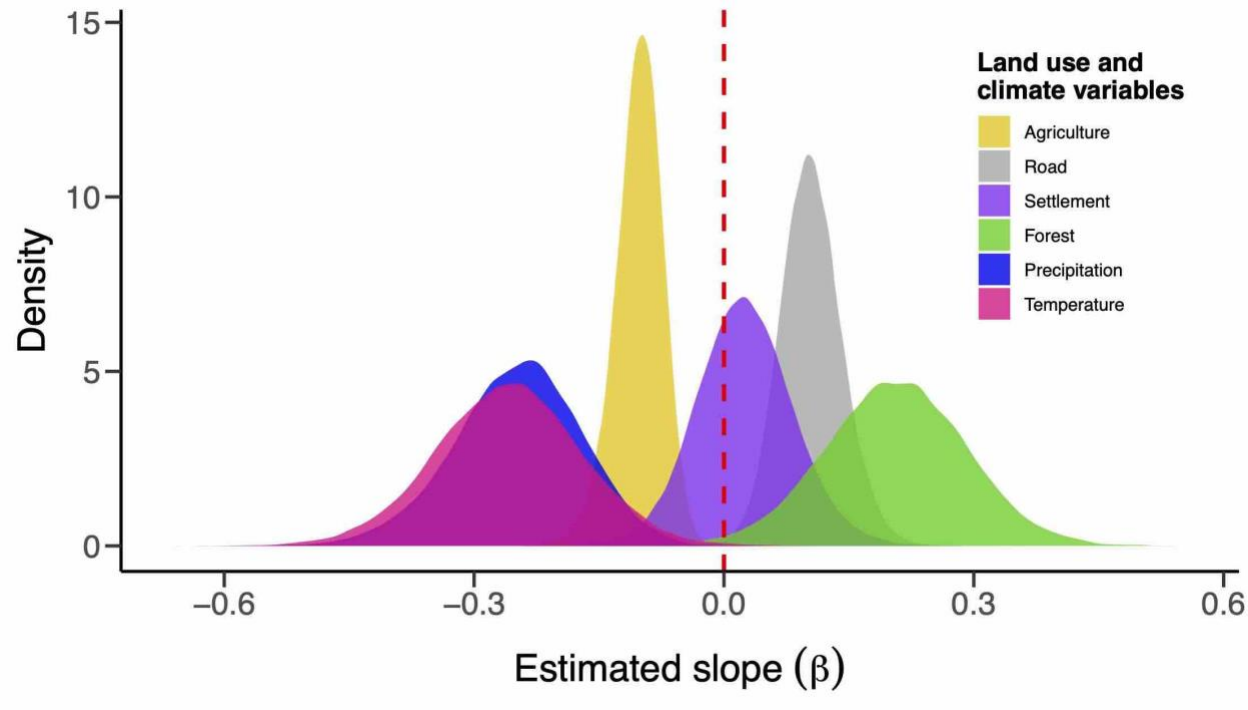
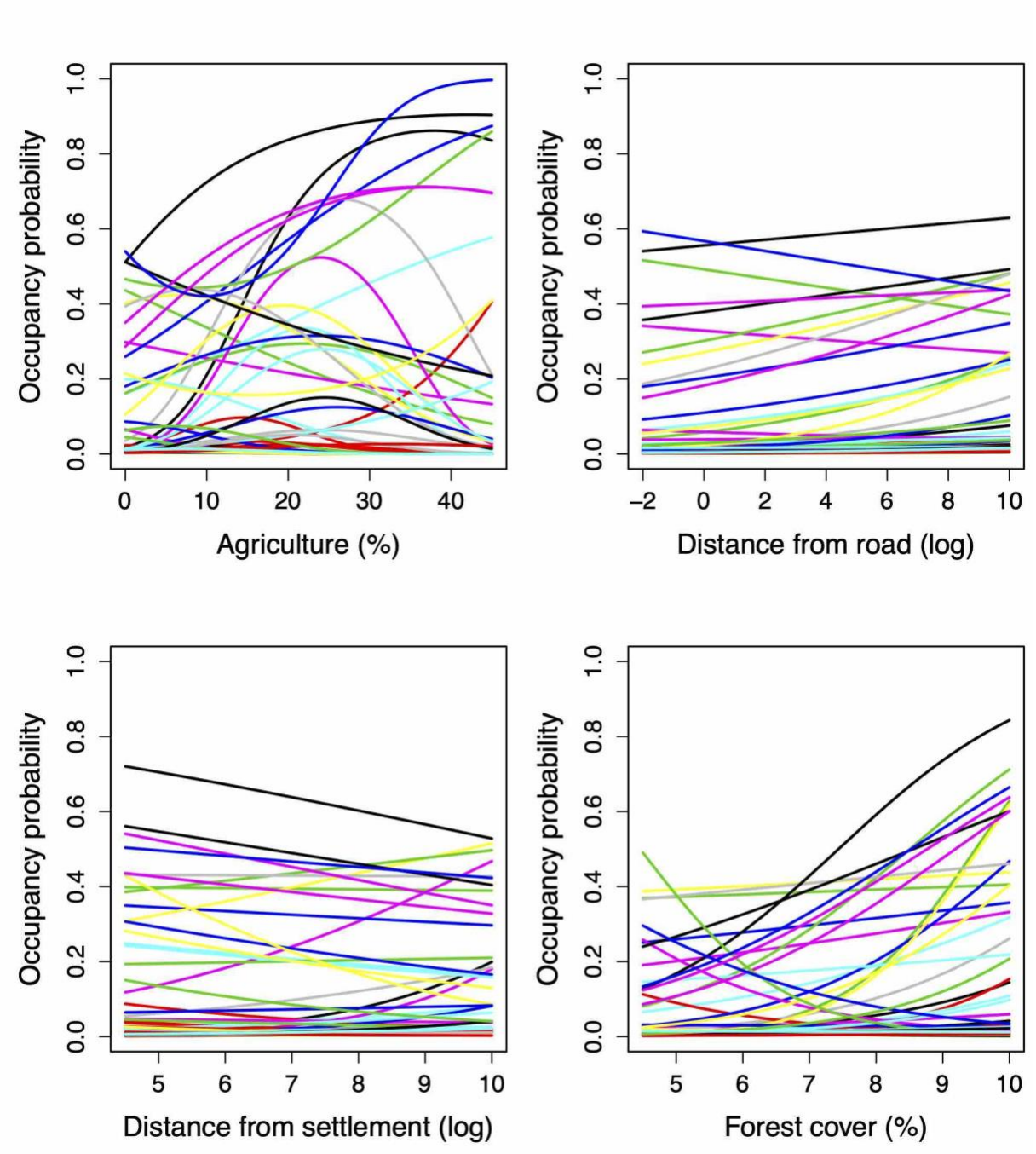


Figure S4. The posterior distribution of slope parameters ($\hat{\beta}$ coefficients) of the overall mammal assemblage in Bhutan. The red dashed line partitions the direction of effect. The plot can be interpreted in conjunction with Table S3. The occupancy probability of each species was modelled as a function of land-use variables (agriculture, distance to road, distance to settlement and forest cover) and climate variables (precipitation and temperature)


Occupancy probability
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
Agriculture (%)
Occupancy probability
0.0
0.2
0.4
0.6
0.8
1.0
−2
0
2
4
6
8
10
Distance from road (log)
Occupancy probability
0.0
0.2
0.4
0.6
0.8
1.0
5
6
7
8
9
10
Distance from settlement (log)
Occupancy probability
0.0
0.2
0.4
0.6
0.8
1.0
5
6
7
8
9
10
Forest cover (%)

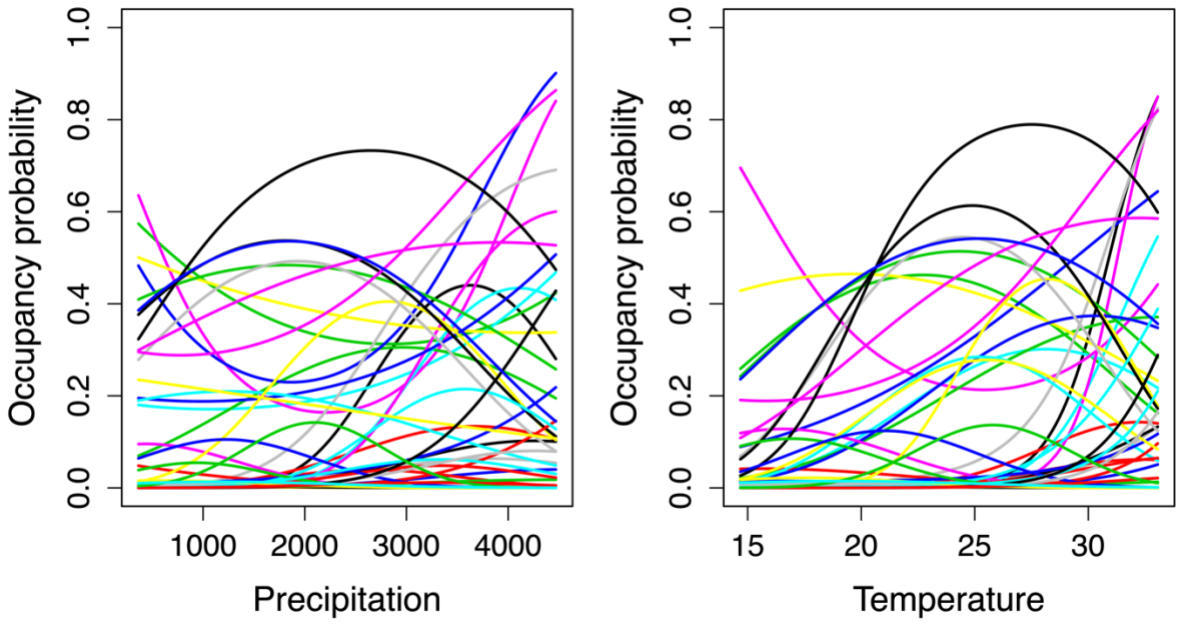


Figure S5. Species-specific predictions of occupancy probability as a function of land use (proportion of land under agriculture, distance from road, distance from settlement and forest cover) and climate (precipitation and temperature) under the community occupancy model of land use. Each line represents one of the 45 observed species

S1. BUGS code for multi-species occupancy model

```
model {

  # Ecological model for latent occurrence (process model)
  for(k in 1:nspec) {
    for(i in 1:nsite) {
     logit(psi[i, k]) <- lpsi[k] + betalpsiAgri[k] * agri[i] +
     betalpsiAgri2[k] * agri2[i] + betalpsiRoad[k] * road[i] +
     betalpsiSettle[k] * settle[i] + betalpsiForest[k] *
     forest[i]

      z[i, k] ~ dbern(psi[i, k])
    }
  }

  # Observation model
  for(k in 1:nspec) {
    for(i in 1:nsite) {
     logit(p[i, k]) <- lp[k] + betalpCamera[camera[i]] +
     betalpTrail[k] * trail[i] #+ betalpDisturb[k] * disturb[i]

      Ysum[i, k] ~ dbin(z[i, k] * p[i, k], nrep[i])
    }
  }

  # Priors
  for(k in 1:nspec) {
    lpsi[k] ~ dnorm(mu.lpsi, tau.lpsi)
    betalpsiAgri[k] ~ dnorm(mu.betalpsiAgri, tau.betalpsiAgri)
    betalpsiAgri2[k] ~ dnorm(mu.betalpsiAgri2,
tau.betalpsiAgri2)
    betalpsiRoad[k] ~ dnorm(mu.betalpsiRoad, tau.betalpsiRoad)
    betalpsiSettle[k] ~ dnorm(mu.betalpsiSettle,
tau.betalpsiSettle)
    betalpsiForest[k] ~ dnorm(mu.betalpsiForest,
tau.betalpsiForest)

    lp[k] ~ dnorm(mu.lp, tau.lp)
    betalpTrail[k] ~ dnorm(mu.betalpTrail, tau.betalpTrail)
  }
```

```
# Hyperpriors
# For the model of occupancy
mu.lpsi ~ dnorm(0, 0.001)
tau.lpsi <- pow(sd.lpsi, -2)
sd.lpsi ~ dt(0, tau, 4) T(0, )

mu.betalpsiAgri ~ dnorm(0, 0.001)
tau.betalpsiAgri <- 1/(sd.betalpsiAgri^2)
sd.betalpsiAgri ~ dt(0, tau, 4) T(0, )
mu.betalpsiAgri2 ~ dnorm(0, 0.001)
tau.betalpsiAgri2 <- 1/(sd.betalpsiAgri2^2)
sd.betalpsiAgri2 ~ dt(0, tau, 4) T(0, )
mu.betalpsiRoad ~ dnorm(0, 0.001)
tau.betalpsiRoad <- 1/(sd.betalpsiRoad^2)
sd.betalpsiRoad ~ dt(0, tau, 4) T(0, )
mu.betalpsiSettle ~ dnorm(0, 0.001)
tau.betalpsiSettle <- 1/(sd.betalpsiSettle^2)
sd.betalpsiSettle ~ dt(0, tau, 4) T(0, )
mu.betalpsiForest ~ dnorm(0, 0.001)
tau.betalpsiForest <- 1/(sd.betalpsiForest^2)
sd.betalpsiForest ~ dt(0, tau, 4) T(0, )

# For the model of detection
mu.lp ~ dnorm(0, 0.001)
tau.lp <- 1/(sd.lp)^2
sd.lp ~ dt(0, tau, 4) T(0, )

# For random camera effect
betalpCamera[1] <- 0
for (c in 2:nCamera) {
  betalpCamera[c] ~ dnorm(0, tau.betalpCamera)
}
tau.betalpCamera <- 1/(sd.betalpCamera^2)
sd.betalpCamera ~ dt(0, tau, 4) T(0, )

mu.betalpTrail ~ dnorm(0, 0.001)
tau.betalpTrail <- 1/(sd.betalpTrail)^2
sd.betalpTrail ~ dt(0, tau, 4) T(0, )

# Derived quantities
```

```
  for(k in 1:nspec) {
    Nocc.fs[k] <- sum(z[, k]) # occupied sites for each species

  }
  for(i in 1:nsite) {
    Nsite[i] <- sum(z[i, ]) # species occurring at each site
  }

  }
}
```

