Sumatran mesocarnivores: small-medium sized wild felids of the Kerinci Seblat Landscape

Iding Achmad Haidir

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A thesis submitted for the degree of
Doctor of Philosophy

Michaelmas 2020

Abstract

The study of mesopredators, their guilds, and conservation has had little attention in the tropics of Southeast Asia. A particularly interesting group, from the point of view of their ecological community and because of their generally threatened status, is the Felidae. This thesis reports an intensive camera-trapping study of small-medium sized wild felids in the Kerinci Seblat landscape in west-central Sumatra. Samples were drawn from seven study areas across a diversity of habitats occupied by clouded leopard, golden cat, marbled cat, leopard cat, and their prey. The papers comprising this thesis report on the ecology, behaviour, population status and trends, core areas and habitat connectivity of this predator-prey community, and prioritizing conservation in a multi-species management approach. Specifically, this thesis has five main results: (i) revealed spatial and temporal interactions between clouded leopard, golden cat, and their respective prey through performing Bayesian two species occupancy modelling and temporal overlap analyses; (ii) estimated population densities of clouded leopard, in the context of human activities, by implementing Bayesian Spatially Explicit Capture Recapture (SECR) and identified and quantified illegal human activities detected by camera traps; (iii) estimated occupancy states as an indicator of clouded leopard and golden cat population dynamics from consecutive surveys in 2009-11 and 2014-16 and anthropogenic pressures from deforestation in the surrounding areas; and (iv) identified high priority areas within and outside protected area networks through estimating multi-species habitat use and least cost path and kernel density estimate analyses for defining core areas and corridor networks. Integrating these four research themes, this thesis contributes to absent information on the felid mesocarnivores of Sumatra, and offers analytical methodologies for assessing their ecology, behaviour, conservation, and management that can be applied throughout the tropics.

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Declaration

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

Iding Achmad Haidir

Acknowledgements

"And these examples We present to the people,
but none will understand them except those of knowledge"

Qur'an, Al-Ankaboot (29) verse 43

I remember my childhood, living in a small village in rural West Java, called Jatisura. The village was surrounded by paddy fields, and although there was no rainforest, it was a very green and natural environment. I had great adventures, playing ground-fishing, hunting insects, swimming in streams, with unlimited playing time with my friends, making my childhood so alive and joyful. Luckily, my profession as a Forester, has allowed me to get enjoy the wilderness, the beauty of the tropical rainforest of Sumatra. Later, these experiences supported the development of my passion for the nebulous '*macan dahan*', the clouded leopard, the 'tree tiger'. My passion for this animal began to translate into action when I first expressed interest in doing research on Sumatran clouded leopard to assess their conservation status. I recall that it was in mid-February 2007, when I wrote down my thoughts and ideas for systematic surveys in Kerinci Seblat National Park (KSNP) to *unclouded the life of the secretive clouded leopards' life.*

My involvement in wildlife population monitoring in Kerinci would not have happened without the encouragement of my boss-colleague-friend, *Mas* Rudijanta Nugraha, and my first GIS tutor and friend- now for the DPhil, one of my academic supervisors, Matthew Linkie. Also, *Ninek* Debbie Martyr, whose role in my career path is obvious: leading my very first jungle trip, a 'Transect Walk' into the Kerinci Seblat forests in Silaut, West Sumatra. More importantly, I would not have reached this stage without the 'approval' and strong motivational support, the stories and wisdom of the then Head of Kerinci Seblat National Park, Mr Soewartono. During these years, my adventures in the Sumatran rainforest, monitoring tiger and prey population with Fauna & Flora International-the first international NGO that I worked with, yielded fruitful and sweet results. In 2007, I was offered a place to attend Certificate Course in Wildlife Management at the Wildlife Institute of India. The three-month course was to open up new academic opportunities in wildlife conservation.

And so here I am now; blessed with the endless support of my academic supervisors, Professor David Macdonald and Dr Matthew Linkie, who from the beginning, have had faith in me finishing this DPhil study. I would not have been able to go through the challenging years of field work and overcoming challenges to grasp new knowledge without their wisdom, patience and matchless advice, which has helped translate my dreams and passion for clouded leopards into reality. I owe a lifetime of thanks to you both.

I thank, too, my colleagues and friends from WildCRU. I offer sincere thanks to Dr Dawn Burnham assisted by Jennifer Spencer and Emma Stewart-Wood, who tirelessly gave their pastoral and administrative support during my years with WildCRU. Susan Cheyne, the first person who introduce me to the Panthera course, and who gave me advice in improving my application for the PG Diploma course. Dr Paul Johnson, Dr Mark Stanley-Price and Prof Claudio Sillero shared their wisdom and lifted my morale and spirit as I pursued my studies. My tutors: Dr Lucy Tallents and Dr Christos Astaras, were the best tutors I've ever had while studying abroad. Jo Ross and Andrew Hearn, the first two WildCRUers who I met - before I too became a member of WildCRU. Ugyen Penjor, who passionately shared experiences, knowledge and skill, jokes, and wisdoms, and, sometimes, the difficulties of living in place far-far away from home and family. Thanks too, to all fellows WildCRU students and all 2010 WildCRU Panthers, for being my friends in exchanging stories, smiles and positive encouragements. Dr Jeremy Cusack and Dr Arjun Gopalaswamy, who, in different time and places, gave their advice or delivered thought-provoking questions regarding my statistical modelling and method. Dr Cedric Tan, Dr Mohammad Farhadinia, Lovemore Sibanda, Eric Ash, my office mates who I met – albeit rarely -at the office, thank you for your kind and silent companionship at the office while being cheering and joyful outside working hours.

This thesis is a product of collaboration of many government agencies, non-government organisations, universities, funding and donor agencies. I thank Karen Povey and Dr Karen Goodrowe-Beck of Point Defiance Zoo & Aquarium, who gave me the chance to attend the clouded leopard workshop in Bangkok and provided financial support particularly towards my field work and to our conservation education project in Kerinci Seblat NP. The Rufford Foundation through their Small Grant programme; Recanati-Kaplan Foundation, Panthera Foundation, Robertson Foundation, and World Animal Protection, for their generous financial support that allowed me to execute my field work, or, to be more precise, my dreams. I thank Darmawan Liswanto, Arozawato Zandroto, Dr Haryo T. Wibisiono, and later their successor at FFI Indonesia Programme who, from the beginning, assisted me in project management and administrative support. WCS Indonesia

Programme for their support both financially and logistically towards my final years of study. Our field project partners: Doddy Saputra, Wido Albert and all members of FFI Tiger Monitoring team, who kindly shared their base camp with my team in Sungai Penuh. Dian Risdianto, Nurhamidi, and all the members of Pelestarian Harimau Sumatra-Kerinci Seblat (PHS-KS) in Jambi and Bengkulu for their cooperation and support. My mentor in the field, Yoan Dinata, and colleagues from ZSL Jambi Office, I thank you all.

I received so much advice and inputs from friends and colleagues towards my field work, not only from my formal circle, on both technical and non-technical matters. I thank my collaborators Żaneta Kaszta, Lara Sousa, Oliver Wearn, M. Irfansyah Lubis, and Wai-Ming Wong. I also thank 11 anonymous reviewers who had kindly given their constructive inputs for the improvement of every data chapter of this thesis. My stats Guru Mike Meredith and Ngumbang Juat for their patience and expertise explaining complex things into very simple and digestible knowledge. Also to Dr Jim Sanderson, Dr Richard Bischof, Dr Azlan Mohamed, for their contribution in knowledge and skill sharing over the phone and emails. I thank friends from PPI Oxford (Indonesian Student Association in Oxford) and students from Universitas Jambi, Universitas Andalas and Institut Teknologi Bandung.

Ms Listya Kusumawardhani, who headed the park when I first joined the service, her guidance and good advice will always be remembered. The Head(s) of Kerinci Seblat National Park Authority and Officers with whom I have crossed paths with in Kerinci, Mr Suyatno Sukandar, Mr Luhut Sihombing, Mr Kholid Indarto, Mr Persada Sitepu, *Kang* Nandang Gumilar, Mr Donal Hutasoit, Mr Arief Toengkagie and Mr Tamen Sitorus. I thank them, particularly to the latter two names, I thank them for giving permission to me to conduct the research and to utilize their field facilities. I thank Mr Wiratno, the DG of KSDAE, and colleagues from Directorate of Biodiversity Conservation (KKH), for their support.

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I thank all my best friends from SKMA (Forestry Vocational School), Batch XIX (2001), for the encouragement and for our old-time stories at school, and for keeping our brotherhood alive. My new friends from Zheng Restaurant and the Perch where I spent my weekends working as a part-timer, I found it was amusing and exciting, but also tiring. I offer my thanks to my hosts in Oxford, and all house mates at the Mansion in University's Accommodation in Court Place Garden, Iffley Village, Oxford.

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".. Allah will exalt those of you who believe,
and those who are given knowledge, in high degrees;
and Allah is aware of what you do"

Qur'an, Al-Mujadilah (58) verse 11

Publications and Contributions

The following published and in press papers have arisen from this thesis, and are presented in Chapters 2, 3, 4, 5 and the Appendices.

Chapter 2

Haidir, I.A., Macdonald, D.W. & Linkie, M. (2018) Assessing the spatiotemporal interactions of mesopredators in Sumatra's tropical rainforest. *PLoS ONE,* **13**.

> I conducted field work and data collection, conceived of the manuscript with feedback from DWM and ML. I carried out the analyses, modelling and wrote the first draft of the manuscript. DWM and ML contributed equally to the review process and improvement of the manuscript in its final form.

Chapter 3

Haidir, I., Macdonald, D.W. & Linkie, M. (2020) Sunda clouded leopard Neofelis diardi densities and human activities in the humid evergreen rainforests of Sumatra. *Oryx***,** 1-8.

> I conducted field work and data collection, conceived of the manuscript with feedback from DWM and ML. I carried out the data analyses, modelling and wrote the first draft of the manuscript. DWM and ML contributed equally to the review process and improvement of the manuscript in its final form.

Chapter 4

Haidir, I., Macdonald, D.W., Wong, W-M., Lubis, M.I., & Linkie, M. (2020) Population dynamics of threatened felids in response to forest cover change in Sumatra, *PLoS ONE* **15**(8): e0236144

> I conducted field work and data collection, conceived of the manuscript with feedback from DWM and ML. I carried out the data analyses, modelling and wrote the first draft of the manuscript. DWM and ML contributed equally to the review process and improvement of the manuscript in its final form. WWM provided data from Survey I and giving inputs for further manuscript development. MIL assisted GIS-related works that include forest cover changes calculation.

Chapter 5

Haidir, I., Kaszta, Ż., Sousa, L., Lubis, M., Macdonald, D.W., & Linkie, M. (2020). Felids, forest and farmland: Identifying high priority conservation areas in Sumatra. Landscape Ecology, doi.org/10.1007/s10980-020-01146-x

> I conducted field work and data collection, conceived of the manuscript with feedback from DWM and ML. I carried out the data analyses, occupancy modelling and wrote the first draft of the manuscript. ZK, LS and I contributed equally to corridor and core area analyses and manuscript advancement. MIL assisted in GIS-related work and spatial analyses. IH, ZK, LS, DWM and ML contributed equally to the review process and improvement of the manuscript in its final form.