BUGS model for MSOM with land use and climate (precipitation) variable

model {

```
  # Ecological model for latent occurrence z (process model)
  for(k in 1:nspec) {
    for(i in 1:nsite) {
                logit(psi[i, k]) <- lpsi[k] + betalpsiAgri[k] *
                agri[i] + betalpsiAgri2[k] * agri2[i] +
               betalpsiRoad[k] * road[i] + betalpsiSettle[k] *
               settle[i] + betalpsiForest[k] * forest[i] +
                 betalpsiPrecipitation[k] * precipitation[i] +
betalpsiPrecipitation2[k] * precipitation2[i]

      z[i, k] ~ dbern(psi[i, k])
    }
  }

  # Observation model
  for(k in 1:nspec) {
    for(i in 1:nsite) {
        logit(p[i, k]) <- lp[k] + betalpCamera[camera[i]] +
betalpTrail[k] * trail[i]

        Ysum[i, k] ~ dbin(z[i, k] * p[i, k], nrep[i])
    }
  }

  # Priors
```

```
  for(k in 1:nspec) {
    lpsi[k] ~ dnorm(mu.lpsi, tau.lpsi)
    betalpsiAgri[k] ~ dnorm(mu.betalpsiAgri, tau.betalpsiAgri)
    betalpsiAgri2[k] ~ dnorm(mu.betalpsiAgri2,
tau.betalpsiAgri2)
    betalpsiRoad[k] ~ dnorm(mu.betalpsiRoad, tau.betalpsiRoad)
    betalpsiSettle[k] ~ dnorm(mu.betalpsiSettle,
tau.betalpsiSettle)
    betalpsiForest[k] ~ dnorm(mu.betalpsiForest,
tau.betalpsiForest)
tau.betalpsiElevation)
    betalpsiPrecipitation[k] ~ dnorm(mu.betalpsiPrecipitation,
tau.betalpsiPrecipitation)
    betalpsiPrecipitation2[k] ~ dnorm(mu.betalpsiPrecipitation2,
tau.betalpsiPrecipitation2)

    lp[k] ~ dnorm(mu.lp, tau.lp)
    betalpTrail[k] ~ dnorm(mu.betalpTrail, tau.betalpTrail)
  }

  # Hyperpriors
  # For the model of occupancy
  mu.lpsi ~ dnorm(0, 0.001)
  tau.lpsi <- pow(sd.lpsi, -2)
  sd.lpsi ~ dt(0, tau, 4) T(0, )

  mu.betalpsiAgri ~ dnorm(0, 0.001)
  tau.betalpsiAgri <- 1/(sd.betalpsiAgri^2)
  sd.betalpsiAgri ~ dt(0, tau, 4) T(0, )
  mu.betalpsiAgri2 ~ dnorm(0, 0.001)
  tau.betalpsiAgri2 <- 1/(sd.betalpsiAgri2^2)
  sd.betalpsiAgri2 ~ dt(0, tau, 4) T(0, )
  mu.betalpsiRoad ~ dnorm(0, 0.001)
  tau.betalpsiRoad <- 1/(sd.betalpsiRoad^2)
  sd.betalpsiRoad ~ dt(0, tau, 4) T(0, )
  mu.betalpsiSettle ~ dnorm(0, 0.001)
  tau.betalpsiSettle <- 1/(sd.betalpsiSettle^2)
  sd.betalpsiSettle ~ dt(0, tau, 4) T(0, )
  mu.betalpsiForest ~ dnorm(0, 0.001)
  tau.betalpsiForest <- 1/(sd.betalpsiForest^2)
  sd.betalpsiForest ~ dt(0, tau, 4) T(0, )
```

```
  mu.betalpsiPrecipitation ~ dnorm(0, 0.001)
  tau.betalpsiPrecipitation <- 1/(sd.betalpsiPrecipitation^2)
  sd.betalpsiPrecipitation ~ dt(0, tau, 4) T(0, )
  mu.betalpsiPrecipitation2 ~ dnorm(0, 0.001)
  tau.betalpsiPrecipitation2 <- 1/(sd.betalpsiPrecipitation2^2)
  sd.betalpsiPrecipitation2 ~ dt(0, tau, 4) T(0, )

  # For the model of detection
  mu.lp ~ dnorm(0, 0.001)
  tau.lp <- 1/(sd.lp)^2
  sd.lp ~ dt(0, tau, 4) T(0, )

  # For random camera effect
  betalpCamera[1] <- 0
  for (c in 2:nCamera) {
    betalpCamera[c] ~ dnorm(0, tau.betalpCamera)
  }
  tau.betalpCamera <- 1/(sd.betalpCamera^2)
  sd.betalpCamera ~ dt(0, tau, 4) T(0, )

  # For trail effect
  mu.betalpTrail ~ dnorm(0, 0.001)
  tau.betalpTrail <- 1/(sd.betalpTrail)^2
  sd.betalpTrail ~ dt(0, tau, 4) T(0, )

  # Derived quantities
  for(k in 1:nspec) {
    Nocc.fs[k] <- sum(z[, k])
  }

  for(i in 1:nsite) {
    Nsite[i] <- sum(z[i, ])
  }
  }
}
```

BUGS model for MSOM with land use and climate (temperature) variable

```
model {

  # Ecological model for latent occurrence z (process model)
  for(k in 1:nspec) {
    for(i in 1:nsite) {
          logit(psi[i, k]) <- lpsi[k] + betalpsiAgri[k] *
          agri[i] + betalpsiAgri2[k] * agri2[i] +
          betalpsiRoad[k] * road[i] + betalpsiSettle[k] *
          settle[i] + betalpsiForest[k] * forest[i] +
          betalpsiTemperature[k] * temperature[i] +
          betalpsiTemperature2[k] * temperature2[i]

      z[i, k] ~ dbern(psi[i, k])
    }
  }

  # Observation model
  for(k in 1:nspec) {
    for(i in 1:nsite) {
        logit(p[i, k]) <- lp[k] + betalpCamera[camera[i]] +
betalpTrail[k] * trail[i]

        Ysum[i, k] ~ dbin(z[i, k] * p[i, k], nrep[i])
    }
  }

  # Priors
  for(k in 1:nspec) {
    lpsi[k] ~ dnorm(mu.lpsi, tau.lpsi)
    betalpsiAgri[k] ~ dnorm(mu.betalpsiAgri, tau.betalpsiAgri)
    betalpsiAgri2[k] ~ dnorm(mu.betalpsiAgri2,
tau.betalpsiAgri2)
    betalpsiRoad[k] ~ dnorm(mu.betalpsiRoad, tau.betalpsiRoad)
    betalpsiSettle[k] ~ dnorm(mu.betalpsiSettle,
tau.betalpsiSettle)
    betalpsiForest[k] ~ dnorm(mu.betalpsiForest,
tau.betalpsiForest)
    betalpsiTemperature[k] ~ dnorm(mu.betalpsiTemperature,
tau.betalpsiTemperature)
```

```
    betalpsiTemperature2[k] ~ dnorm(mu.betalpsiTemperature2,
tau.betalpsiTemperature2)

    lp[k] ~ dnorm(mu.lp, tau.lp)
    betalpTrail[k] ~ dnorm(mu.betalpTrail, tau.betalpTrail)
  }

  # Hyperpriors
  # For the model of occupancy
  mu.lpsi ~ dnorm(0, 0.001)
  tau.lpsi <- pow(sd.lpsi, -2)
  sd.lpsi ~ dt(0, tau, 4) T(0, )
  mu.betalpsiAgri ~ dnorm(0, 0.001)
  tau.betalpsiAgri <- 1/(sd.betalpsiAgri^2)
  sd.betalpsiAgri ~ dt(0, tau, 4) T(0, )
  mu.betalpsiAgri2 ~ dnorm(0, 0.001)
  tau.betalpsiAgri2 <- 1/(sd.betalpsiAgri2^2)
  sd.betalpsiAgri2 ~ dt(0, tau, 4) T(0, )
  mu.betalpsiRoad ~ dnorm(0, 0.001)
  tau.betalpsiRoad <- 1/(sd.betalpsiRoad^2)
  sd.betalpsiRoad ~ dt(0, tau, 4) T(0, )
  mu.betalpsiSettle ~ dnorm(0, 0.001)
  tau.betalpsiSettle <- 1/(sd.betalpsiSettle^2)
  sd.betalpsiSettle ~ dt(0, tau, 4) T(0, )
  mu.betalpsiForest ~ dnorm(0, 0.001)
  tau.betalpsiForest <- 1/(sd.betalpsiForest^2)
  sd.betalpsiForest ~ dt(0, tau, 4) T(0, )
  mu.betalpsiTemperature ~ dnorm(0, 0.001)
  tau.betalpsiTemperature <- 1/(sd.betalpsiTemperature^2)
  sd.betalpsiTemperature ~ dt(0, tau, 4) T(0, )
  mu.betalpsiTemperature2 ~ dnorm(0, 0.001)
  tau.betalpsiTemperature2 <- 1/(sd.betalpsiTemperature2^2)
  sd.betalpsiTemperature2 ~ dt(0, tau, 4) T(0, )

  # For the model of detection
  mu.lp ~ dnorm(0, 0.001)
  tau.lp <- 1/(sd.lp)^2
  sd.lp ~ dt(0, tau, 4) T(0, )

  # For random camera effect
  betalpCamera[1] <- 0
```

```
  for (c in 2:nCamera) {
    betalpCamera[c] ~ dnorm(0, tau.betalpCamera)
  }
  tau.betalpCamera <- 1/(sd.betalpCamera^2)
  sd.betalpCamera ~ dt(0, tau, 4) T(0, )

  # For trail effect
  mu.betalpTrail ~ dnorm(0, 0.001)
  tau.betalpTrail <- 1/(sd.betalpTrail)^2
  sd.betalpTrail ~ dt(0, tau, 4) T(0, )

  # Derived quantities
  for(k in 1:nspec) {
    Nocc.fs[k] <- sum(z[, k])
  }

  for(i in 1:nsite) {
    Nsite[i] <- sum(z[i, ])
  }
  }
}
```

Supplementary material for Supplementary Chapter 2

Multispecies occupancy model - Priors

We used normal priors on intercept and slopes, $\beta_k \sim Normal(\mu_{\beta_k}, \tau_{\beta_k})$, $\alpha_k \sim Normal(\mu_{\alpha_k}, \tau_{\alpha_k})$ for ecological and observation processes, respectively treating each species as a random effect. For hyperparameters that describe the community, we used normal priors on means of the intercept and slope, $\mu_{\beta_k} \sim Normal(0, \tau_{\mu_{\beta_k}})$ for occupancy, $\mu_{\alpha_k} \sim Normal(0, \tau_{\mu_{\alpha_k}})$ for detection, and weakly informative half-Cauchy distribution with $\sigma = 2.25$ on standard deviations with precision, $\tau_{\mu_{\beta_k}} = \frac{1}{\sigma^2_{\mu_{\beta_k}}}$ with $\sigma^2_{\mu_{\beta_k}} \sim half\text{-}Cauchy(2.25^2)$ for occupancy and where, $\tau_{\mu_{\alpha_k}} = \frac{1}{\sigma^2_{\mu_{\alpha_k}}}$ with $\sigma^2_{\mu_{\alpha_k}} \sim half\text{-}Cauchy(2.25^2)$ for detectability. To cope with the small sample size for most species in MSOMs, we used weakly informative priors on the variance of hyperparameters. We specified half-Cauchy distributions with $\sigma = 2.25$ which is similar in range for standard deviations that the mean parameters have on the logit scale and assigns low probabilities to large effects on the logit scale (Gelman, 2006b, Dorazio et al., 2011, Broms et al., 2016) such that $\mu_{\beta_k} \sim Normal(0, \tau_{\mu_{\beta_k}})$ where, $\tau_{\mu_{\beta_k}} = 1/\sigma^2_{\mu_{\beta_k}}$ and $\sigma^2_{\mu_{\beta_k}} \sim half\text{-}Cauchy(2.25^2)$. The use of weakly informative priors provides a small amount of information based on data and model but less than the actual knowledge without influencing the posteriors (Gelman et al., 2013, Banner et al., 2020).