Appendix 1

Risdianto, D., Martyr, D.J., Nugraha, R.T., Harihar, A., Wibisono, H.T., **Haidir, I.A.**, Macdonald, D.W., D'Cruze, N. & Linkie, M. (2016) Examining the shifting patterns of poaching from a long-term law enforcement intervention in Sumatra. Biological Conservation. http://dx.doi.org/10.1016/j.biocon.2016.10.029.

Appendix 2

Macdonald, D.W., Bothwell, H.M., Hearn, A.J., Cheyne, S.M., **Haidir, I.A**, Hunter, L.T.B., Kaszta, Ż., Linkie, M., Macdonald, E.A., Ross, J. & Cushman, S.A. (2018) Multi-scale habitat selection modeling identifies threats and conservation opportunities for the Sunda clouded leopard (*Neofelis diardi*). *Biological Conservation,* 227, 92-103.

Abstract

The study of mesopredators, their guilds, and conservation has had little attention in the tropics of Southeast Asia. A particularly interesting group, from the point of view of their ecological community and because of their generally threatened status, is the Felidae. This thesis reports an intensive camera-trapping study of small-medium sized wild felids in the Kerinci Seblat landscape in west-central Sumatra. Samples were drawn from seven study areas across a diversity of habitats occupied by clouded leopard, golden cat, marbled cat, leopard cat, and their prey. The papers comprising this thesis report on the ecology, behaviour, population status and trends, core areas and habitat connectivity of this predator-prey community, and prioritizing conservation in a multi-species management approach. Specifically, this thesis has five main results: (i) revealed spatial and temporal interactions between clouded leopard, golden cat, and their respective prey through performing Bayesian two species occupancy modelling and temporal overlap analyses; (ii) estimated population densities of clouded leopard, in the context of human activities, by implementing Bayesian Spatially Explicit Capture Recapture (SECR) and identified and quantified illegal human activities detected by camera traps; (iii) estimated occupancy states as an indicator of clouded leopard and golden cat population dynamics from consecutive surveys in 2009-11 and 2014-16 and anthropogenic pressures from deforestation in the surrounding areas; and (iv) identified high priority areas within and outside protected area networks through estimating multi-species habitat use and least cost path and kernel density estimate analyses for defining core areas and corridor networks. Integrating these four research themes, this thesis contributes to absent information on the felid mesocarnivores of Sumatra, and offers analytical methodologies for assessing their ecology, behaviour, conservation, and management that can be applied throughout the tropics.

Contents

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A mural on a wall in Bangko, capital of Merangin Regency, Jambi,
portraying a clouded leopard with a message: "not to be hunted…!! but to be protected'

1
Introduction

Background

Carnivores, and in particular felids, have attracted attention and evoked passion because of their iconic appearance, charisma, and, in some cases, the danger they pose and damage they can cause (Nowak 2005, Macdonald 2009). A handful of charismatic felids have been studied in depth, such as tigers (*Panthera tigris*) in India, lions (*Panthera leo*) in Africa, and jaguars (*Panthera onca*) in Southern America, and much evidence underpins efforts to conserve them (Singh and Gibson 2011, Tobler et al. 2013, Meena et al. 2014, Jędrzejewski et al. 2017a). Nonetheless, each continues to decline, and knowledge of their behavioural ecology must be matched with local and global commitment to save their populations (Dinerstein et al. 2006). For the great majority of wild felids there is no such evidence-base, although, encouragingly, the last two decades have witnessed increasing attention to the lesser known felids of Southeast Asia, and some of this work has begun to reveal their ecology, behaviour, conservation and conflict with humans. This thesis focuses on these issues on the island of Sumatra, Indonesia (Nyhus and Tilson 2004, Inskip and Zimmermann 2009, Wibisono and Pusparini 2010, Wibisono et al. 2011).

Sumatra is part of the Sunda plateau in western Indonesia. It contains endemic and charismatic species, such as Sumatran tiger (*Panthera tigris sumatrae*), Sumatran rhino (*Dicerorhinos sumatrensis*), Sumatran orang-utan (*Pongo abelii*), endemic birds and amphibians, not to mention various species of flora (Whitten et al. 2000). Other carnivores present within this area are Asiatic wild dogs (*Cuon alpinus*), the omnivorous Malayan sun bear (*Helarctos malayanus*), and a diversity of mustelids and viverids (Holden et al. 2003). While the Sumatran tiger has been the focus of conservation, its smaller relatives have been neglected: Sumatran clouded leopard (*Neofelis diardi diardi*) (hereafter clouded leopard), Asiatic golden cat (*Catopuma temminckii*) (hereafter golden cat), marbled cat (*Pardofelis marmorata*), leopard cat (*Prionailurus bengalensis*), and flat-headed cat (*Prionailurus planiceps*). Information on the bio-ecology and conservation of these species is minimal or non-existent (Pusparini et al. 2014, Sunarto et al. 2015, Luskin 2016, Struebig et al. 2018). This gap is being filled by emerging research on small- and medium-sized cats, concerning their distributions, diets, habitat ranges, and behaviours (Kawanishi and E. Sunquist 2008, Lynam et al. 2013, Mohamad et al. 2015), including finer-scale predator-prey interactions (Hearn 2013, Ross et al. 2013) to inform conservation and protected area management (Sollmann et al. 2014); this thesis contributes to this emerging corpus.

The study of small- and medium-sized felids – difficult to trap and track for telemetry studies - has been revolutionised by camera trapping and associated analytical techniques. Camera-traps were introduced to the Kerinci Seblat (KS) landscape in west-central Sumatra nearly twenty years ago, when Holden et al. (2003) successfully documented high conservation value species: tiger, Malayan tapir (*Tapirus indicus*), Malayan sun bear, Sumatran elephant (*Elephas maximus sumatrensis*), and many other smaller species. Subsequently, successive camera trap surveys have been progressively more systematic and achieved wider coverage, yielding records of rare elusive species (Linkie et al. 2008). Against this background, the aim of this thesis is to describe intra-guild relations amongst the felids in Kerinci Seblat National Park (KSNP) and its surrounding areas. The research had five main foci: (i) investigate spatial and temporal interactions between clouded leopard, golden cat, and their respective putative prey; (ii) estimate clouded leopard densities in sampled areas within KSNP; (iii) investigate trends in their populations between 2010 and 2015, based on two camera trap surveys conducted in 2009-11 and 2014-16; and (iv) identify high value conservation areas within KSNP and the surrounding forests.

Filling in the gap: secretive Sumatran mesocarnivores

Felid populations have been increasingly confined to protected areas that function as dispersed islands amidst a sea of human-dominated landscapes (Wikramanayake et al. 2011, Ripple et al. 2014). Too often, these small, scattered protected areas have neither the space nor the infrastructure to sustain viable populations of large bodied animals that need extensive areas to thrive (Chundawat et al. 2016, Williams et al. 2017, Espinosa et al. 2018). This problem besets the small- to medium-sized felid guild in Sumatra. Increasingly, the research priority is not the autecology of individual species, but rather the functioning of their multi-species guilds (Macdonald 2005, Macdonald and Loveridge 2014). Sumatra is home to 5 species of felid (Sunquist and Sunquist 2002), of which I particularly focused on clouded leopard and golden cat, with a lesser emphasis on marbled cat and leopard cat. The following is a brief introduction to these species and their putative prey:

Sumatran clouded leopard

The forest-dependant, heavily arboreal clouded leopard is a medium-sized cat weighing 9 to 18 kg, with a distinctive appearance due to its pattern of large grey-black rosettes, and its elongated canines and long tail (Sunquist and Sunquist 2002). The clouded leopard occurs as two species, of which the mainland form occurs from open forest in eastern India to peninsular Malaysia, with historical evidence in China and Taiwan (Grassman et al. 2016), whereas the Sunda species spans Borneo and the Indonesian island of Sumatra, but not Java. Their diet is little known, but thought to range from primates to pangolin, and includes Indian hog deer (*Axis porcinus*), slow Loris, porcupine (*Hystrix brachyura*), squirrel, great argus pheasant (*Argusianus argus*), macaque and muntjac (Grassman et al. 2005, Austin et al. 2007). Radio-tracking in national parks in Thailand revealed clouded leopard's home ranges between 30-40 km^2 with a core area of 3-5 km^2 (Austin et al. 2007), while Hearn (2013) radio tracking study on the Island of Borneo concluded 95% and 50% of fixed-kernel estimator respectively at 16.1 km^2 home range with core-range 5.4 km^2. Estimates of clouded leopard population densities tend to be higher in areas where tiger and leopard occur in low densities, as these species are assumed to be their competitors. The population size and distribution of clouded leopard have both contracted globally due to high pressures from illegal hunting, forest fragmentation, and habitat degradation (Sunarto et al. 2008). On-going deforestation in their range has contributed to an estimated global reduction of at least 30% in the last three generations

(IUCN, 2016). According to captivity data, clouded leopard reach maturity when aged between five and six years (Yamada and Durrant 1989). The Sunda clouded leopard exists as two subspecies, inhabiting Sumatra (*Neofelis diardi diardi*) and Borneo (*N. diardi bornensis*) (Kitchener et al. 2006, Christiansen and Kitchener 2011). The Sunda clouded leopard is protected under Indonesian national law and under the legislation of Malaysian Borneo and Brunei, meaning it cannot legally be hunted, and is included in CITES Appendix I of global wildlife trade and listed as Vulnerable on the IUCN Red List (Sunarto et al. 2008).

Asiatic golden cat

In contrast to the strident 'clouded' appearance of the clouded leopard, the Asiatic golden cat's pelage is a more uniform golden or red-brown; although there are occasional records of melanistic individuals in KSNP (Holden et al. 2003). There are no population estimates of golden cat anywhere from mainland Asia through to the island of Sumatra, but recent surveys indicate steep declines in Cambodia, Vietnam, Laos, and South China (Inskip and Zimmermann 2009, Johnson et al. 2016, Rasphone et al. 2019). As with the clouded leopard, there is increasing concern that the golden cat faces escalating pressure from illegal trade, with increasing instances of pelts being confiscated at the international borders of Indo-Chinese countries: Vietnam, Laos, and Myanmar (Willcox et al. 2014). Alarmingly, a ten-year span of camera trapping in Cambodia revealed a rapid decline in golden cat detections (Gray et al. 2012). The Asiatic golden cat is assessed by IUCN criteria as Near Threatened, with obvious evidence of population declines between 20-30% due to extensive habitat loss and poaching across their range; the species' status seems set to deteriorate to Vulnerable in the next several years (Hearn et al. 2015). The Golden cat has been recorded widely and although it is probably in decline in Sumatra, populations are stable on other Indonesian islands (Linkie and Ridout 2011, McCarthy et al. 2015, Sunarto et al. 2015). Golden cats are thought to favour forested areas, occasionally including secondary forests, and have some unpublished incidents of conflict with local people (Haidir et al. 2013). There is an unknown level of indirect mortality as bycatch from bush meat hunting and a fear of increasing retaliatory killings provoked by livestock (mainly poultry) predation (McCarthy 2013). The difficulty of identifying individuals, combined with a low detection rate, has thwarted attempts at producing golden cat population estimates. The general impression is that their abundance is comparable to that of the sympatric Sumatran clouded leopard.

Potential prey species

The only systematic dietary study of either clouded leopard or golden cat was undertaken in Thailand by Grassman et al. (2005), who report that both ate prey ranging in size from *Muridae* (0.1 kg) to Indian hog deer (~40 kg) in the case of the clouded leopard and Indian muntjac (*Muntiacus muntjac*) (~30 kg) in the case of the golden cat. In Malaysia, Kawanishi and E. Sunquist (2008) recorded golden cats predating on *Tragulus Spp.* (~4.5 kg), *Muridae* (~0.2 kg), and dusky leaf monkey (*Trachypithecus obscurus*) (~6.5 kg). A record from Borneo confirmed that clouded leopard predates on both pig-tailed macaque (*Macaca nemestrina*) and long-tailed macaque (*M. fascicularis*) (Macdonald 2009, Burnham et al. 2012). In Southern Sumatra, golden cat are occasionally involved in human-wildlife conflict after attacks on poultry (McCarthy 2013). On the basis of this fragmentary evidence, the current best assessment of the most likely prey of these two felids is: muntjac (*M. muntjac* and *M. montanus*), mouse deer (*Tragulus napu* and *T. kanchil*), pig-tailed macaque, porcupine, and great argus pheasant.

Questions and thesis overview

To remedy the knowledge gap hindering both ecological understanding and conservation planning for small- to medium-sized felids in Southeast Asia, I tackled five major research themes spanning ecology, behaviour, population densities and trends, the definition of core areas, and potential corridors, for which these felids may be umbrella species. Therefore, following this Introduction, I structured the thesis as follows:

In Chapter 2, I reported the spatial interactions (Cusack et al. 2016) and temporal patterns (Ridout and Linkie 2009, Linkie and Ridout 2011) of clouded leopard, golden cat, and their potential prey species in Sumatran rainforest (Grassman et al. 2005, Lynam et al. 2013, Ross et al. 2013). This chapter documents patterns in co-occurrence amongst clouded leopard and golden cat, as published in (Haidir et al. 2013), and predator-prey pairwise coefficients of temporal overlap for each putative prey species.

In Chapter 3, I investigated clouded leopard population densities across a selection of study areas within and around KSNP, and the effect of deforestation in surrounding forests. I estimated clouded leopard density using spatial capture-recapture analyses, employing a Bayesian approach (Gopalaswamy et al. 2012) and building on an earlier study by (Sollmann et al. 2014). I estimated population parameters for each study area. Despite the massive camera trapping effort underpinning these analyses, the data were insufficient to enable me to derive sex-specific density estimates (Tobler and Powell 2013), as attempted by (Jędrzejewski et al. 2017b) using long-term monitoring data for jaguars. My study suggests that illegal human activities did impact clouded leopard density, as higher human activity was associated with lower clouded leopard density and larger ranges.

In Chapter 4, I further analysed the effects of deforestation on mesopredator populations. Following two camera trapping surveys in 2009 to 2011 (survey 1) and 2014 to 2016 (survey 2), I used occupancy modelling to reveal trends in occupancy by Sumatran mesopredators in response to forest loss and in the absence of threats from poaching (Wong et al. 2013). By comparing the two survey periods, I quantified trends in occupancy of three sympatric felid species (clouded leopard, golden cat, and marbled cat) in the tropical rainforest landscape of KSNP. I found that the occupancy of these three species has remained stable, despite deforestation encircling the park to within 15 km.

In Chapter 5, I raised questions on how to identify core areas and potential corridors using camera trap data to inform analyses of detection/non-detection (occupancy) (Linkie et al. 2007, Cove et al. 2013, Bailey et al. 2014). This research question is particularly relevant to my professional obligations because I am a member of the protected area management authority. This authority urgently needs these analyses to underpin planning for protected area and wildlife population management (Harihar and Pandav 2012); key information includes the location of core habitat patches (Cushman et al. 2013, Cushman et al. 2018), the dispersal corridors (Sloan et al. 2019) revealed by species distribution modelling (Kéry et al. 2010), and the risk they face from key threats, notably deforestation (Pusparini et al. 2014, Wong et al. 2015, Haidir et al. 2020).

Finally, in **Chapter 6**, I offered a synthesis of Chapters 2 to 5 to illustrate how my findings can guide science-based wildlife management and conservation in Sumatra, and have the potential to be expanded from KSNP to a national scale. I concluded by emphasising the power of camera trapping surveys to fill important knowledge gaps regarding Sumatran mesopredators, and argued that intensive camera trapping surveys have an important role to play in wildlife conservation and management in tropical habitats.

In this introductory chapter, I have not provided an extensive formal literature review, as this information is embedded in Chapters 2 to 5.

A clouded leopard on a 'dahan' (Indonesian for branch),
drawn by a team of high school students in a mural competition held in Bangko,
as part of celebrating the International Year of Forest, 2012

2

Sumatra's mesopredators spatiotemporal interactions

RESEARCH ARTICLE

Assessing the spatiotemporal interactions of mesopredators in Sumatra's tropical rainforest

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Check for updates

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Abstract

Co-occurrence between mesopredators can be achieved by differentiation of prey, temporal activity, and spatial habitat use. The study of mesopredator interactions is a growing area of research in tropical forests and shedding new light on inter-guild competition between threatened vertebrate species that were previously little understood. Here, we investigate sympatry between the Sunda clouded leopard (*Neofelis diardi*) and Asiatic golden cat (*Pardofelis temminckii*) living in the Sumatran rainforests of Indonesia. We investigate: i) spatial overlap of predator-prey species using a combination of single-species occupancy modelling and Bayesian two-species modelling, while controlling for the possible influence of several confounding landscape variables; and, ii) temporal overlap between mesopredators and their shared prey through calculating their kernel density estimate associations. From four study areas, representing lowland, hill, sub-montane and montane forest, 28,404 camera trap nights were sampled. Clouded leopard and golden cat were respectively detected in 24.3% and 22.6% of the 292 sampling sites (camera stations) and co-occurred in 29.6% of the sites where they were detected. Golden cat occupancy was highest in the study area where clouded leopard occupancy was lowest and conversely lowest in the study area where clouded leopard occupancy was highest. However, our fine-scale (camera trap site) analyses found no evidence of avoidance between these two felid species. While both mesopredators exhibited highest spatial overlap with the larger-bodied prey species, temporal niche separation was also found. Clouded leopard was more nocturnal and, consequently, had higher temporal overlap with the more nocturnal prey species, such as porcupine and mouse deer, whereas the more diurnal golden cat had higher overlap with the strictly diurnal great argus pheasant. The Bayesian two species occupancy modelling approach applied in our study fills several important knowledge gaps of Sumatra's lesser known mesopredators and provides a replicable methodology for studying interspecific competition for other small-medium sized carnivore species in the tropics.

Introduction

Co-occurrence within a predator guild can be achieved through the differentiation of prey base composition, segregating temporal activity, and segregating spatial overlap within habitat patches [1, 2]. For example, spotted hyaenas *Crocuta crocuta* segregate their temporal movement patterns from the apex predator, lion *Panthera leo*, in order to reduce the likelihood of direct confrontations [3]. When there is direct interaction in resource-rich patches, such as water holes, prairies and open grasslands, competing predators may become less tolerant and more aggressive [4]. Within carnivores community, habitat differentially would be expected by the mesopredator in response to the habitat use of the apex predator, such as leopards (*Panthera pardus*) foraging in forest patches with lower prey abundance in order to avoid tigers (*Panthera tigris*) that dominate prey-rich areas [5]. These behavioural mechanisms have been demonstrated to promote such co-existence in a variety of felid communities [6, 7].

In Asia, the majority of terrestrial carnivore species are at risk of extinction. Understanding their population status and inter-guild interactions is therefore important for conservation managers, especially when the species in competition are both threatened [8]. Most studies on predator interactions in Asia have focussed on the high profile conservation flagship species of tiger and leopard and most have come from the dry deciduous forests of South Asia [6, 8]. Thus, little attention has been paid to the mesopredators, such as the smaller felids species living in Southeast Asia's humid evergreen rainforest, which are also under threat, lack data but are presumed to be in need of active management.

Existing in-depth references for clouded leopard and golden cat, and other mesopredator, spatiotemporal interactions from Sumatra are scarce. In other parts of the world however, research on these interactions amongst mesopredators and also with their prey is growing. A camera trap study on multi-species occupancies in three national parks from northern Pakistan, revealed that the Altai mountain weasel *Mustela altaica* is associated with its prey, the pika *Ochotona dauurica*, and segregates spatiotemporal activity with red fox *Vulves vulves* and stone marten *Martes fiona* [9]. Moreover, a combined survey of camera trap, distance sampling and faecal analyses is advancing understanding of tiger and leopard density as well as shifting temporal and spatial patterns of both species over time and areas [8].

In this study we investigate interspecific competition between two threatened felid species, the Near Threatened (NT) golden cat (*Pardofelis temminckii*) [10] and the Vulnerable Sunda clouded leopard (*Neofelis diardi*) [11] from the rainforests of Sumatra, Indonesia. These species have similar body sizes, semi-arboreal behaviour and prey base, therefore neither species is obviously dominant. Previously, Linkie and Ridout [12] investigated the temporal overlap of clouded leopard, golden cat and tiger (*Panthera tigris*) using a camera trap-based sampling technique in multiple study areas that revealed temporal separation to be 10–20% greater between the two smaller felid species. A comparison using single-species, single-season occupancy models then revealed that clouded leopard tended to use forest at higher elevation and further from the non-forest edge, whereas golden cat preferred lower elevation forest with no such edge effect, thereby suggesting the presence of spatial separation [13]. However, these two preliminary studies did not consider how interspecific competition was influenced by prey availability and activity patterns in space and time, nor did they explicitly test spatial interactions between the two carnivore species. Thus, fundamentally important ecological questions remain unanswered, such as whether predator species occupancy is more strongly influenced either by competitor co-occurrence, by prey availability or indeed abiotic landscape factors.

Other carnivore species that might compete with the clouded leopard and golden cat include Sumatran tiger, Asiatic wild dog (*Cuon alpinus*) and sun bear (*Helarctos malayanus*). However, it is unlikely that these three species are true competitors with the two medium-sized felids for several reasons. Tiger and dhole are strictly ground dwelling [2] and the pack-hunting dhole is able to hunt larger-sized prey, such as adult sambar [14, 15], which would be difficult to capture, at least as adults, for the smaller solitary felids. The sun bear is omnivorous with a diet largely consisting of fruits and invertebrates, rather than ungulate prey [16]. The remaining, also solitary, Sumatran felid species are marbled cat (*Pardofelis marmorata*), leopard cat (*Prionailiurus bengalensis*) and flat-headed cat (*Prionailurus planiceps*). The average body size for each species is approximately 50 per cent smaller than golden cat and clouded leopard which makes them unlikely competitors.

To investigate interspecific competition, we use a combination of single-species occupancy modelling and Bayesian two-species occupancy modelling with parameterization, which tests for species dominance as a proxy for co-existence [17]. From this, we measure the potential of predator-prey interactions due to spatial overlap, while analytically controlling for the possible influence of confounding landscape factors. Once we have understood the spatial relationship between these cats, we then calculate kernel densities for the two predator species and their shared prey species to explore overlap in activity patterns. More specifically, this study investigates: 1) level of spatial overlap of clouded leopard and golden cat using a combination of single-species occupancy modelling and Bayesian two-species modelling that incorporate controlled landscape factors; and, 2) measure clouded leopard and golden cat activity patterns; given that their occurrences and activity patterns are affected by shared potential prey.

Materials and methods

Study area

The study was conducted in Kerinci Seblat National Park and its adjacent forest that are under State land authority. We have secured permit to conduct the fieldwork from Indonesia Ministry of Environment and Forestry (MoEF) technical unit in Jambi, West Sumatra, South Sumatra and Bengkulu, of whom the first author is an employee of MoEF.