Model selection and validation

We wanted to infer the response of species to anthropogenic and environmental variables and for this, we built a set of competing models (see Table S1 for details). In the first model (Model1), we aim to test the effect of the settlement on bird occupancy probability along the elevational gradient with the assumption that human settlement will have an overall negative effect on

community occupancy. The second model (Model2) tests the effects of agriculture and forest cover on occupancy probability along the elevational gradient. We assumed that some species (mainly generalists, e.g., crows, pigeons, etc) will be positively associated with agriculture while forest cover will have mostly habitat specialists affiliated to it. The third model is our global model with all covariates aimed to evaluate the effects of different land-use types along the elevational gradient. The limited model contains only a single covariate (i.e., elevation) essentially to check the performance of the univariate model against the multivariate models. Finally, the 'extra' model has a randomly generated standard normal variable added to check if the model selection criteria were able to adequately discriminate superfluous variables.

Since we did not have out-of-sample data to test and validate the true predictive performance, we performed k-fold cross-validation using the same data set (Hooten and Hobbs, 2015, Broms et al., 2016). We split our data into five equal subsets, withheld one subset and fitted the model to the rest, and compared predictions for the withheld subset with the observed data. This was sequentially repeated for each subset. Models with different covariate structures were ranked against each other using several scoring rules such as AUC, Log-likelihood, Brier score and 0-1 score. The area under the receiver operating characteristic curve (AUC) is a rank-based rule that assigns a high score when predicted probabilities of successes are consistently higher than probabilities of failures (Zipkin et al., 2012). The Brier score and 0-1 score are traditionally used for logistic regression models of binary data (Broms et al., 2016). Although other scoring rules, besides AUC, may not be optimal for occupancy models, we used them to compare with AUC. We built five sets of models, from parsimonious to full model with all

covariates and selected the best performing based on the selection criteria mentioned above for further prediction and interpretation (Table S1).

To evaluate how well our best model fit the data, we compared the observed response variables to the values predicted by the model using the Freeman-Tukey discrepancy (Kéry and Royle, 2016). Since the true occurrence status of our sites is unknown, we do not have true values to compare against. Instead, we compared observed detections to posterior predicted detections. We calculated the Bayesian *p*-value (as a summary of Posterior Predictive Check) to measure the goodness of fit of the full model (Hooten and Hobbs, 2015). The full model adequately fitted our data (Bayesian *p*-value = 0.32, AUC = 0.92).

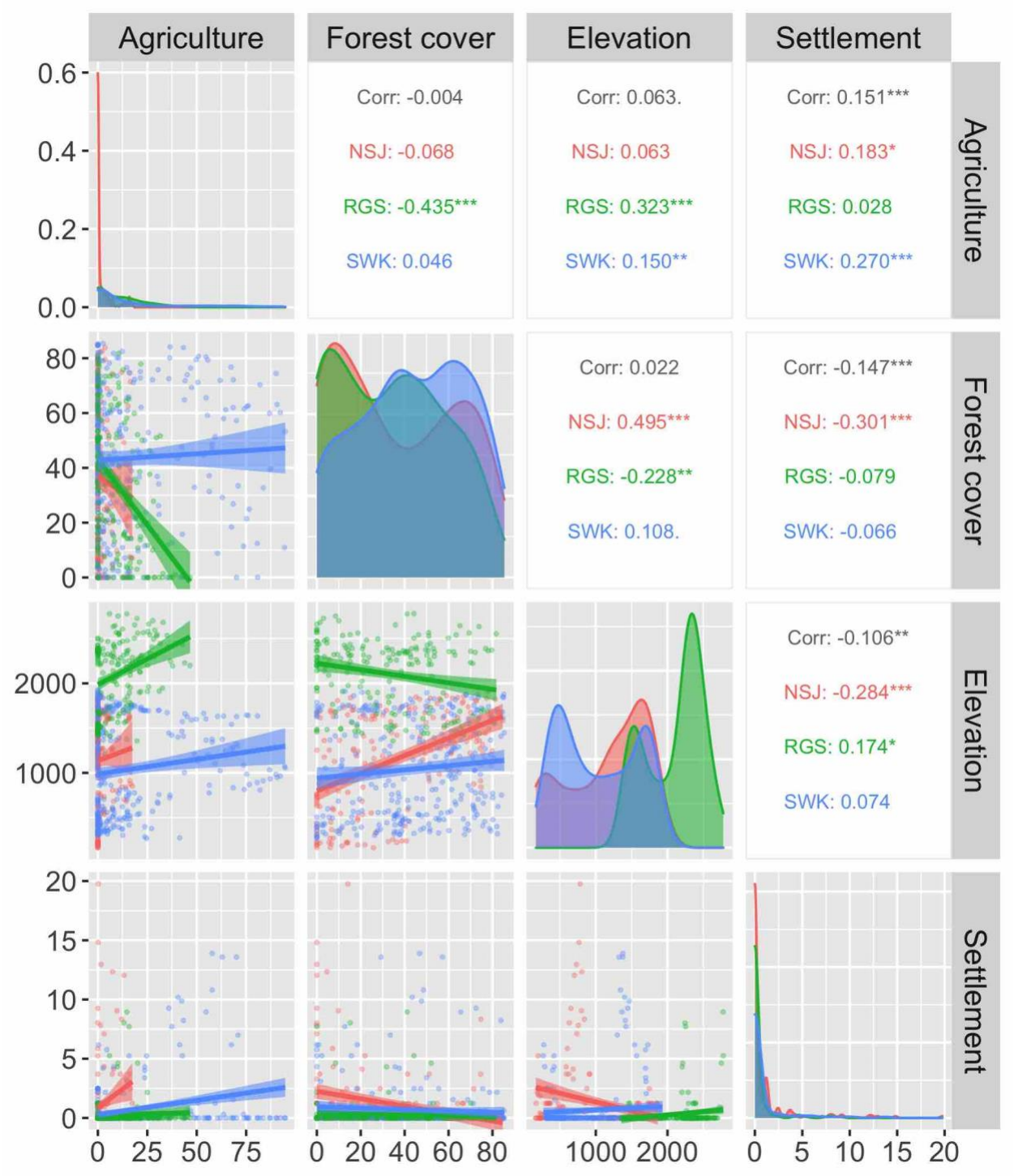


Figure S1. Pearson's correlation coefficient of predictor variables. Routes are NSJ = Narphu-Samdrupjongkhar, RGS = Rimchu-Gasa, and SWK = Shechamthang-Waklaytar

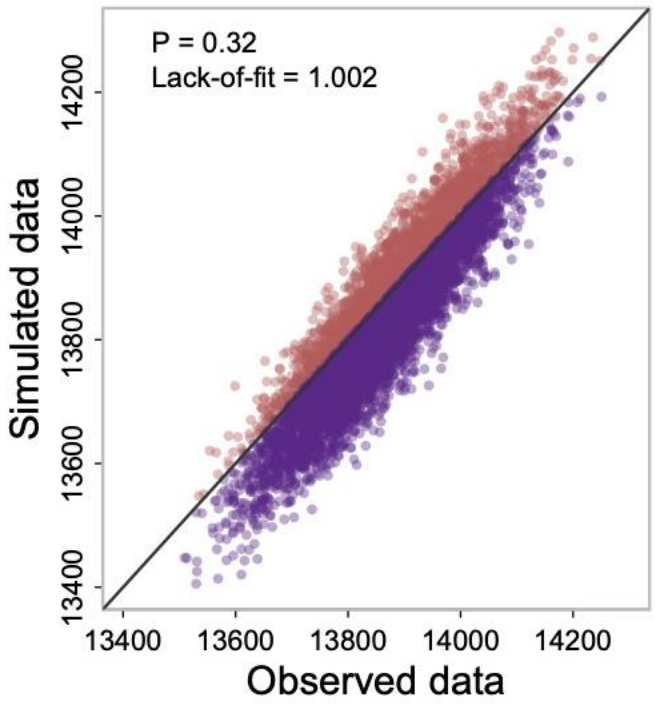


Figure S2. Posterior predictive check of the full model of bird community occupancy in Bhutan. Red and blue points show the simulated and observed data, respectively. The poor fit model will have these points on the either side of the diagonal line and *p*-value <0.05 or >0.9