Camera trap surveys were conducted in four humid evergreen rainforest study areas located in west-central Sumatra, Indonesia. The ~26,000 km^2 Kerinci Seblat landscape lies between E 100˚ 35' 00" and E 102˚ 54' 00", and S 1˚ 30' 00" and S 3˚ 37' 00". Two areas were situated entirely inside the 13,900 km^2 Kerinci Seblat National Park, whereas the other two areas straddled the park border (Figs 1–5, Table 1). The four study areas represent the main forest types in the landscape (lowland, hill, sub-montane and montane), which are characterized by their varying elevation. The national park stretches for ~370 km from north to south and 40–70 km from east to west. The park is situated on the central spine of the Bukit Barisan mountain range and spans elevations of 250 to 3,805 m asl (above sea level), the peak of Mount Kerinci. The average monthly rainfall is high, only dropping below 1500 mm during the months of July and August [18].

Field data collection

For each of the four study areas, 80 paired camera trap placements were set across 1 km^2 grid cells that formed a ~60 km^2 sampling area. Cameras were set at a height of 30–40 cm off the ground, a distance of 2–3 meters from the target trail and at a spacing of 0.8–1.0 km between paired traps. Two brands of heat-motion sensor camera traps were used: Cuddeback Ambush IR (Non Typical Inc., WI, USA) and Panthera IV (Panthera Foundation). Each pair consisted of the same brand at each station, without bait or other lure. Cameras were set by the side of animal trails as indicated by the presence of focal species signs. Camera traps collected data in the field continuously for three months and were visited every two weeks for maintenance and data retrieval.

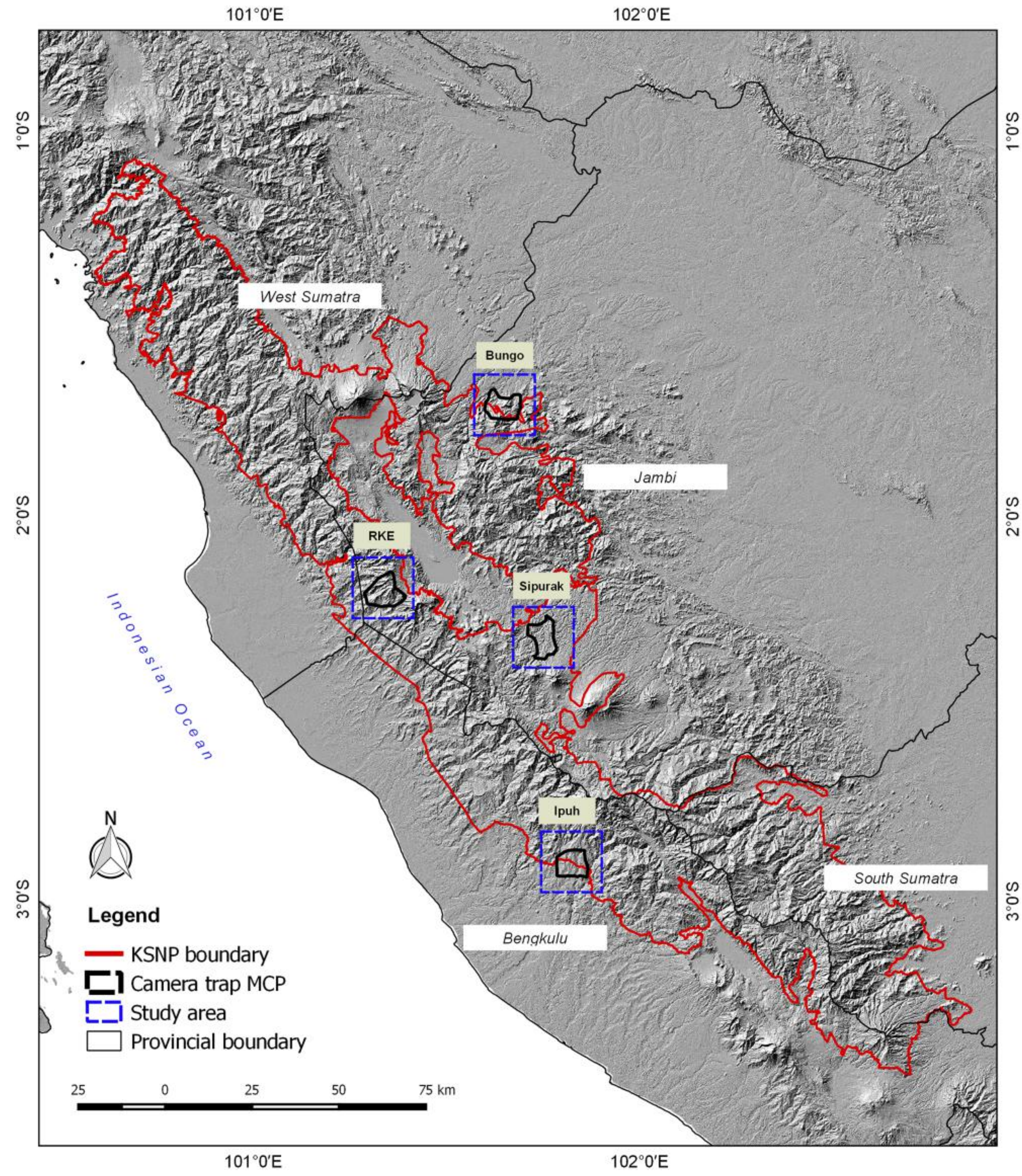

Fig 1. Location of the four-rainforest study areas, of varying elevation in and around Kerinci Seblat National Park, west-central Sumatra.

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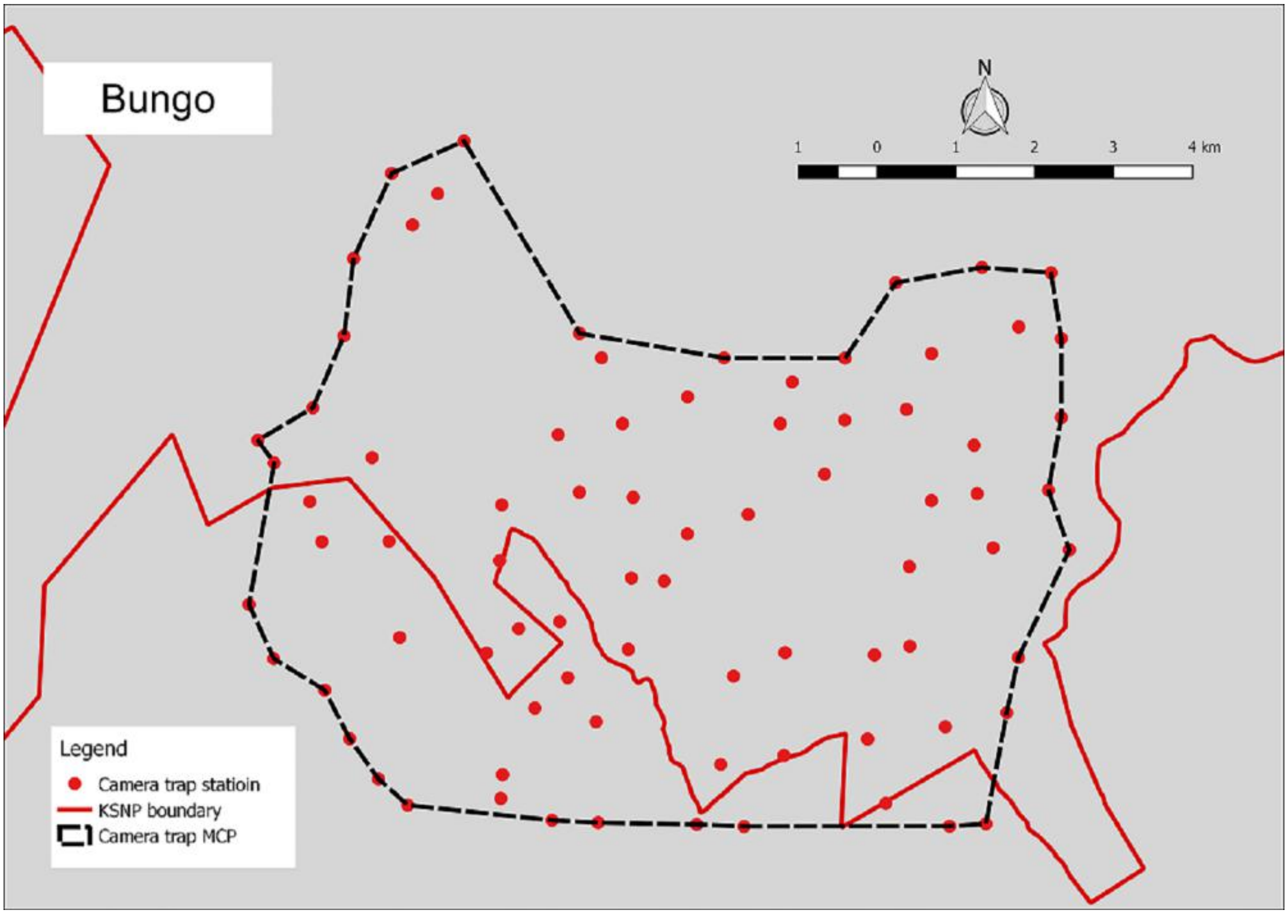

Fig 2. Camera trap location in Bungo.

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Understanding interactions amongst mesopredators requires knowledge of their diets. In Southeast Asia, there are only a few published dietary studies on clouded leopard and golden cat. From Thailand, these felids were found to consume prey as small as Muridae (0.1 kg) and as big as Indian hog deer (*Axis porcinus*, ~40 kg) for clouded leopard and muntjac (*Muntiacus muntjac*, ~30 kg) for golden cat [19]. From Malaysia, golden cat was found to hunt mouse deer (*Tragulus* spp., ~4.5 kg), Muridae (~0.2 kg) and dusky leaf monkey (*Trachypithecus obscurus*, ~6.5 kg) [20]. A record from Borneo confirmed that clouded leopard attacked both pig-tailed macaque (*Macaca nemestrina*, 5–15 kg) and long-tailed macaque (*M. fascicularis*, 4–8 kg) [21]. In Sumatra, golden cat have been recorded attacking poultry [22]. Based on these records and the known prey from our study area, we selected five species as potentially preferred prey: muntjac (*M. muntjac* and *M. montanus*), mouse deer, pig-tailed macaque, porcupine (*Hystrix brachyura*) and great argus pheasant (*Argusianus argus*).

Spatial data analysis. For each camera trap placement, information on the landscape covariates of elevation, distance to forest edge and distance to river were generated using a GIS. These variables were chosen because they have been found to have an effect on felid distribution elsewhere in Sumatra [22, 23]. Elevation data, at 90 m resolution, were obtained from the Shuttle Radar Topography Mission [24]. River data were obtained from the Indonesian National Coordination Agency for Surveys and Mapping for Sumatra (UTM 47 S, scale

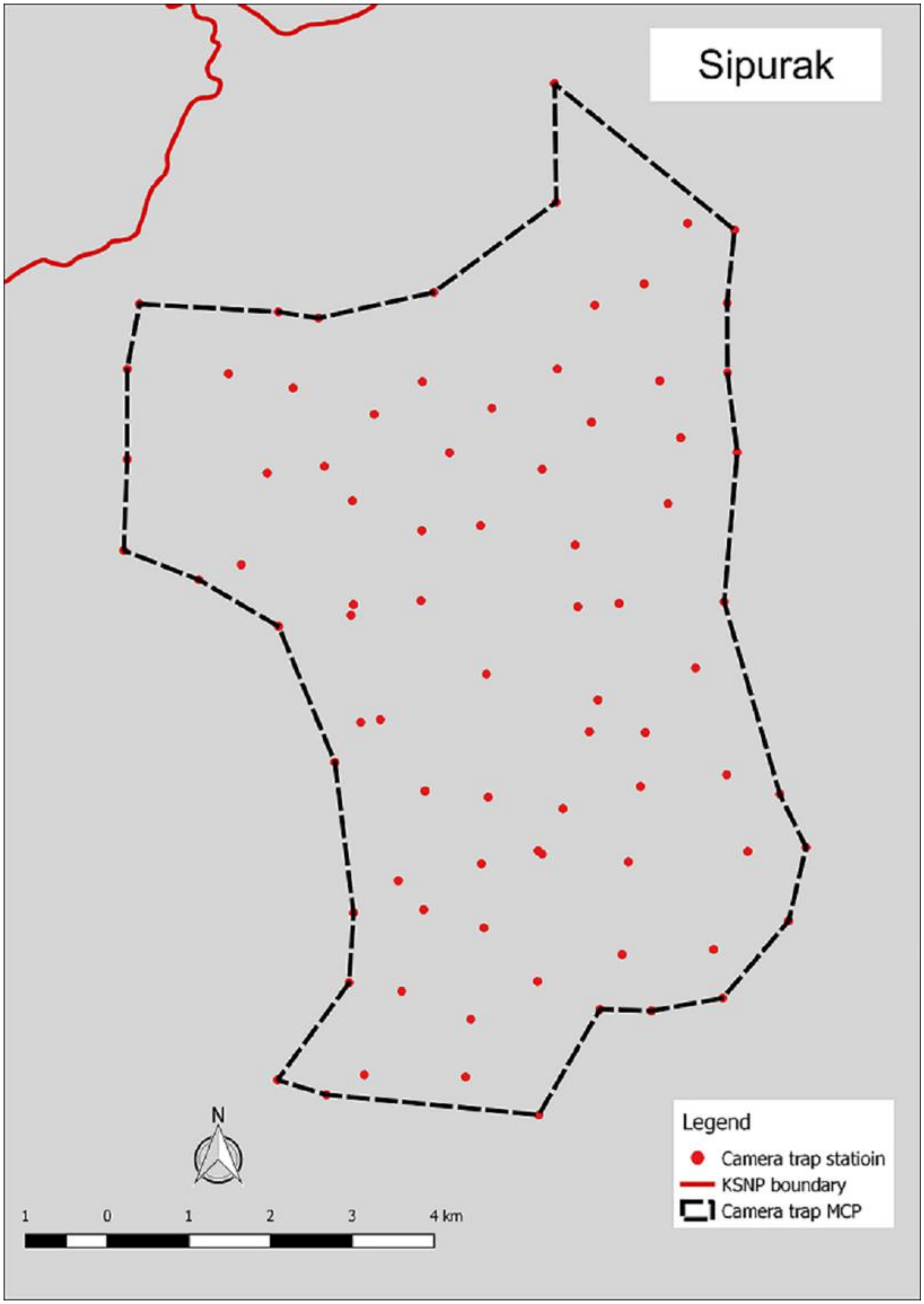

Fig 3. Camera trap location in Sipurak.

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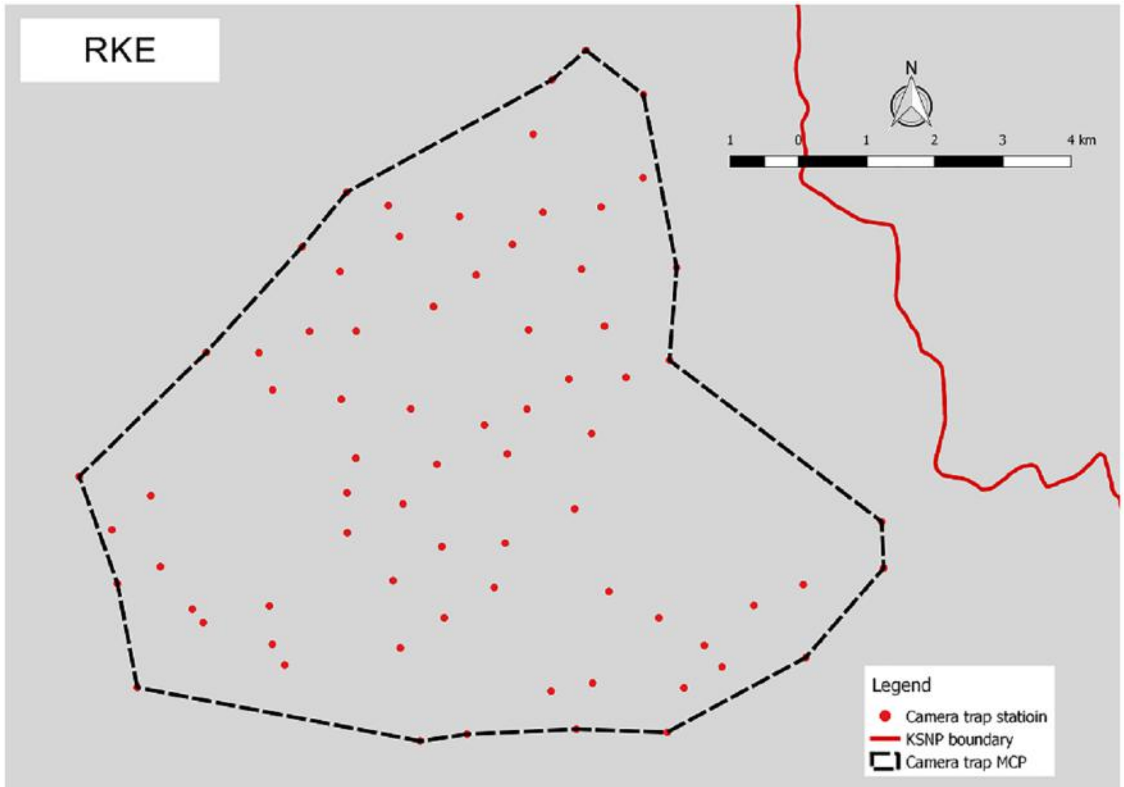

Fig 4. Camera trap location in Renah Kayu Embun (RKE).

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1:50,000). Forest edge data, converted to shapefile format, were obtained from a forest cover map that was produced in 2013 [25].

To investigate species spatial occurrence, an occupancy-modelling framework based on the following assumptions was used: i) demographic population closure—sites have a constant species occupancy status over the sampling period (i.e. there are no births, deaths, immigrations or emigrations); ii) sites and replicates (occasions) are spatially and temporally independent; and, iii) the influence of species detectability and spatial sampling are accounted for in the models [26]. Individual detection matrices ('1' = detected and '0' = undetected) were constructed for the focal species using 14 day sampling occasions [13]. Clouded leopard and golden cat gestation period is 80–90 days [27], in order to anticipate that there would have been new births during our study we recorded only adult individuals in our detection matrices within ~100 days of survey.

A Bayesian multi-species occupancy-modelling framework that enables the modelling of interactions between paired species was used to assess spatial associations between clouded leopard and golden cat and then individually with each of the prey species [17]. Four co-occupancy scenarios were considered: i) golden cat occupancy is influenced by the occupancy of the slightly larger clouded leopard; ii) clouded leopard occupancy is influenced by prey occupancy; iii) golden cat occupancy is influenced by prey occupancy; and, iv) prey and predator occupancies are both influenced by site covariates.

For the multi-species occupancy modelling, we used Bayesian 95% credible density intervals (CDI) for the mean of the posterior distribution for parameter estimates to make inferences about effects on the occupancy of predator species [3, 9]. We used packages R2jags and

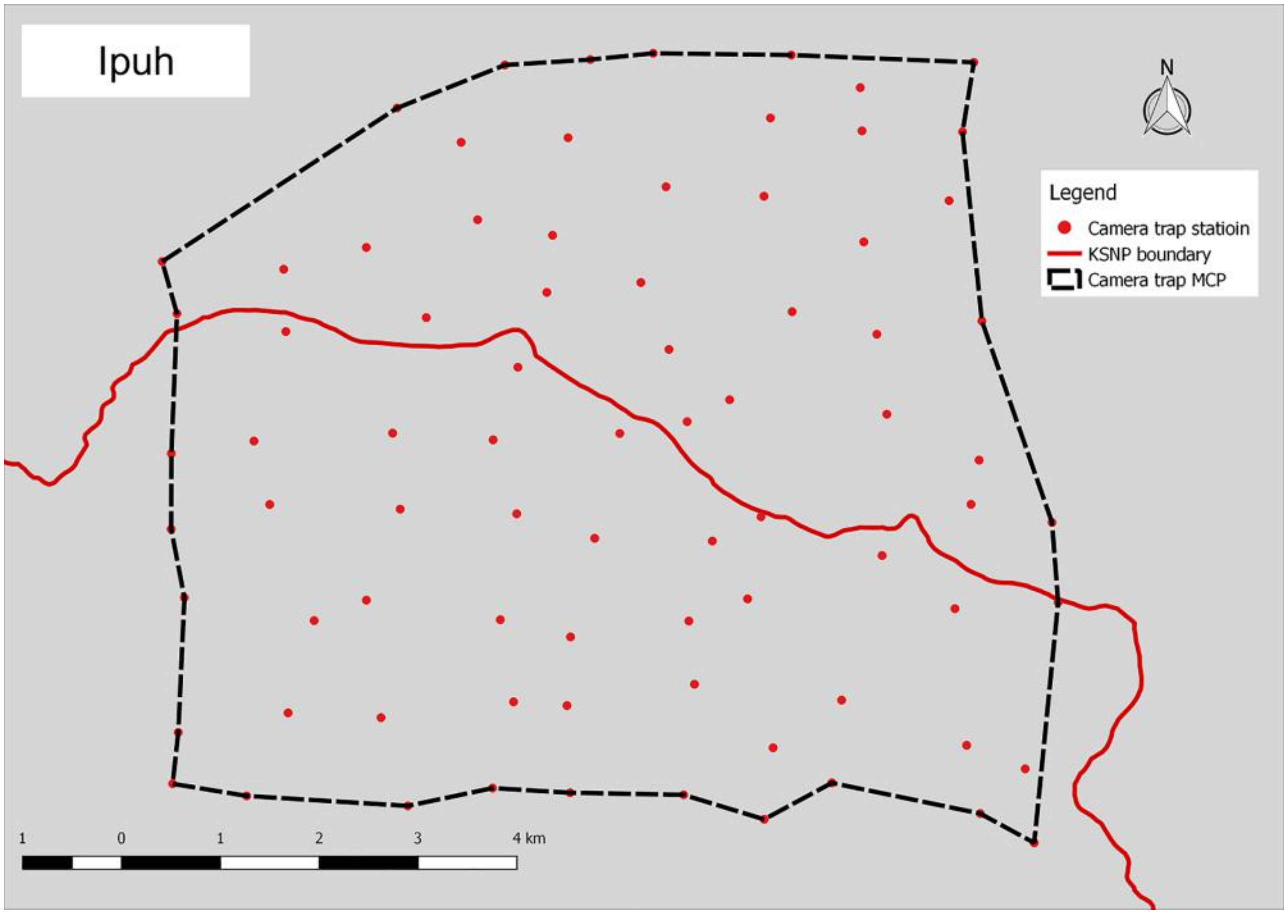

Fig 5. Camera trap location in Ipuh.

https://doi.org/10.1371/journal.pone.0202876.g005

rjags in R statistical software to run the multi-species occupancy models [28, 29]. Uninformative-uniform priors defined by the log-odds interval [−10,10] for all parameter distributions with four chains of 50,000 iterations each, including 10,000 iteration burn-ins, were run. Based on the calculation, we assessed model convergence using the $\hat{R}$ value (closer to 1.0 indicating a more plausible convergence) and from a visual inspection of chain trace plots [30].