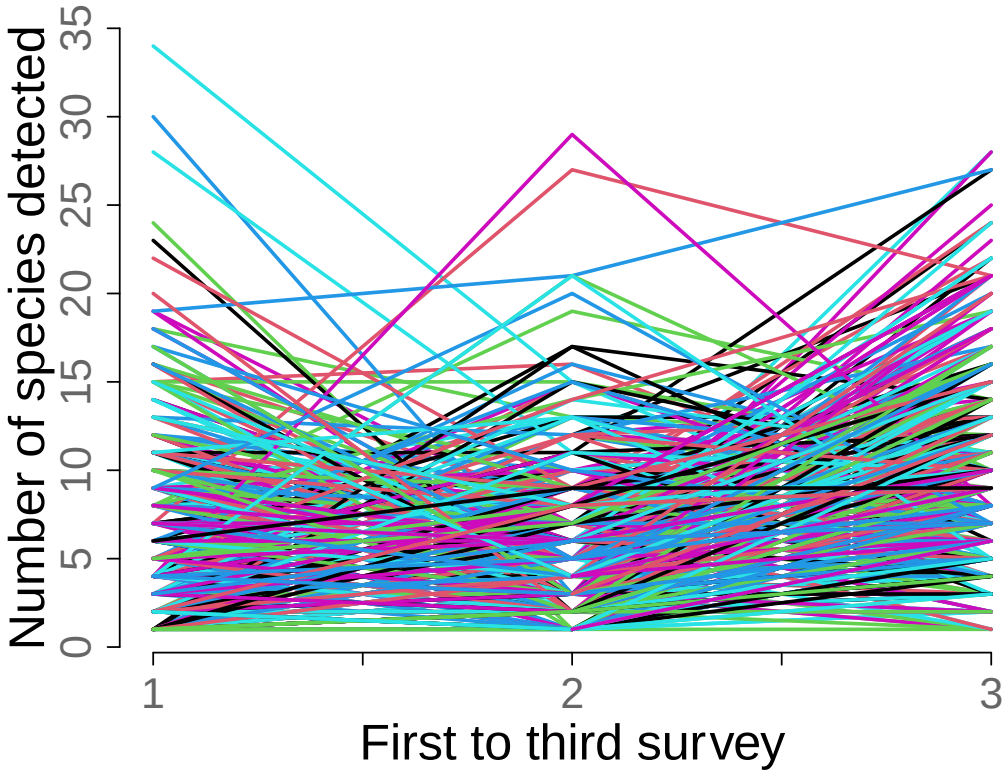


Figure S3. Number of species detected per site and survey during 2019-20

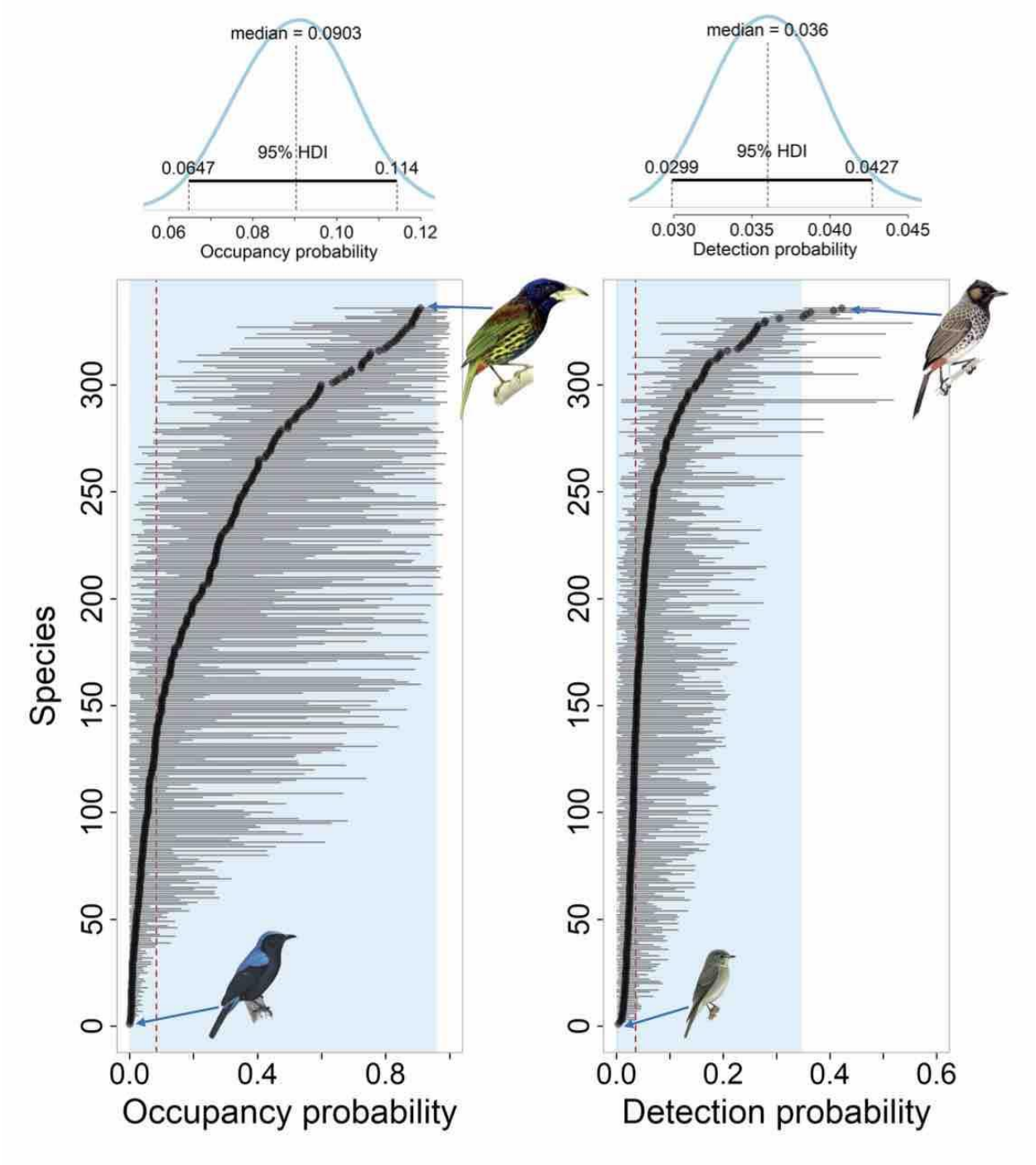


Figure S4. Occupancy and detection probability estimates of individual species. Black circles represent mean estimates and grey horizontal bars show 95% CRI. Red lines are community median estimate and light blue shades represent 95% CRI. Histograms show overall community (median) occupancy and detection probability estimates. Illustrated birds are great barbet (top

left) and Asian fairy bluebird (bottom left), and red-vented bulbul (top right) and dark-sided flycatcher (bottom right)

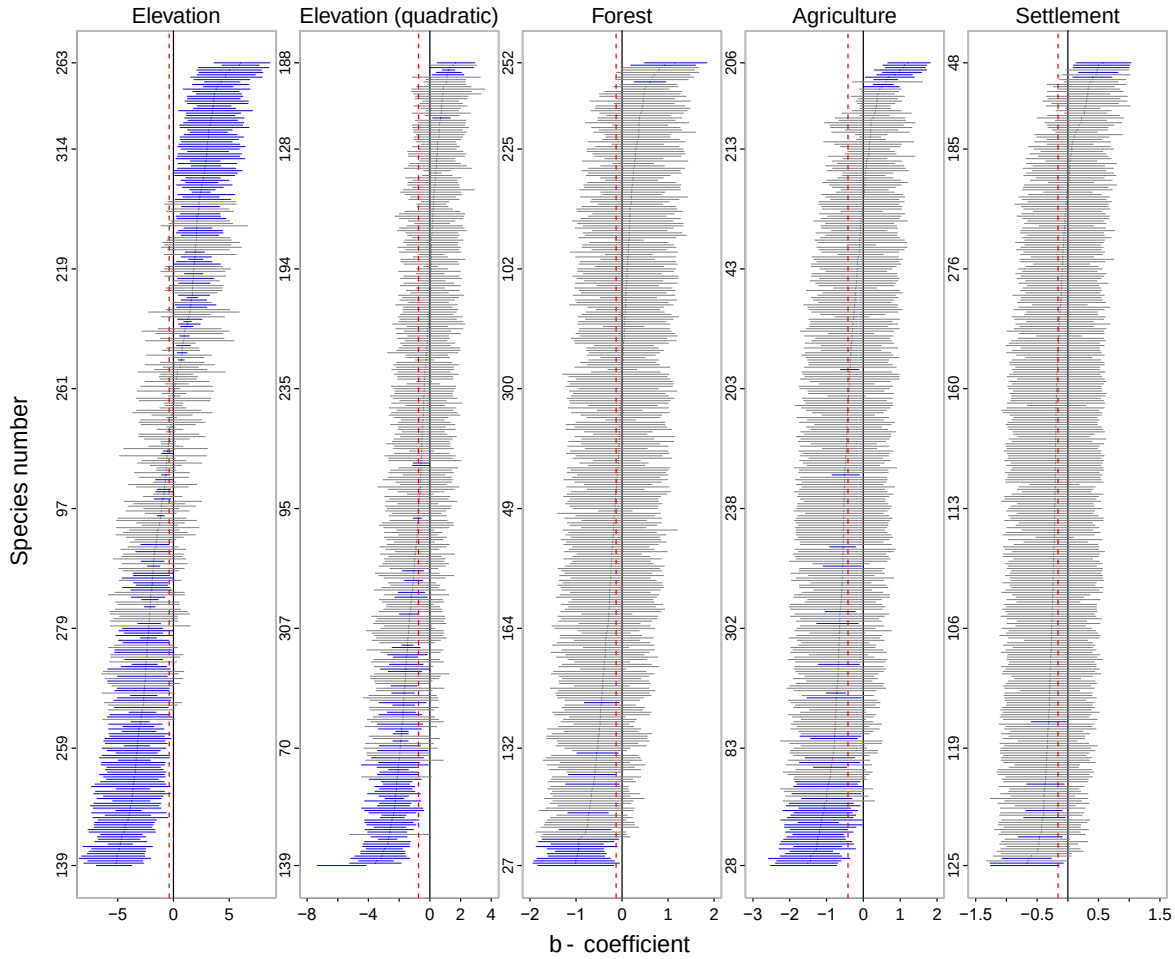


Figure S5. Species-specific coefficient estimates of environmental and anthropogenic variables. Black circles show a mean coefficient estimate with 95% CRI in grey horizontal bars. Red vertical lines are the overall means, and 95% CRI are shaded in light blue. Species with a significant response (95% CRI non-overlapping zero) are highlighted in blue horizontal bar

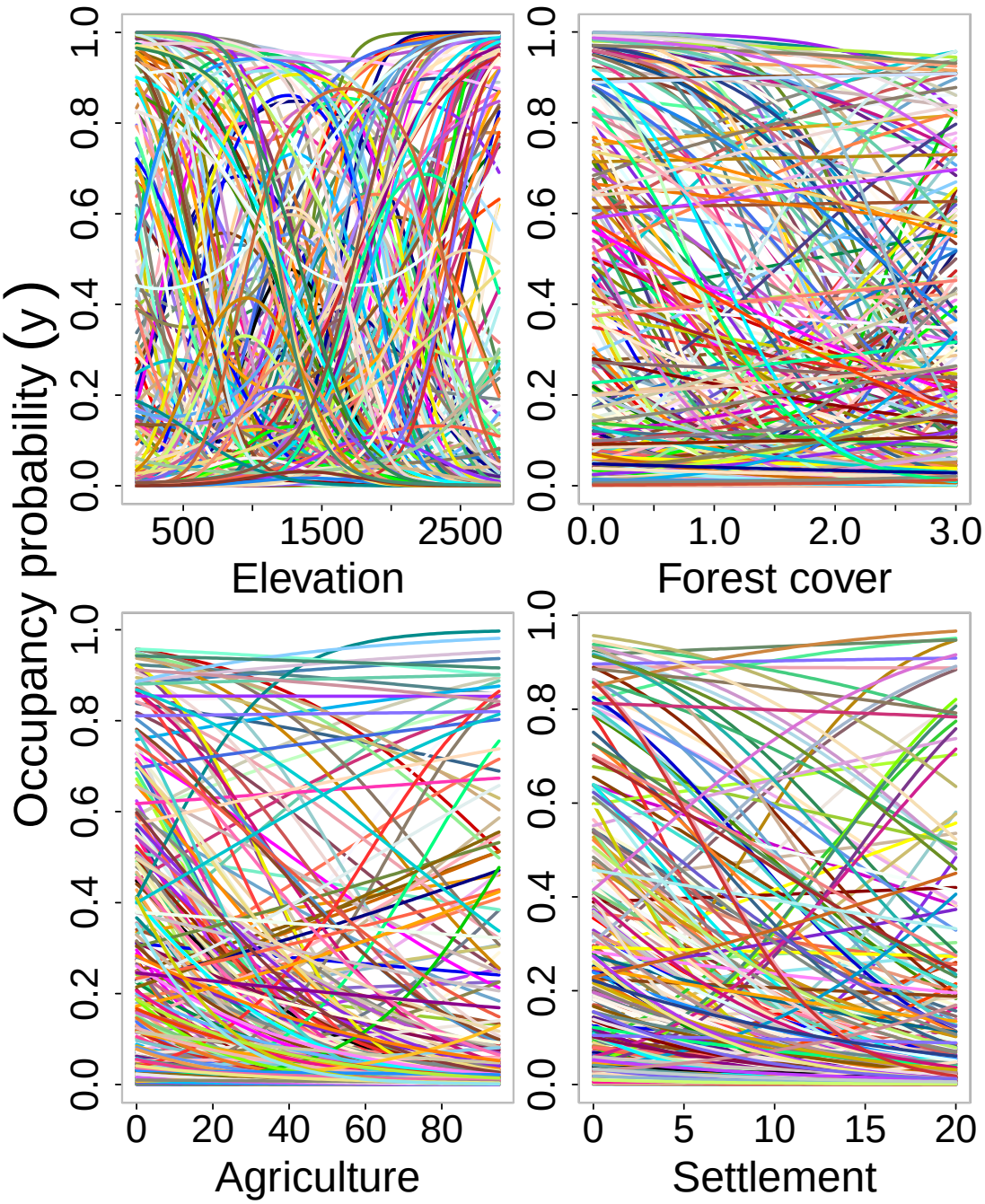


Figure S6. Species-specific response to environmental and anthropogenic variables. Prediction of each species for each variable is made while holding others at their mean values