Overlap in activity pattern. To investigate temporal interactions between the two felid species and then paired individually with each prey species, study area data were separately

Table 1. Camera trap study area characteristics and sampling effort.

Feature	Study area			
	Bungo	Sipurak	RKE	Ipuh
Mean elevation (min.—max.) in metres	630 (310–1,120)	800 (370–1,070)	1,190 (490–2,000)	430 (230–670)
Main forest types	Hill–submontane	Hill–submontane	Hill–montane	Lowland–hill
Minimum convex polygon (km^2)	63.9	62.5	63.2	60.6
# trap nights	8,399	7,053	6,674	6,278
# paired camera trap stations	76	76	65	75
Mean camera trap spacing (m)	777	814	1,027	793
Survey period	June-Nov 2014	Nov 2014-Mar 2015	Apr-Aug 2015	Sept-Dec 2015

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analysed to investigate differences in species temporal pattern. Independent photographs were treated as a random sample from the underlying distribution that describes the probability of a photograph being taken within any particular interval of the day [12, 31].

To analyse species interaction data from camera trapping, we follow Ridout and Linkie [31] that used Kernel Density Estimate (KDE) for finite data smoothing with three delta estimators.

Results

Species detection

From 292 paired-camera trap stations, 39 vertebrate species from 20 families were recorded over 28,404 trap nights from the four study areas (S1 Table). Combined data from four study areas included independent photographs of clouded leopard (n = 163), golden cat (107), macaque (1,215), great argus pheasant (1,090), muntjac (803), porcupine (513), and mouse deer (189).

Spatial occurrence patterns

From the combined camera trap data set, clouded leopard was detected at 71/292 stations, yielding a naïve occupancy (percent of occurrence) estimate of 0.24, whereas golden cat was detected at 66/292 stations (0.23). For the focal prey species, naïve occupancy estimates were recorded for pig-tailed macaque (0.73), muntjac (0.63), great argus pheasant (0.47), porcupine (0.38) and mouse deer (0.19), but these varied between study areas. In the individual study areas, clouded leopard occupancy was highest in RKE (0.57) and lowest in Ipuh (0.26) with varying study area detection probabilities ($\hat{p}$ = 0.09–0.23; Table 2). Golden cat occupancy was highest (0.53) in Sipurak where clouded leopard occupancy was lowest, but was lowest (0.39) in RKE where clouded leopard occupancy was highest (Table 2). Both species had low occurrence in the Ipuh study area. See S2 Table for details on the occupancy models for each species.

Investigating predator-prey co-occurrence revealed that clouded leopard was detected with all prey combined in 22.2% (62/292) of the sampling units. For individual prey species, it overlapped most with macaque (16.4%), then muntjac (12.6%), porcupine (10.6%), great argus pheasant (9.6%) and mouse deer (2.4%). There was a similar overlap pattern for golden cat with all prey combined in 20.8% of the units and individually for macaque (18.8%), muntjac (15.0%), porcupine (13.0%), great argus pheasant (11.6%) and mouse deer (7.5%).

Spatial co-occurrence between mesopredators and individual prey species, as indicated by beta coefficient (β) and the proportion of spatial overlap (quantity) varied between study areas (Table 3). The multi-species occupancy models revealed that both clouded leopard and golden cat were more likely to use sites at which muntjac and macaque were present, with weak evidence of golden cat occupancy being influenced by clouded leopard presence. The Bayesian multi-species occupancy calculated log odds values between pairwise species hierarchically to determine relationships between species. The proportions of negative log odds values were found higher for clouded leopard and muntjac, mouse deer, macaque and great argus pheasant indicate avoidance by the prey, where golden cat had higher percentage of positive log odds values, which indicates spatial association (Figs 6 and 7; Table 3 and S2 Table).

Temporal patterns

Combined camera trap data from all four study areas, revealed that golden cat was more diurnal (61.9% of observations between 6:30–17:30hrs) than clouded leopard (36.1%, Fig 8). For the prey species, strongly diurnal patterns were shown by macaque (97.5%) and great argus

Table 2. Single season-single species occupancy estimates ($\hat{\psi}$), detection probability (p) and associated landscape covariates for two other predator species and their potential prey.

Species/Study Area	$\hat{\psi}$ (95%CI)	$\hat{p}$ (95%CI)	β Coefficient (95%CI)		
			Elevation	*Dist. to river*	*Dist. to forest edge*
Clouded leopard					
Bungo	0.49	0.09	-0.57	-0.70	-
	(0.22–0.76)	(0.04–0.17)	(-1.22)-(-0.20)	((-1.31)-(-0.77))	
Sipurak	0.26	0.12	-	-	-
	(0.12–0.49)	(0.05–0.24)			
RKE	0.56	0.20	-	1.20	1.50
	(0.37–0.74)	(0.14–0.29)		(0.21–2.18)	(0.44–2.57)
Ipuh	0.25	0.23	-	-	-
	(0.16–0.39)	(0.15–0.34)			
Golden cat					
Bungo	0.46	0.06	-	-	-
	(0.12–0.85)	(0.02–0.16)			
Sipurak	0.53	0.12	-	-	-
	(0.29–0.76)	(0.07–0.19)			
RKE	0.39	0.14	-	-	-
	(0.19–0.64)	(0.14–0.25)			
Ipuh	0.39	0.07	-	-	-
	(0.11–0.76)	(0.03–0.20)			
Muntjac					
Bungo	0.75	0.30	1.10	1.14	1.31
	(0.62–0.84)	(0.26–0.35)	(0.48–1.73)	(0.52–1.76)	(0.61–2.01)
Sipurak	0.88	0.31	-	-	-
	(0.75–0.95)	(0.27–0.36)			
RKE	0.31	0.22	-1.87	-2.09	-2.06
	(0.18–0.47)	(0.14–0.33)	(-2.93-(-0.80)	(-2.94)-(-1.24)	(-2.91)-(-1.21)
Ipuh	0.74	0.24	-	-	-
	(0.57–0.86)	(0.19–0.30)			
Mouse deer					
Bungo	0.46	0.11	-0.90	-0.90	-0.83
	(0.25–0.68)	(0.06–0.19)	(-1.43 –(-0.37)	(-1.41)-(-0.39)	(-1.37)-(0.29)
Sipurak	0.24	0.16	-	-	-
	(0.13–0.41)	(0.09–0.28)			
RKE	0.04	0.19	-2.44	-2.44	-2.41
	(0.01–0.20)	(0.03–0.62)	(-4.11)-(-0.77)	(-3.55)-(-0.94)	(-3.91)-(-0.90)
Ipuh	0.27	0.34	-	-	-
	(0.18–0.38)	(0.32–0.37)			
Macaque					
Bungo	0.71	0.29	-	-	-
	(0.58–0.81)	(0.24–0.34)			
Sipurak	0.89	0.43	-	-	-
	(0.79–0.95)	(0.38–0.47)			
RKE	0.36	0.38	-	-1.34	-1.39
	(0.25–0.49)	(0.35–0.42)		((-2.07)-(-0.60))	((-2.14)-(-0.65))

(*Continued*)

Table 2. (Continued)

Species/Study Area	$\hat{\psi}$ (95%CI)	$\hat{p}$ (95%CI)	β Coefficient (95%CI)		
			Elevation	*Dist. to river*	*Dist. to forest edge*
Ipuh	0.98	0.28	-	-	-
	(0.23–0.99)	(0.23–0.33)			
Porcupine					
Bungo	0.53	0.25	-0.36	-	-
	(040–0.65)	(0.20–0.31)	((-0.88)-0.16)		
Sipurak	0.53	0.35	-1.92	-1.03	-
	(0.41–0.64)	(0.29–0.41)	((-2.78)-(-1.06))	((-1.75)-(-0.31))	
RKE	0.26	0.36	0.44	-0.96	-1.21
	(0.17–0.39)	(0.32–0.41)	((-0.55)-1.43)	((-1.71)-(-0.22))	((-2.02)-(-0.41))
Ipuh	0.30	0.21	0.86	0.13	0.81
	(0.18–0.44)	(0.14–0.31)	(0.10–1.63)	((-0.55)-0.81)	(0.04–1.58)
Argus pheasant					
Bungo	0.50	0.29	-	-	-
	(0.38–0.62)	(0.24–0.35)			
Sipurak	0.46	0.37	-	1.20	1.33
	(0.34–0.58)	(0.31–0.44)		(0.46–1.95)	(0.47–2.19)
RKE	0.27	0.33	-	-0.93	-0.99
	(0.17–0.40)	(0.23–0.45)		((-1.68)-(-0.17))	((-1.75)-(-0.24))
Ipuh	0.73	0.36	0.84	-	-
	(0.60–0.82)	(0.31–0.42)	(0.05–1.63)		

Note: $\hat{\psi}$ represents occupancy values for the top ranked model from a list of candidate models that incorporate different site covariates for Psi/ ($\hat{\psi}$) and for a constant detection probability (p̂), only significant results (do not contain zero) are shown. The β-coefficient is an intercept values of the linear models that indicates the relationship between occupancy values and the covariates derived from the occupancy modelling

https://doi.org/10.1371/journal.pone.0202876.t002

Table 3. Spatial co-occurrence between clouded leopard and golden cat with individual prey species, as indicated by their beta coefficients (β) and the proportion of spatial overlap between study areas.

Species pairs	Bungo	Sipurak	RKE	Ipuh	Overall
	β (% overlap)	β (% overlap)	β (% overlap)	β (% overlap)	β (% overlap)
Clouded leopard+					
golden cat	0.91 (56.7%)	-0.43 (44.9%)	5.47 (89.0%)	2.22 (67.3%)	6.33 (98.2%)
muntjac	2.26 (66.4%)	2.20 (66.2%)	-1.97 (30.8%)	-0.76 (42.8%)	-0.59 (15.3%)
mousedeer	-2.35 (32.2%)	0.35 (52.6%)	-4.42 (16.8%)	-4.88 (6.0%)	-1.59 (0.1%)
porcupine	3.35 (75.4%)	4.27 (86.0%)	7.28 (98.5%)	7.92 (99.6%)	1.63 (99.8%)
macaque	-2.59 (29.0%)	-1.98 (34.4%)	4.29 (84.1%)	-2.9 (27.2%)	-1.75 (1.4%)
argus	1.81 (62.8%)	-2.37 (29.1%)	-4.24 (13.8%)	2.03 (74.5%)	-0.23 (21.6%)
Golden cat+					
muntjac	0.21 (50.8%)	1.35 (61.6%)	-2.45 (30.1%)	1.87 (64.4%)	-2.14 (36.0%)
mousedeer	0.32 (51.8%)	-4.26 (16.9%)	-1.24 (40.7%)	4.62 (85.0%)	4.87 (99.8%)
porcupine	4.20 (83.8%)	7.73 (99.0%)	2.39 (68.3%)	3.07 (73.5%)	4.71 (88.8%)
macaque	4.84 (85.5%)	0.03 (51.5%)	5.53 (91.3%)	0.75 (56.0%)	4.87 (94.4%)
argus	1.98 (65.8%)	5.20 (93.2%)	0.72 (55.2%)	-0.99 (41.0%)	1.71 (71.7%)

Note: Beta coefficient β (range from 1–10 as stated in the model calculation) indicates the degree of positive (+) interaction (overlap) or negative (-) interaction (avoidance), and the percentage of overlap based on log-odds effects from Bayesian hierarchical multi-species occupancy. Grey cells indicate >75% of overlap or avoidance.