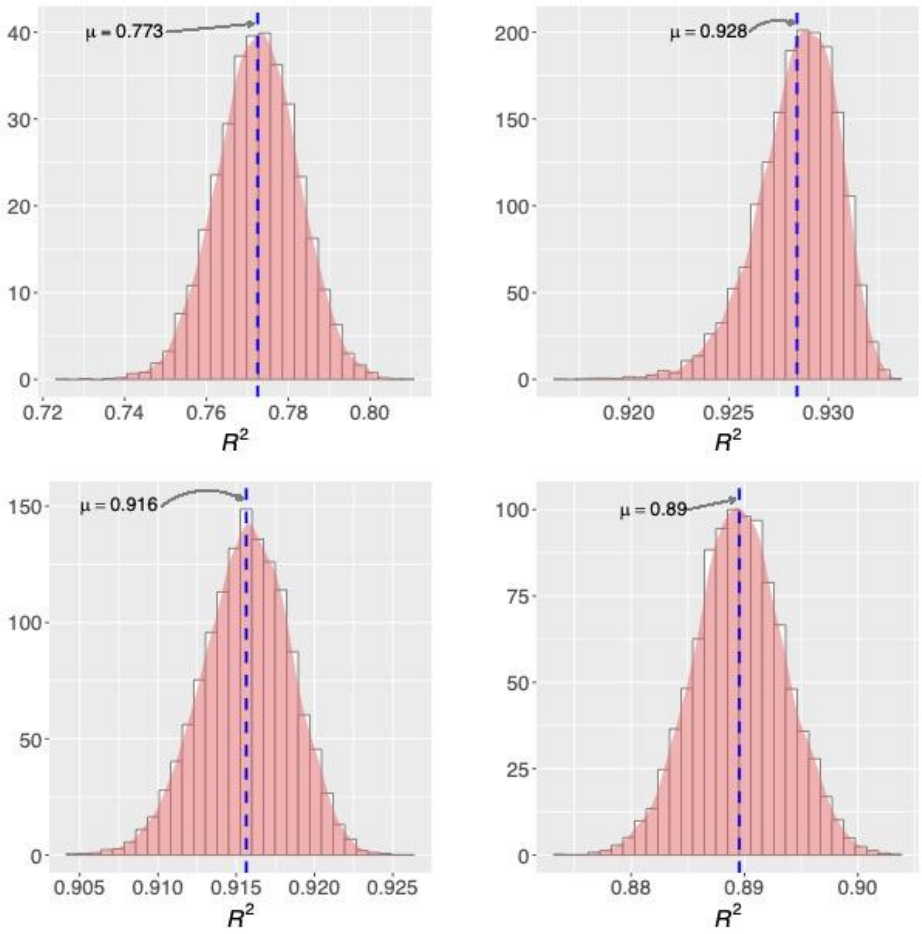


Figure S7. Posterior distributions of Bayesian R^2 for the linear mixed-effect models of diversity metrics. Vertical lines indicate posterior means. R^2 was calculated as, $R^2 = \frac{explained\ variance}{explained\ variance + residual\ variance}$, where *explained variance* is estimated from the modelled predictive means and *residual variance* is the modelled residual variance (Gelman et al., 2019)

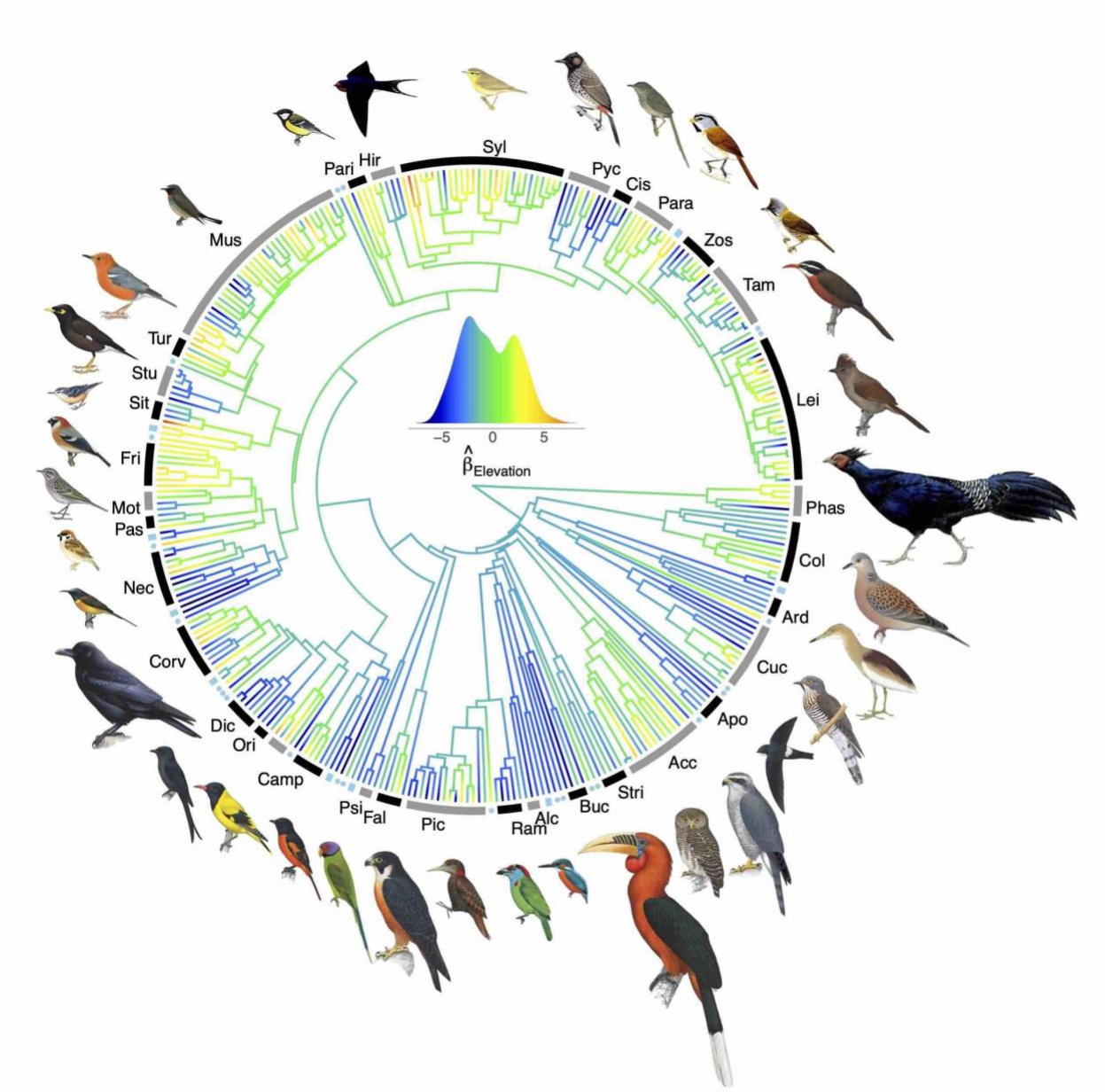


Figure S8. Modelled altitudinal distribution of 336 species. Negative ($\hat{\beta}$) indicates low altitudinal affiliate and vice versa for positive. Contracted family names are shown (please refer to the main text for expansion). Only representative species are illustrated. Image courtesy of (Robson, 2005, Arlott, 2015, Grimmett et al., 2016)

Table S1. Model selection results of the five models fit to point count data. The scores are calculated and averaged from 5-fold cross-validation

Model	**Occupancy covariates**	**Detection covariates**	**0-1 score**	**LogLik score**	**AUC**	**Brier**
Limited	Elevation	Date	4327.003	18235.97	0.890	2165.971
Model1	Elevation, Elevation^2, Settlement	Date, Date^2	4133.692	17175.83	0.907	2064.728
Model2	Elevation, Elevation^2, Agriculture, Forest	Duration	4222.635	17457.42	0.906	2117.279
Full	Elevation, Elevation^2, Forest, Agriculture, Settlement	Date, Date^2, Duration, Habitat	**4032.575**	**16542.34**	**0.918**	**2024.343**
Extra*	Elevation, Random	Constant	4308.826	18106.35	0.893	2156.178

**Extra model has a randomly generated standard normal variable. This was added to check if the model selection criteria could adequately discriminate superfluous variables*

Table S2 Hypothesised *a priori* model set for regression analysis of diversity metric as a function of environmental and anthropogenic predictors. The response variable was each of the functional and phylogenetic diversity metrics (SES.FD, SES.fMPD, SES.PD, SES.MPD)

Model	**Parameters**
M1	Elevation + Elevation^2
M2	Forest
M3	Agriculture
M4	Settlement
M5	Elevation + Elevation^2 + Forest
M6	Elevation + Elevation^2 + Agriculture
M7	Elevation + Elevation^2 + Settlement
M8	Agriculture + Forest
M9	Agriculture + Settlement
M10	Forest + Settlement
M11	Elevation + Elevation^2 + Forest + Agriculture
M12	Elevation + Elevation^2 + Forest + Settlement
M13	Elevation + Elevation^2 + Agriculture + Settlement
M14	Forest + Agriculture + Settlement
M15	Elevation + Elevation^2 + Forest + Agriculture + Settlement
M16	Elevation + Forest + Agriculture + Settlement

Table S3 Model selection result for SES.FD (functional diversity). Refer to Table S2 for the details of each model. K= no. of parameters

Model	K	LogLik	AICc	DeltaAICc	Weight
M6	6	564.487 -	-1116.8	0.00	0.460
M11	7	564.773	-1115.4	1.47	0.221
M13	7	564.651	-1115.1	1.71	0.195
M15	8	565.228	-1114.2	2.61	0.125
M16	7	556.279	-1098.4	18.46	0.000
M5	6	535.651	-1059.2	57.67	0.000
M12	7	535.817	-1057.5	59.38	0.000
M7	6	532.606 -	-1053.1	63.76	0.000
M1	5	530.799	-1051.5	65.34	0.000
M8	5	14.529	-19.0	1097.88	0.000
M2	4	13.330	-18.6	1098.25	0.000
M14	6	14.530	-16.9	1099.91	0.000
M10	5	13.338	-16.6	1100.26	0.000
M4	4	2.073	3.9	1120.76	0.000
M9	5	2.073	5.9	1122.79	0.000
M3	4	0.085	7.9	1124.74	0.000

Table S4 Model selection result for SES.fMPD (functional structure). Refer to Table S2 for the details of each model. K= no. of parameters

Model	K	LogLik	AICc	DeltaAICc	Weight
M15	8	597.391	-1178.6	0.00	0.810
M13	7	594.907	-1175.6	2.92	0.188
M11	7	589.971	-1165.8	12.79	0.001
M6	6	581.787	-1151.4	27.12	0.000
M12	7	577.554	-1140.9	37.63	0.000
M5	6	570.613	-1129.1	49.47	0.000
M7	6	564.038	-1116.0	62.62	0.000
M1	5	542.846	-1075.6	102.97	0.000
M16	7	466.167	-918.2	260.40	0.000
M8	5	-119.859	249.8	1428.38	0.000
M14	6	-119.830	251.8	1430.35	0.000
M2	4	-134.568	277.2	-1455.76	0.000
M10	5	-134.440	279.0	-1457.54	0.000
M9	5	-178.234	366.6	-1545.13	0.000
M4	4	-180.235	368.5	1547.10	0.000
M3	4	-186.339	380.7	1559.30	0.000

Table S5 Model selection result for SES.PD (phylogenetic diversity). Refer to Table S2 for the details of each model. K= no. of parameters

Model	K	LogLik	AICc	DeltaAICc	Weight
M15	8	550.329 -	-1084.4	0.00	0.982
M13	7	545.295 -	-1076.4	8.02	0.018
M6	6	532.265 -	-1052.4	32.04	0.000
M11	7	532.611	-1051.1	33.39	0.000
M12	7	476.091	-938.0	146.43	0.000
M7	6	473.631	-935.1	149.31	0.000
M16	7	465.416	-916.7	167.78	0.000
M5	6	461.146	-910.2	174.28	0.000
M1	5	448.521	-887.0	197.49	0.000
M8	5	-232.494	475.1	1559.52	0.000
M14	6	-232.303	476.7	1561.18	0.000
M2	4	-236.886	481.8	1566.28	0.000
M10	5	-236.779	483.6	1568.09	0.000
M4	4	-265.066	538.2	1622.64	0.000
M9	5	-264.929	539.9	1624.39	0.000
M3	4	-272.460	553.0	1637.42	0.000

Table S6 Model selection result for SES.MPD (functional structure). Refer to Table S2 for the details of each model. K= no. of parameters

Model	K	LogLik	AICc	DeltaAICc	Weight
M13	7	398.300	-782.4	0.00	0.726
M15	8	398.347	-780.5	1.95	0.274
M11	7	389.617	-765.1	17.37	0.000
M6	6	388.520	-764.9	17.52	0.000
M12	7	373.863	-733.6	48.87	0.000
M7	6	369.574	-727.0	55.41	0.000
M5	6	366.137	-720.1	62.28	0.000
M1	5	353.031	-696.0	86.46	0.000
M16	7	275.463	-536.8	245.67	0.000
M8	5	-360.862	731.8	1514.25	0.000
M14	6	-360.850	733.8	1516.26	0.000
M2	4	-373.711	755.5	1537.91	0.000
M10	5	-373.630	757.3	1539.78	0.000
M9	5	-407.330	824.7	1607.18	0.000
M4	4	-409.464	827.0	1609.42	0.000
M3	4	-414.117	836.3	1618.73	0.000

Table S7 Parameter estimate from the top model for each diversity metric presented as median (95% credible intervals). (-) indicates that these variables did not feature in the top model