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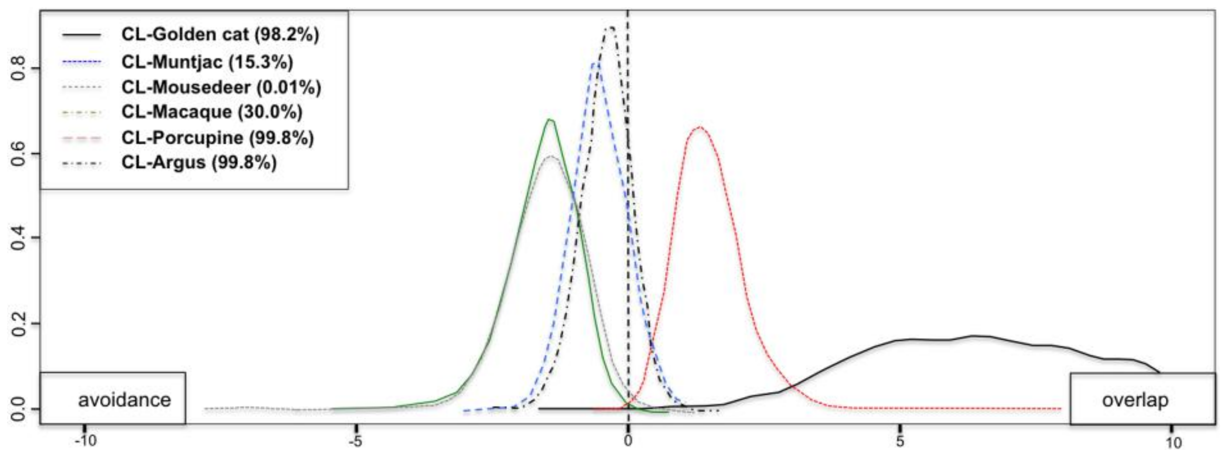

Fig 6. Pair-wise spatial overlap between clouded leopard, golden cat, and prey. Clouded leopard and golden cat (solid black line), and clouded leopard and prey; muntjac (blue dotted line), mouse deer (green dotted line) macaque (blue dashed-dotted line), porcupine (red-dashed line), and argus pheasant (black dashed-dotted line). The right side from straight-dashed line of the graph indicates overlap, whereas the left side indicates avoidance.

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pheasant (88.2%), and followed by muntjac (65.7%) while porcupine exhibited strongly nocturnal patterns with 93.2% of detections being at night and followed by mouse deer at 63.5%), (19.00–05.00hrs).

Comparing between study areas, the temporal overlap between clouded leopard and golden cat showed little variation, being lowest in Sipurak ($\Delta_4 = 0.58$) and highest in Bungo and Ipuh ($\Delta_4 = 0.62$). The predator-prey temporal patterns revealed that clouded leopard, although with some variations across study areas, had the highest overlap with muntjac and mouse deer than with the more diurnal macaque and great argus pheasant. Similarly golden cat had the highest temporal overlap with muntjac but second to that is the more diurnal macaque and great argus pheasant followed by the more nocturnal mouse deer (Table 4; S1 Fig).

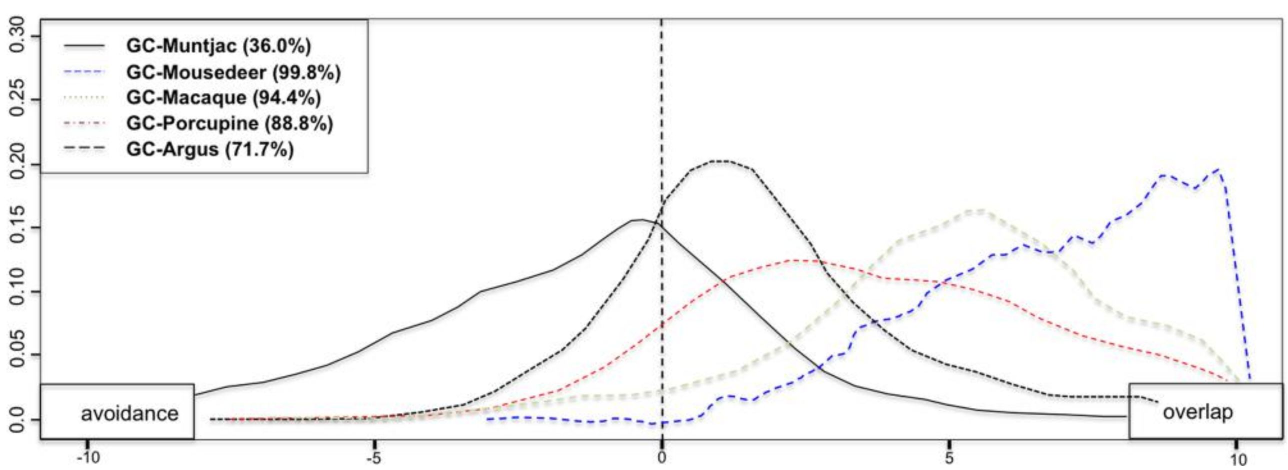

Fig 7. Pair-wise spatial overlap between golden cat and prey. Spatial overlap proportion between golden cat and muntjac (black solid line), mouse deer (blue dashed line), macaque (grey dotted line), porcupine (red-dashed line), and argus pheasant (black dashed line). The right side from straight-dashed line of the graph indicates overlap, whereas the left side indicates avoidance.

https://doi.org/10.1371/journal.pone.0202876.g007

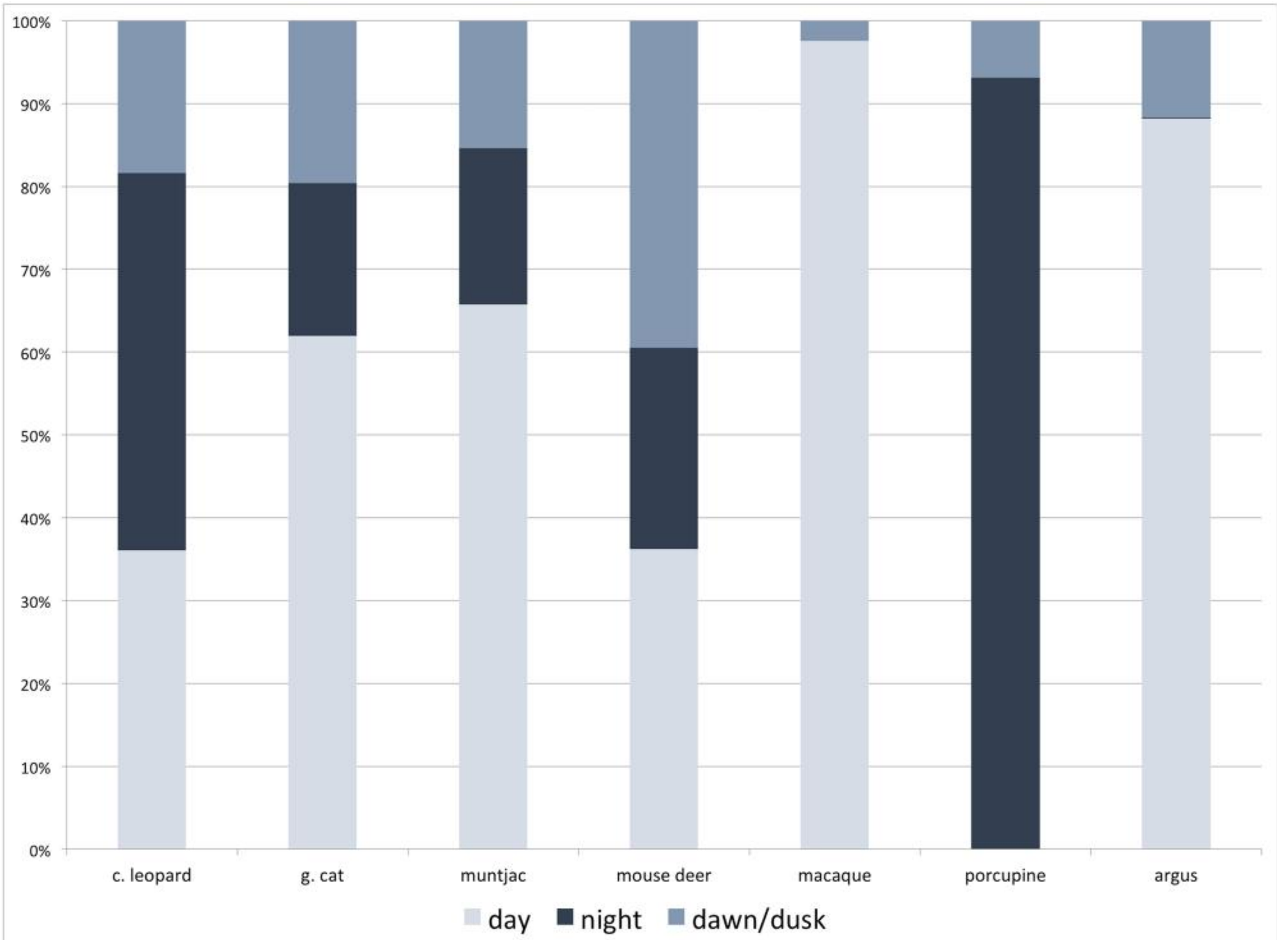

Fig 8. Temporal patterns of clouded leopard (c. leopard), golden cat (g. cat) and their prey. Temporal categorizations for diurnal (06:30–17:30hrs), nocturnal (19:00–05:00hrs) and crepuscular (05:00–06:30hrs and 17:30–19:00hrs).

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Discussion

We found differences in the extent to which clouded leopard and golden cat spatially overlapped with different prey species. The two felids exhibited different temporal activity patterns, which may have enabled a greater degree of spatial overlap. Although detailed dietary studies are lacking, we identified potential prey species whose spatial and temporal activity patterns had a higher degree of overlap with that of the predators' thereby suggesting specific associations.

Spatial and temporal overlap patterns

Camera trapping revealed weak evidence for niche partitioning between clouded leopard and golden cat. Although there were signs of habitat partitioning with clouded leopards tending to avoid forest edge patches, whilst golden cats did not, the habitat of the two species overlapped extensively in the forest interior. This builds on the earlier work of Haidir et al. (2013) that found clouded leopard occupancy being higher in patches that were further from the forest edge and at higher elevations. Our study also found that the forest edge had a positive influence

Table 4. Estimates of temporal overlap between clouded leopard and golden cat with their individual prey species, as indicated by their Kernel density ($\hat{D}$) estimates and the proportion of overlap between study areas.