	SES.FD	**SES.fMPD**	**SES.PD**	**SES.MPD**
Intercept	-0.352 (-0.366, -0.339)	-0.129 (-0.143, -0.114)	-0.321 (-0.337, -0.306)	-0.180 (-0.199, -0.161)
Elevation	-0.302 (-0.312, -0.292)	-0.349 (-0.358, -0.338)	-0.431 (-0.442, -0.419)	-0.505 (-0.520, -0.489)
Elevation^2	-0.023 (-0.032, -0.015)	0.087 (0.078, 0.097)	0.073 (0.063, 0.083)	0.112 (0.101, 0.124)
Forest	-	-0.012 (-0.022, -0.001)	0.019 (0.007, 0.030)	-
Agriculture	0.035 (0.027, 0.043)	0.028 (0.019, 0.038)	0.064 (0.054, 0.074)	0.043 (0.032, 0.054)
Settlement	-	0.017 (0.009, 0.025)	0.029 (0.020, 0.038)	0.024 (0.013, 0.035)

Table S8 Species list (n=336) with common and Latin names detected across the survey in Bhutan during 2019-2020

Common Name	Latin Name	Family
Black Eagle	*Ictinaetus malayensis*	Accipitridae
Golden Eagle	*Aquila chrysaetos*	Accipitridae
Crested Serpent Eagle	*Spilornis cheela*	Accipitridae
Rufous-bellied Eagle	*Lophotriorchis kienerii*	Accipitridae
Changeable Hawk Eagle	*Nisaetus limnaetus*	Accipitridae
Mountain Hawk Eagle	*Nisaetus nipalensis*	Accipitridae
Himalayan Vulture	*Gyps himalayensis*	Accipitridae
Bearded Vulture	*Gypaetus barbatus*	Accipitridae
Oriental Honey-buzzard	*Pernis ptilorhynchus*	Accipitridae
Northern Goshawk	*Accipiter gentilis*	Accipitridae
Crested Goshawk	*Accipiter trivirgatus*	Accipitridae
Eurasian Sparrowhawk	*Accipiter nisus*	Accipitridae
Besra	*Accipiter virgatus*	Accipitridae
Shikra	*Accipiter badius*	Accipitridae
Common Iora	*Aegithina tiphia*	Aegithinidae
Crested Kingfisher	*Megaceryle lugubris*	Alcedinidae
Common Kingfisher	*Alcedo atthis*	Alcedinidae
White-throated Kingfisher	*Halcyon smyrnensis*	Alcedinidae
Dark-rumped Swift	*Apus acuticauda*	Apopidae
Asian Palm Swift	*Cypsiurus balasiensis*	Apopidae
House Swift	*Apus nipalensis*	Apopidae
Himalayan Swiftlet	*Collocalia brevirostris*	Apopidae
Fork-tailed Swift	*Apus pacificus*	Apopidae
Striated Heron	*Butorides striata*	Ardeidae
White-bellied Heron	*Ardea insignis*	Ardeidae
Indian Pond Heron	*Ardeola grayii*	Ardeidae
Little Egret	*Egretta garzetta*	Ardeidae
Rufous-necked Hornbill	*Aceros nipalensis*	Bucerotidae
Great Hornbill	*Buceros bicornis*	Bucerotidae
Wreathed Hornbill	*Rhyticeros undulatus*	Bucerotidae
Oriental Pied Hornbill	*Anthracoceros albirostris*	Bucerotidae
Grey-chinned Minivet	*Pericrocotus solaris*	Campephagidae
Scarlet Minivet	*Pericrocotus flammeus*	Campephagidae
Short-billed Minivet	*Pericrocotus brevirostris*	Campephagidae
Long-tailed Minivet	*Pericrocotus ethologus*	Campephagidae

Black-winged Cuckooshrike	*Coracina melaschistos*	Campephagidae
Large Cuckooshrike	*Coracina macei*	Campephagidae
Grey Nightjar	*Caprimulgus jotaka*	Caprimulgidae
Rusty-flanked Treecreeper	*Certhia nipalensis*	Certhiidae
Brown-throated Treecreeper	*Certhia discolor*	Certhiidae
Slaty-bellied Tesia	*Tesia olivea*	Cettiidae
Grey-bellied Tesia	*Tesia cyaniventer*	Cettiidae
Chestnut-headed Tesia	*Oligura castaneocoronata*	Cettiidae
River Lapwing	*Vanellus duvaucelii*	Charadriidae
Orange-bellied Leafbird	*Chloropsis hardwickii*	Chloropseidae
Golden-fronted Leafbird	*Chloropsis aurifrons*	Chloropseidae
Brown Dipper	*Cinclus pallasii*	Cinclidae
Common Tailorbird	*Orthotomus sutorius*	Cisticolidae
Mountain Tailorbird	*Phyllergates cucullatus*	Cisticolidae
Black-throated Prinia	*Prinia atrogularis*	Cisticolidae
Rufescent Prinia	*Prinia rufescens*	Cisticolidae
Striated Prinia	*Prinia crinigera*	Cisticolidae
Barred Cuckoo Dove	*Macropygia unchall*	Columbidae
Oriental Turtle Dove	*Streptopelia orientalis*	Columbidae
Emerald Dove	*Chalcophaps indica*	Columbidae
Spotted Dove	*Stigmatopelia chinensis*	Columbidae
Wedge-tailed Green Pigeon	*Treron sphenurus*	Columbidae
Mountain Imperial Pigeon	*Ducula badia*	Columbidae
Pin-tailed Green Pigeon	*Treron apicauda*	Columbidae
Thick-billed Green Pigeon	*Treron curvirostra*	Columbidae
Common Pigeon	*Columba livia*	Columbidae
Speckled Wood Pigeon	*Columba hodgsonii*	Columbidae
Snow Pigeon	*Columba leuconata*	Columbidae
Indian Roller	*Coracias benghalensis*	Coraciidae
Dollarbird	*Eurystomus orientalis*	Coraciidae
Large-billed Crow	*Corvus macrorhynchos*	Corvidae
Eastern Jungle Crow	*Corvus levaillantii*	Corvidae
Grey Treepie	*Dendrocitta formosae*	Corvidae
Rufous Treepie	*Dendrocitta vagabunda*	Corvidae
Collared Treepie	*Dendrocitta frontalis*	Corvidae
Common Green Magpie	*Cissa chinensis*	Corvidae
Yellow-billed Blue Magpie	*Urocissa flavirostris*	Corvidae
Spotted Nutcracker	*Nucifraga caryocatactes*	Corvidae
Eurasian Jay	*Garrulus glandarius*	Corvidae
Red-billed Chough	*Pyrrhocorax pyrrhocorax*	Corvidae

Chestnut-winged Cuckoo	*Clamator coromandus*	Cuculidae
Plaintive Cuckoo	*Cacomantis merulinus*	Cuculidae
Banded Bay Cuckoo	*Cacomantis sonneratii*	Cuculidae
Indian Cuckoo	*Cuculus micropterus*	Cuculidae
Himalayan Cuckoo	*Cuculus saturatus*	Cuculidae
Eurasian Cuckoo	*Cuculus canorus*	Cuculidae
Large Hawk Cuckoo	*Hierococcyx sparverioides*	Cuculidae
Hodgson's Hawk Cuckoo	*Hierococcyx fugax*	Cuculidae
Common Hawk Cuckoo	*Hierococcyx varius*	Cuculidae
Green-billed Malkoha	*Phaenicophaeus tristis*	Cuculidae
Lesser Coucal	*Centropus bengalensis*	Cuculidae
Asian Koel	*Eudynamys scolopaceus*	Cuculidae
Fire-breasted Flowerpecker	*Dicaeum ignipectus*	Dicaeidae
Plain Flowerpecker	*Dicaeum concolor*	Dicaeidae
Yellow-vented Flowerpecker	*Dicaeum chrysorrheum*	Dicaeidae
Ashy Drongo	*Dicrurus leucophaeus*	Dicruridae
Lesser Racket-tailed Drongo	*Dicrurus remifer*	Dicruridae
Bronzed Drongo	*Dicrurus aeneus*	Dicruridae
Greater Racket-tailed Drongo	*Dicrurus paradiseus*	Dicruridae
Hair-crested Drongo	*Dicrurus hottentottus*	Dicruridae
Crow-billed Drongo	*Dicrurus annectens*	Dicruridae
Spotted Elachura	*Elachura formosa*	Elachuridae
Scaly-breasted Munia	*Lonchura punctulata*	Estrildidae
White-rumped Munia	*Lonchura striata*	Estrildidae
Long-tailed Broadbill	*Psarisomus dalhousiae*	Eurylaimidae
Eurasian Hobby	*Falco subbuteo*	Falconidae
Oriental Hobby	*Falco severus*	Falconidae
Peregrine Falcon	*Falco peregrinus*	Falconidae
Common Kestrel	*Falco tinnunculus*	Falconidae
Collared Falconet	*Microhierax caerulescens*	Falconidae
Scarlet Finch	*Carpodacus sipahi*	Fringillidae
Golden-naped Finch	*Pyrrhoplectes epauletta*	Fringillidae
Red-headed Bullfinch	*Pyrrhula erythrocephala*	Fringillidae
Grey-headed Bullfinch	*Pyrrhula erythaca*	Fringillidae
Dark-rumped Rosefinch	*Carpodacus edwardsii*	Fringillidae
Dark-breasted Rosefinch	*Carpodacus nipalensis*	Fringillidae
Yellow-breasted Greenfinch	*Chloris spinoides*	Fringillidae
Spot-winged Grosbeak	*Mycerobas melanozanthos*	Fringillidae
Barn Swallow	*Hirundo rustica*	Hirundinidae
Ashy Wood Swallow	*Artama fuscus*	Hirundinidae

Red-rumped Swallow	*Cecropis daurica*	Hirundinidae
Nepal House Martin	*Delichon nipalense*	Hirundinidae
Asian House Martin	*Delichon dasypus*	Hirundinidae
Eurasian Crag Martin	*Ptyonoprogne rupestris*	Hirundinidae
Yellow-rumped Honeyguide	*Indicator xanthonotus*	Indicatoridae
Asian Fairy Bluebird	*Irena puella*	Irenidae
Grey-backed Shrike	*Lanius tephronotus*	Laniidae
Long-tailed Shrike	*Lanius schach*	Laniidae
Bay-backed Shrike	*Lanius vittatus*	Laniidae
Striated Laughingthrush	*Garrulax striatus*	Leiothrichidae
White-crested Laughingthrush	*Garrulax leucolophus*	Leiothrichidae
Rufous-chinned Laughingthrush	*Garrulax rufogularis*	Leiothrichidae
Chestnut-crowned Laughingthrush	*Garrulax erythrocephalus*	Leiothrichidae
Blue-winged Laughingthrush	*Garrulax squamatus*	Leiothrichidae
White-throated Laughingthrush	*Garrulax albogularis*	Leiothrichidae
Scaly Laughingthrush	*Garrulax subunicolor*	Leiothrichidae
Rufous-necked Laughingthrush	*Garrulax ruficollis*	Leiothrichidae
Grey-sided Laughingthrush	*Garrulax caerulatus*	Leiothrichidae
Greater Necklaced Laughingthrush	*Garrulax pectoralis*	Leiothrichidae
Black-faced Laughingthrush	*Garrulax affinis*	Leiothrichidae
Lesser Necklaced Laughingthrush	*Garrulax monileger*	Leiothrichidae
Bhutan Laughingthrush	*Garrulax imbricatus*	Leiothrichidae
Rufous Sibia	*Heterophasia capistrata*	Leiothrichidae
Long-tailed Sibia	*Heterophasia picaoides*	Leiothrichidae
Rusty-fronted Barwing	*Actinodura egertoni*	Leiothrichidae
Hoary-throated Barwing	*Actinodura nipalensis*	Leiothrichidae
Blue-winged Siva	*Siva cyanouroptera*	Leiothrichidae
Bar-throated Siva	*Siva strigula*	Leiothrichidae
Red-tailed Minla	*Minla ignotincta*	Leiothrichidae
Red-billed Leiothrix	*Leiothrix lutea*	Leiothrichidae
Silver-eared Mesia	*Leiothrix argentauris*	Leiothrichidae
Red-faced Liocichla	*Liocichla phoenicea*	Leiothrichidae
Himalayan Cutia	*Cutia nipalensis*	Leiothrichidae
Blue-bearded Bee-eater	*Nyctyornis athertoni*	Meropidae
Chestnut-headed Bee-eater	*Merops leschenaulti*	Meropidae
Black-naped Monarch	*Hypothymis azurea*	Monarchidae
White Wagtail	*Motacilla alba*	Motacillidae
White-browed Wagtail	*Motacilla maderaspatensis*	Motacillidae
Olive-backed Pipit	*Anthus hodgsoni*	Motacillidae
Rosy Pipit	*Anthus roseatus*	Motacillidae

Dark-sided Flycatcher	*Muscicapa sibirica*	Muscicapidae
Little Pied Flycatcher	*Ficedula westermanni*	Muscicapidae
Ultramarine Flycatcher	*Ficedula superciliaris*	Muscicapidae
Rufous-gorgeted Flycatcher	*Ficedula strophiata*	Muscicapidae
Pygmy Blue Flycatcher	*Ficedula hodgsoni*	Muscicapidae
Slaty-blue Flycatcher	*Ficedula tricolor*	Muscicapidae
Pale Blue Flycatcher	*Cyornis unicolor*	Muscicapidae
Blue-throated Blue Flycatcher	*Cyornis rubeculoides*	Muscicapidae
Pale-chinned Flycatcher	*Cyornis poliogenys*	Muscicapidae
White-gorgeted Flycatcher	*Anthipes monileger*	Muscicapidae
Large Niltava	*Niltava grandis*	Muscicapidae
Small Niltava	*Niltava macgrigoriae*	Muscicapidae
Rufous-bellied Niltava	*Niltava sundara*	Muscicapidae
Spotted Forktail	*Enicurus maculatus*	Muscicapidae
Slaty-backed Forktail	*Enicurus schistaceus*	Muscicapidae
Little Forktail	*Enicurus scouleri*	Muscicapidae
Black-backed Forktail	*Enicurus immaculatus*	Muscicapidae
White-capped Redstart	*Phoenicurus leucocephalus*	Muscicapidae
Blue-fronted Redstart	*Phoenicurus frontalis*	Muscicapidae
Plumbeous Water Redstart	*Rhyacornis fuliginosa*	Muscicapidae
Oriental Magpie Robin	*Copsychus saularis*	Muscicapidae
White-tailed Robin	*Myiomela leucura*	Muscicapidae
Blue-fronted Robin	*Cinclidium frontale*	Muscicapidae
Golden Bush Robin	*Tarsiger chrysaeus*	Muscicapidae
Rufous-breasted Bush Robin	*Tarsiger hyperythrus*	Muscicapidae
White-browed Bush Robin	*Tarsiger indicus*	Muscicapidae
Pied Bushchat	*Saxicola caprata*	Muscicapidae
Grey Bushchat	*Saxicola ferreus*	Muscicapidae
Common Stonechat	*Saxicola torquatus*	Muscicapidae
White-rumped Shama	*Copsychus malabaricus*	Muscicapidae
Himalayan Bluetail	*Tarsiger rufilatus*	Muscicapidae
Chestnut-bellied Rock Thrush	*Monticola rufiventris*	Muscicapidae
Green-tailed Sunbird	*Aethopyga nipalensis*	Nectariniidae
Black-throated Sunbird	*Aethopyga saturata*	Nectariniidae
Crimson Sunbird	*Aethopyga siparaja*	Nectariniidae
Mrs Gould's Sunbird	*Aethopyga gouldiae*	Nectariniidae
Fire-tailed Sunbird	*Aethopyga ignicauda*	Nectariniidae
Ruby-cheeked Sunbird	*Chalcoparia singalensis*	Nectariniidae
Streaked Spiderhunter	*Arachnothera magna*	Nectariniidae
Maroon Oriole	*Oriolus traillii*	Oriolidae

Black-hooded Oriole	*Oriolus xanthornus*	Oriolidae
Slender-billed Oriole	*Oriolus tenuirostris*	Oriolidae
Yellow-throated Fulvetta	*Pseudominla cinerea*	Paradoxornithidae
Nepal Fulvetta	*Alcippe nipalensis*	Paradoxornithidae
Rufous-winged Fulvetta	*Alcippe castaneceps*	Paradoxornithidae
White-browed Fulvetta	*Fulvetta vinipectus*	Paradoxornithidae
Greater Rufous-headed Parrotbill	*Psittiparus ruficeps*	Paradoxornithidae
Grey-headed Parrotbill	*Psittiparus gularis*	Paradoxornithidae
Brown Parrotbill	*Cholornis unicolor*	Paradoxornithidae
Black-throated Parrotbill	*Suthora nipalensis*	Paradoxornithidae
Green-backed Tit	*Parus monticolus*	Paridae
Yellow-cheeked Tit	*Parus spilonotus*	Paridae
Black-throated Tit	*Aegithalos concinnus*	Paridae
Rufous-fronted Tit	*Aegithalos iouschistos*	Paridae
Sultan Tit	*Melanochlora sultanea*	Paridae
Yellow-browed Tit	*Sylviparus modestus*	Paridae
Eurasian Tree Sparrow	*Passer montanus*	Passeridae
Russet Sparrow	*Passer cinnamomeus*	Passeridae
House Sparrow	*Passer domesticus*	Passeridae
Long-billed Wren Babbler	*Rimator malacoptilus*	Pellorneidae
Great Cormorant	*Phalacrocorax carbo*	Phalacrocoracidae
Little Cormorant	*Phalacrocorax niger*	Phalacrocoracidae
Rufous-throated Partridge	*Arborophila rufogularis*	Phasianidae
Chestnut-breasted Partridge	*Arborophila mandellii*	Phasianidae
Hill Partridge	*Arborophila torqueola*	Phasianidae
Kalij Pheasant	*Lophura leucomelanos*	Phasianidae
Red Junglefowl	*Gallus gallus*	Phasianidae
Grey Peacock Pheasant	*Polyplectron bicalcaratum*	Phasianidae
Tickell's Leaf Warbler	*Phylloscopus affinis*	Phylloscopidae
Grey-capped Pygmy Woodpecker	*Dendrocopos canicapillus*	Picidae
Crimson-breasted Woodpecker	*Dendrocopos cathpharius*	Picidae
Darjeeling Woodpecker	*Dendrocopos darjellensis*	Picidae
Rufous-bellied Woodpecker	*Dendrocopos hyperythrus*	Picidae
Fulvous-breasted Woodpecker	*Dendrocopos macei*	Picidae
Bay Woodpecker	*Blythipicus pyrrhotis*	Picidae
Grey-headed Woodpecker	*Picus canus*	Picidae
Rufous Woodpecker	*Micropternus brachyurus*	Picidae
Pale-headed Woodpecker	*Gecinulus grantia*	Picidae
Greater Yellownape	*Picus flavinucha*	Picidae
Lesser Yellownape	*Picus chlorolophus*	Picidae

Greater Goldenback	*Chrysocolaptes lucidus*	Picidae
Speckled Piculet	*Picumnus innominatus*	Picidae
White-browed Piculet	*Sasia ochracea*	Picidae
Blue-naped Pitta	*Pitta nipalensis*	Pittidae
Pygmy Wren Babbler	*Pnoepyga pusilla*	Pnoepygidae
Scaly-breasted Wren Babbler	*Pnoepyga albiventer*	Pnoepygidae
Hodgson's Frogmouth	*Batrachostomus hodgsoni*	Podargidae
Rufous-breasted Accentor	*Prunella strophiata*	Prunellidae
Red-breasted Parakeet	*Psittacula alexandri*	Psittacidae
Slaty-headed Parakeet	*Psittacula himalayana*	Psittacidae
Plum-headed Parakeet	*Psittacula cyanocephala*	Psittacidae
Striated Bulbul	*Pycnonotus striatus*	Pycnonotidae
Red-vented Bulbul	*Pycnonotus cafer*	Pycnonotidae
Black-crested Bulbul	*Pycnonotus flaviventris*	Pycnonotidae
Red-whiskered Bulbul	*Pycnonotus jocosus*	Pycnonotidae
Black Bulbul	*Hypsipetes leucocephalus*	Pycnonotidae
Ashy Bulbul	*Hemixos flavala*	Pycnonotidae
White-throated Bulbul	*Alophoixus flaveolus*	Pycnonotidae
Mountain Bulbul	*Ixos mcclellandii*	Pycnonotidae
Black-tailed Crake	*Porzana bicolor*	Rallidae
Great Barbet	*Megalaima virens*	Ramphastidae
Blue-throated Barbet	*Megalaima asiatica*	Ramphastidae
Golden-throated Barbet	*Megalaima franklinii*	Ramphastidae
Lineated Barbet	*Megalaima lineata*	Ramphastidae
Blue-eared Barbet	*Megalaima australis*	Ramphastidae
White-throated Fantail	*Rhipidura albicollis*	Rhipiduridae
Yellow-bellied Fantail	*Chelidorhynx hypoxanthus*	Rhipiduridae
White-tailed Nuthatch	*Sitta himalayensis*	Sittidae
Chestnut-bellied Nuthatch	*Sitta cinnamoventris*	Sittidae
Beautiful Nuthatch	*Sitta formosa*	Sittidae
Velvet-fronted Nuthatch	*Sitta frontalis*	Sittidae
Grey-headed Canary Flycatcher	*Culicicapa ceylonensis*	Stenostiridae
Asian Barred Owlet	*Glaucidium cuculoides*	Strigidae
Collared Owlet	*Glaucidium brodiei*	Strigidae
Mountain Scops Owl	*Otus spilocephalus*	Strigidae
Brown Wood Owl	*Strix leptogrammica*	Strigidae
Spot-bellied Eagle Owl	*Bubo nipalensis*	Strigidae
Common Myna	*Acridotheres tristis*	Sturnidae
Jungle Myna	*Acridotheres fuscus*	Sturnidae
Great Myna	*Acridotheres grandis*	Sturnidae

Common Hill Myna	*Gracula religiosa*	Sturnidae
Asian Pied Starling	*Gracupica contra*	Sturnidae
Chestnut-tailed Starling	*Sturnia malabarica*	Sturnidae
Yellow-vented Warbler	*Phylloscopus cantator*	Sylviidae
Grey-hooded Warbler	*Phylloscopus xanthoschistos*	Sylviidae
Grey-cheeked Warbler	*Phylloscopus poliogenys*	Sylviidae
Chestnut-crowned Warbler	*Phylloscopus castaniceps*	Sylviidae
Green-crowned Warbler	*Phylloscopus burkii*	Sylviidae
Ashy-throated Warbler	*Phylloscopus maculipennis*	Sylviidae
Lemon-rumped Warbler	*Phylloscopus chloronotus*	Sylviidae
Buff-barred Warbler	*Phylloscopus pulcher*	Sylviidae
Greenish Warbler	*Phylloscopus trochiloides*	Sylviidae
Hume's Warbler	*Phylloscopus humei*	Sylviidae
Whistler's Warbler	*Seicercus whistleri*	Sylviidae
White-spectacled Warbler	*Seicerus affinis*	Sylviidae
Yellow-bellied Warbler	*Abroscopus superciliaris*	Sylviidae
Black-faced Warbler	*Abroscopus schisticeps*	Sylviidae
Broad-billed Warbler	*Tickellia hodgsoni*	Sylviidae
Large-billed Leaf Warbler	*Phylloscopus magnirostris*	Sylviidae
Blyth's Leaf Warbler	*Phylloscopus reguloides*	Sylviidae
Brown-flanked Bush Warbler	*Cettia fortipes*	Sylviidae
Grey-sided Bush Warbler	*Cettia brunnifrons*	Sylviidae
Aberrant Bush Warbler	*Horornis flavolivaceus*	Sylviidae
Russet Bush Warbler	*Bradypterus mandelli*	Sylviidae
Rusty-cheeked Scimitar Babbler	*Pomatorhinus erythrogenys*	Timaliidae
Streak-breasted Scimitar Babbler	*Pomatorhinus ruficollis*	Timaliidae
Coral-billed Scimitar Babbler	*Pomatorhinus ferruginosus*	Timaliidae
White-browed Scimitar Babbler	*Pomatorhinus schisticeps*	Timaliidae
Slender-billed Scimitar Babbler	*Pomatorhinus superciliaris*	Timaliidae
Golden Babbler	*Stachyridopsis chrysaea*	Timaliidae
Rufous-capped Babbler	*Stachyridopsis ruficeps*	Timaliidae
Rufous-fronted Babbler	*Stachyridopsis rufifrons*	Timaliidae
Jungle Babbler	*Turdoides striata*	Timaliidae
Grey-throated Babbler	*Stachyris nigriceps*	Timaliidae
Puff-throated Babbler	*Pellorneum ruficeps*	Timaliidae
Black-eared Shrike Babbler	*Pteruthius melanotis*	Timaliidae
Black-headed Shrike Babbler	*Pteruthius rufiventer*	Timaliidae
White-browed Shrike Babbler	*Pteruthius flaviscapis*	Timaliidae
Green Shrike Babbler	*Pteruthius xanthochlorus*	Timaliidae
Pin-striped Tit Babbler	*Macronus gularis*	Timaliidae

Rufous-throated Wren Babbler	*Spelaeornis caudatus*	Tamiliidae
Winter Wren	*Troglodytes troglodytes*	Troglodytidae
Red-headed Trogon	*Harpactes erythrocephalus*	Trogonidae
Plain-backed Thrush	*Zoothera mollissima*	Turdidae
Orange-headed Thrush	*Zoothera citrina*	Turdidae
Blue Whistling Thrush	*Myophonus caeruleus*	Turdidae
White-browed Shortwing	*Brachypteryx montana*	Turdidae
Lesser Shortwing	*Brachypteryx leucophris*	Turdidae
Grey-winged Blackbird	*Turdus boulboul*	Turdidae
Green Cochoa	*Cochoa viridis*	Turdidae
Common Hoopoe	*Upupa epops*	Upupidae
Bar-winged Flycatcher-shrike	*Hemipus picatus*	Vangidae
Large Woodshrike	*Tephrodornis virgatus*	Vangidae
White-bellied Erpornis	*Erpornis zantholeuca*	Vireonidae
Oriental White-Eye	*Zosterops palpebrosus*	Zosteropidae
Whiskered Yuhina	*Yuhina flavicollis*	Zosteropidae
White-naped Yuhina	*Yuhina bakeri*	Zosteropidae
Black-chinned Yuhina	*Yuhinia nigrimenta*	Zosteropidae
Stripe-throated Yuhina	*Yuhina gularis*	Zosteropidae
Rufous-vented Yuhina	*Yuhina occipitalis*	Zosteropidae
Striated Yuhina	*Staphida castaniceps*	Zosteropidae

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Other Publications (between 2019 and 2022)

Understanding the environmental and anthropogenic correlates of tiger presence in a montane conservation landscape

Penjor, U., Tan, C. K. W., Wangdi, S., & Macdonald, D. W. (2019).

Published in *Biological Conservation, 238, 108196*.

https://doi.org/10.1016/j.biocon.2019.108196

Abstract

Management of tigers is a response to a global conservation crisis. Range contraction, population decline, habitat fragmentation, prey loss, and poaching cause and aggravate this crisis. There is a debate as to whether conserving source sites or maintaining landscape connectivity is the greater priority. Both approaches rely on understanding environmental and anthropogenic factors. We used a large dataset from a nation-wide camera trapping survey to investigate factors affecting habitat use of tigers across the montane landscape of Bhutan. We tested the effects of environmental and anthropogenic covariates on habitat use while accounting for imperfect detection using a hierarchical occupancy model. Tiger habitat use showed a strong positive association with closeness to protected area, greater distance from human settlement and availability of abundant large prey. Our findings can help to identify the drivers of tiger decline and contribute to the refinement of conservation strategies to combat that decline in this montane conservation landscape. We provide a general approach to tiger conservation by highlighting the importance of understanding the basic ecology of this apex predator, including the relationship between environmental and anthropogenic variables and habitat use. Bhutan, with unusually strong environmental legislation, and a high percentage of its area protected and under contiguous forest cover, set the global standard in large carnivore conservation and is an important component of a wider conservation complex in South Asia.

Multi-scale habitat modelling identifies spatial conservation priorities for mainland clouded leopards (*Neofelis nebulosa*)

Macdonald, D.W., Bothwell, H. M., Kaszta, Z., Ash, E., Bolongon, G., Burnham., D., Can, O. M., Campos-Arceiz, A., Channa, P., Clements, G. R., Hearn, A. J., Hedges, L., Htun, S., Kamler, J., Kawanishi., K., Macdonald., E. A., Mohamad., S. W., Moore, J., Naing, H., Onuma, M., **Penjor, U.,** Rasphone, A., Rayan, D. M., Ross, J., Singh, P., Tan, C. K. W., Wadey, J., Yadav, B. P. and Cushman, S. A. (2019).

Published in *Diversity and Distributions, 25(10), 1639 – 1654.* https://doi.org/10.1111/ddi.12967

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 and capacity to act as powerful levers for broader forest conservation programmes. Thus, identifying core habitat and conservation opportunities are critical for curbing further *Neofelis* declines and extending umbrella protection for diverse forest biota similarly threatened by widespread habitat loss. Furthermore, a recent comprehensive habitat assessment of Sunda clouded leopards (*N. diardi*) highlights the lack of such information for the mainland species (*N. nebulosa*) and facilitates a comparative assessment.

Location

Southeast Asia.

Methods

Species–habitat relationships are scale-dependent, yet <5% of all recent habitat modelling papers apply robust approaches to optimize multivariate scale relationships. Using one of the largest

camera trap datasets ever collected, we developed scale-optimized species distribution models for two con-generic carnivores, and quantitatively compared their habitat niches.

Results

We identified core habitat, connectivity corridors, and ranked remaining habitat patches for conservation prioritization. Closed-canopy forest was the strongest predictor, with ~25% lower *Neofelis* detections when forest cover declined from 100 to 65%. A strong, positive association with increasing precipitation suggests ongoing climate change as a growing threat along drier edges of the species' range. While deforestation and land use conversion were deleterious for both species, *N. nebulosa* was uniquely associated with shrublands and grasslands. We identified 800 km^2 as a minimum patch size for supporting clouded leopard conservation.

Main conclusions

We illustrate the utility of multi-scale modelling for identifying key habitat requirements, optimal scales of use and critical targets for guiding conservation prioritization. Curbing deforestation and development within remaining core habitat and dispersal corridors, particularly in Myanmar, Laos and Malaysia, is critical for supporting evolutionary potential of clouded leopards and conservation of associated forest biodiversity.

Habitat requirements of the Himalayan red panda (*Ailurus fulgens*) and threat analysis in Jigme Dorji National Park, Bhutan

Dendup, P., Humle, T., Bista, D., **Penjor, U**., Lham, C., & Gyeltshen, J. (2020).

Published in *Ecology and Evolution, 10(17), 9444 – 9453*. https://doi.org/10.1002/ece3.6632

Abstract

Understanding the influence of anthropogenic disturbances on species' habitat use and distribution is critical to conservation managers in planning effective conservation strategies and mitigating the impact of development. Few studies have focused on the Himalayan red panda (*Ailurus fulgens*) in Bhutan. This study aimed to assess the habitat requirements and threats to this endangered species in the Khamaed subdistrict of the Jigme Dorji National Park, Bhutan. We employed a transect walk and plot-sampling survey design across two seasons, that is, winter and spring. In total, we surveyed 84 × 50 m radius circular plots along 51 km of existing trails within a 25.4 km^2 study area. At 500 m intervals, we established plots at random distances and direction from the trail. We recorded direct sightings (n = 2) and indirect signs (n = *14*), such as droppings and footprints as evidence of red panda presence within an altitudinal range of 2,414–3,618 m. We also noted 21 tree and 12 understory species within plots with red panda evidence; the dominant tree species was the Himalayan hemlock (*Tsuga dumosa*) and the Asian barberry (*Berberis asiatica*) as an understory species. Red panda presence showed a significant positive association with distance to water sources and fir forests. Plant disturbance and infrastructure, such as power transmission lines, were identified as prominent anthropogenic threats in the study area. Based on our findings, we recommend the development and implementation of local forest management plans, livestock intensification programs, and strict application of environmental impact assessment regulations to promote the conservation of the red panda in the region.

How effective are tiger conservation areas at managing their sites against the conservation assured| tiger standards (CA|TS)?

Dudley, N., Stolton, S., Pasha, M. K. S., Baltser, M., Yap, W. L., Sharma, M., Long, B., Yadav, S. P., Gopal, R., Bonal, B. S., Kapoor, M., Roy, S., Paxton, M., Khadka, M., Bhatta, S. R., Chapagain, D., Chapman, S., Roberts, J., Verma, N., Wangdi, S., **Penjor, U.,** Tandin, T., Dhaka, M., Oli, B. N., Tenzin., K., Peiqi, L., Bose, J., Widodo, F. A., Novalina, R., Darmaraj., M. R., Hagir, R., Kostyria, A. V., Rafhan, H., Shrestha, M., Duangchantrasiri, S., Vinitpornsawan, S., Phoonjampa R. and Boron, V. (2020).

Published in *Parks, 26(2), 115 – 128*. http://dx.doi.org/10.2305/IUCN.CH.2020.PARKS-26-2ND.en

Abstract

A global pledge to double wild Tiger populations by 2022 has focused attention on the need for effective conservation management. Conservation Assured | Tiger Standards (CA|TS) was established to identify good management standards for Tigers and promote these within Tiger conservation areas (TCAs). The study reported here assessed TCA management against a simplified version of CA|TS to uncover potential shortfalls in management and provide recommendations for future practices. From 11 Tiger range countries (TRCs), 111 TCAs were surveyed on their implementation of 40 strategic Tiger management activities, making it the largest Tiger management study to date. The study found that over a third of TCAs have major management deficiencies, threatening the survival of wild Tigers, biodiversity and natural resources. These deficiencies are especially prominent in South East Asian countries compared to other TRCs. Non-South East Asian countries had a significantly higher percentage of TCAs that had fully implemented the activities outlined in the survey. The lowest scoring elements of management, excluding tourism since that did not apply to all TCAs, were infrastructure, equipment and facilities, protection, and community relations. Recommendations include increased government funding, capacity building, and the implementation of CA|TS to secure the future of wild Tigers.

Investigating Carnivore Guild Structure: Spatial and Temporal Relationships amongst Threatened Felids in Myanmar

Kyaw, P. P., Macdonald, D. W., **Penjor, U**., Htun, S., Naing, H., Burnham, D., Kaszta, Ż., & Cushman, S. A. (2021).

Published in *ISPRS International Journal of Geo-Information, 10(2), 808*.

https://doi.org/10.3390/ijgi10120808

Abstract

The co-occurrence of felid species in Southeast Asia provides an unusual opportunity to investigate guild structure and the factors controlling it. Using camera-trap data, we quantified the space use, temporal activity, and multi-dimensional niche overlap of the tiger, clouded leopard, Asiatic golden cat, marbled cat, and leopard cat in the Htamanthi Wildlife Sanctuary, Myanmar. We hypothesised that the spatio-temporal behaviour of smaller cats would reflect the avoidance of the larger cats, and similar-sized guild members would partition their niches in space or time to reduce resource competition. Our approach involved modelling single-species occupancy, pairwise spatial overlap using Bayesian inference, activity overlap with kernel density estimation, and multivariate analyses. The felid assembly appeared to be partitioned mainly on a spatial rather than temporal dimension, and no significant evidence of mesopredator release was observed. Nonetheless, the temporal association between the three mesopredators was inversely related to the similarity in their body sizes. The largest niche differences in the use of space and time occurred between the three smallest species. This study offers new insight into carnivore guild assembly and adds substantially to knowledge of five of the least known felids of conservation concern.

Density and occupancy of leopard cats across different forest types in Cambodia

Pin, C., Phan, C., Kamler, J. F., Rostro-García, S., **Penjor, U.**, In, V., Crouthers, R., Macdonald, E. A., Chou, S., & Macdonald, D. W. (2022).

Published in *Mammal Research*. https://doi.org/10.1007/s13364-022-00634-6

Abstract

The leopard cat (*Prionailurus bengalensis*) is the most common wild felid in Southeast Asia, yet little is known about the factors that affect their population density and occupancy in natural habitats. Although leopard cats are highly adaptable and reportedly can attain high densities in human-modified habitats, it is not clear which natural habitat is optimal for the species. Also, this felid has been preyed upon by large carnivores in Southeast Asia, yet the intra-guild effects of large carnivore presence on leopard cats are almost unknown. To shed light on these fundamental questions, we used data from camera trap surveys for felids to determine the leopard cat densities in three different forest types within Cambodia: continuous evergreen, mosaic dominated by evergreen (hereafter evergreen mosaic), and mosaic dominated by open dry deciduous forests (hereafter DDF mosaic). We also conducted occupancy analyses to evaluate the interactions of the leopard cats with three large carnivores: leopards (*Panthera pardus*), dholes (*Cuon alpinus*), and domestic dogs (*Canis familiaris*). The estimated density (individuals/100 $km^2 \pm$ SE) was highest in the continuous evergreen (27.83 ± 7.68), followed by evergreen mosaic (22.06 ± 5.35) and DDF mosaic (13.53 ± 3.23). Densities in all three forest types were relatively high compared to previous studies. Domestic dogs were detected on all 3 sites, and leopards and dholes had sufficient records on only one site each. The occupancy probability of leopard cats was not affected by the presence or absence of any large carnivore, indicating that large carnivores and leopard cats occurred independently of each other. Our findings support the claim that leopard cats are habitat generalists, but we show that evergreen forest is the optimum natural habitat for this species in the region. The DDF mosaic appears to sustain lower densities of leopard cats, probably due to the harsh dry season and wildfires that led to reduced prey base, although this generalist felid was still able to occupy DDF in relatively

moderate numbers. Overall, the adaptability of leopard cats to various forest types, and lack of negative interaction with large carnivores, helps to explain why this species is the most common and widespread felid in Southeast Asia.