Species	Study area			
	Bungo	Sipurak	RKE	Ipuh
	$\hat{D}$ with 95% CI			
Clouded leopard				
Golden cat	0.62	0.58	0.61	0.62
	0.50–0.83	0.39–0.77	0.45–0.79	0.47–0.77
Muntjac	0.69	0.54	0.69	0.61
	0.58–0.84	0.37–0.72	0.57–0.82	0.50–0.70
Mouse deer	0.74	0.56	0.53	0.68
	0.67–0.93	0.35–0.78	0.35–0.75	0.54–0.82
Macaque	0.47	0.24	0.49	0.33
	0.32–0.61	0.03–0.35	0.34–0.58	0.20–0.38
Porcupine	0.57	0.62	0.48	0.53
	0.42–0.71	0.46–0.80	0.36–0.61	0.35–0.65
Great argus pheasant	0.42	0.34	0.43	0.56
	0.29–0.57	0.12–0.48	0.31–0.53	0.44–0.70
Golden cat				
Muntjac	0.73	0.70	0.66	0.68
	0.62–0.91	0.58–0.85	0.54–0.87	0.59–0.85
Mouse deer	0.61	0.61	0.39	0.58
	0.47–0.80	0.47–0.82	0.19–0.64	0.44–0.73
Macaque	0.72	0.48	0.64	0.56
	0.58–0.92	0.31–0.59	0.48–0.86	0.40–0.75
Porcupine	0.26	0.43	0.26	0.26
	0.10–0.37	0.25–0.55	0.05–0.39	0.10–0.39
Great argus pheasant	0.63	0.61	0.59	0.68
	0.49–0.82	0.49–0.75	0.43–0.83	0.55–0.85

Each cell indicates a density overlap value, with 95% confidence intervals (CIs) below the averaged value. The value of the trigonometric sum of density overlap ($\hat{D}$) between two species within the different study areas are shaded from lighter to darker indicating low to high overlap.

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on clouded leopard occupancy only at higher elevation where prey abundance was lower, such as in the sub-montane study area of RKE.

Clouded leopard and golden cat are likely to concentrate their hunting where prey is abundant and accessible [32]. The reciprocal results for Sipurak and RKE, where the highest occupancy for one felid species occurred alongside the lowest occupancy of the other, and vice versa, suggests that there is a broad level competition between them. Conversely, in Ipuh, both species had low occupancies, despite the presence of a rich and widespread prey base, which is possibly a result of the much higher human disturbance here [33, 34]. Ipuh contains large tracts of lowland forests that are highly accessible and borders an ex-logging concession. The neighbouring forests in Ipuh also had the highest forest degradation rate amongst the four study areas [13, 35].

In Bungo, the two felid species shared similar and relatively high occupancy rates. Tiger densities were almost twice as high in Bungo than in Ipuh. A relatively higher occupancy rate of tiger, clouded leopard and golden cat could be indicative of higher prey biomass and lower threats to felid species that reduce interspecies competition, especially on prey species amongst the three felid species. Additionally, higher occupancy of both clouded leopard and golden cat might be due to higher prey abundance within secondary forests [33, 36] that would result in tiger exerting a lower influence on mesopredators' co-occurrence. Documenting the influence of larger predators towards smaller ones is difficult in the dense Sumatran rainforest. This is, unlike in more open habitats in India or central African countries, where studies on predator-prey interactions and their preferred diet can be conducted through direct observations [37, 38]. Studying these interactions in dense tropical rainforests is particularly difficult because inferences are drawn solely from the observed patterns that are derived from remote device, such as camera traps. Nevertheless, our camera trap data revealed a distinction in the temporal activity patterns between the more nocturnal clouded leopard and the more diurnal golden cat would have further reduced interference competition between the two species. These results are consistent with the patterns observed by previous studies conducted in Sumatra [23, 39].

Clouded leopards exhibited the closest spatial and temporal associations with muntjac. A study in Borneo on the interactions between felids and primates reported a clouded leopard killing a pig-tailed macaque [40]. Physiologically, clouded leopards have the longest canines, of any felid species relative to their body size and are likely to have evolved to be able to kill larger-bodied prey such as young muntjac, adult mouse deer and great argus pheasant.

In the case of the golden cat, its diet is less certain but it might target mouse deer and argus pheasant. Unlike the clouded leopard's spatial occurrence with muntjac and mousedeer, golden cat showed a positive association with these species. A positive association between golden cat and the prey does not necessarily mean that these species, especially those weighing >10 kg, are key prey for golden cat. On the contrary, a strong positive spatial association might suggest that these species are neither threatened nor hunted by golden cat. This possibility may be supported by the findings from a similar evergreen rainforest habitat in Taman Negara, Malaysia, which reported the golden cat's diet to consist of avian body parts, mouse deer, lizards, snakes, rats and langur [19].

There are several possible limitations in our study that we tried to control. Firstly, the camera trap set on the forest floor would not detect arboreal activities of the two felid species. This may include hunting arboreal prey, such as birds and lizards, which camera traps would also not record [19]. Secondly, despite amassing a large data set of independent photographs (>100 for each species) from a substantial sampling effort (28,040 trap nights), only 1.8% of the 13.900 km^2 Kerinci Seblat National Park was sampled.

Clouded leopards, golden cats and their potential prey species exhibit various activity patterns that indicate the temporal elasticity of both predators. Predators might maximize their hunting effort within prey-rich timing [1, 7]. Similarly, prey might become more active when fewer predators are inactive [1, 3]. Based on these activity patterns there are three possible explanations. First, the spatial niche separation between clouded leopards and golden cats exist, but it was not detected. However, given the high sampling intensity of the study, we judge this to be unlikely. Second, the spatial niche separation between clouded leopards and golden cat does not exist. A considered explanation that niche separation between both cats could be because the mesopredator suppression keeps both species at a density below which competition manifests. However, there is inadequate evidence to support this possibility, and we have not investigated the influence of tigers on these two smaller felids. Third, the interspecific competition between clouded leopards and golden cats is lower due to their temporal separation and the relatively high occurrence of a variety of nocturnal and diurnal prey. Here is the most likely conclusion, considering also that we judge that poaching pressure on these two felids species is low, nevertheless the low occurrence of both cat species in the highly disturbed Ipuh site emphasises the importance of safeguarding forest habitat in Kerinci Seblat landscape.

Our study lends support to calls to not only protect primary rainforest, but also not to disregard the importance of secondary forest to threatened vertebrate communities in the tropics [41, 42]. However, besides ensuring forest integrity and avoiding further degradation, controlling poaching of their ungulate prey will also be a determining factor in the survival of Sumatra's mesopredators.

Supporting information

S1 Dataset.
(ZIP)

S1 Fig. Temporal pattern of studied species across study areas.
(DOCX)

S1 Table. Species photographed during the surveys conducted between April 2014 and December 2016 in the Kerinci Seblat Landscape, Sumatra.
(DOCX)

S2 Table. List of models with 50,000 iterations and 10,000 burn for the two-species single season occupancy in pooled study areas.
(DOCX)

S3 Table. Top five occupancy models for focal species, using single season, single species model with the following covariates; elevation, distance to forest edge and distance to river.
(DOCX)

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The first ever collared male 'macan dahan',
released in area next to Berbak-Sembilang NP, Jambi, the collar last only two weeks

3

Sunda clouded leopard densities and human encounter

Sunda clouded leopard *Neofelis diardi* densities and human activities in the humid evergreen rainforests of Sumatra

IDING HAIDIR, DAVID W. MACDONALD and MATTHEW LINKIE

Abstract Most species of wild felids are threatened, but for many little is known about their status in the wild. For the cryptic and elusive Vulnerable Sunda clouded leopard *Neofelis diardi*, key metrics such as abundance and occupancy have been challenging to obtain. We conducted an intensive survey for this species on the Indonesian island of Sumatra. We deployed camera traps across four study areas that varied in elevation and threats, for a total of 28,404 trap nights, resulting in 114 independent clouded leopard photographs, in which we identified 18 individuals. Using a Bayesian spatially explicit capture–recapture analysis, we estimated clouded leopard density to be 0.8–2.4 individuals/100 km^2. The highest predicted occurrence of people was at lower altitudes and closer to the forest edge, where we categorized more than two-thirds of people recorded by camera traps as bird poachers, 12.5% each as ungulate/tiger poachers and non-timber collectors, and $< 2\%$ as fishers. Our findings provide important insights into the status of this little known species in Sumatra. We recommend that the large volume of camera-trap data from other Sumatran landscapes be used for an island-wide assessment of the clouded leopard population, to provide up-to-date and reliable information for guiding future conservation planning.

Keywords Camera trap, clouded leopard, felid, Kerinci Seblat National Park, *Neofelis diardi*, poaching, spatially explicit capture–recapture

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Introduction

Across the tropics of Latin America, Africa and Asia, information on wild felids tends to be based on indirect signs because dense vegetation typically precludes direct observations and because these species tend to be rare as a result of their trophic status (Carter et al., 2015; Rayan & Linkie, 2015; Jędrzejewski et al., 2017). Remote detection devices, primarily camera traps, facilitate surveying felids that are otherwise difficult to detect, enabling researchers to investigate felid ecology and population status, and gain a better understanding of the threats to these species (Linkie et al., 2006; Kawanishi et al., 2010; Henschel et al., 2011; Rich et al., 2014). There are 10 felid species in South-east Asia, occurring in open savannahs, deciduous forests and humid evergreen forests along the equator (Sunquist & Sunquist, 2002). Little is known about most of these species, particularly the smaller-bodied ones. However, recent camera-trap surveys have provided new information on the relative abundance, occupancy and/or habitat preference of the Sunda clouded leopard *Neofelis diardi*, Asiatic golden cat *Catopuma temminckii*, Bornean bay cat *Catopuma badia*, marbled cat *Pardofelis marmorata*, leopard cat *Prionailurus bengalensis* and flat-headed cat *Prionailurus planiceps* (Haidir et al., 2013; Wearn et al., 2013; McCarthy et al., 2015; Hearn et al., 2016a; Rustam et al., 2016).

To date, wildlife research in Sumatra has mainly focused on the Indonesian Ministry of Environment and Forestry's priority species, the Sumatran tiger *Panthera tigris sumatrae*, Sumatran elephant *Elephas maximus sumatranus*, Sumatran rhinoceros *Dicerorhinus sumatrensis*, Sumatran orangutan *Pongo abelii* and, most recently, the newly discovered Tapanuli orangutan *Pongo tapanuliensis* (Hedges et al., 2005; Wibisono & Pusparini, 2010; Pusparini et al., 2015; Sunarto et al., 2015; Nowak et al., 2017). This attention is justified because these flagship species or subspecies are endemic, categorized as Critically Endangered on the IUCN Red List, and able to attract international attention and conservation funds that provide wider benefits to the wildlife, rainforest habitats and protected areas within their range. However, the Sunda clouded leopard can also play a role as a wildlife conservation ambassador, as shown elsewhere in Asia, through its ability to generate political support for both the species itself and the protected areas it inhabits (Macdonald et al., 2017).

Here we investigate demographic parameters of Sunda clouded leopards in four rainforest areas in one of

South-east Asia's largest protected areas, Kerinci Seblat National Park in west-central Sumatra. The study areas are characterized by different forest types, elevation gradients and human disturbance levels. Our study builds on earlier work that was based on bycatch data from a tiger survey in four study areas in the Park, with estimated Sunda clouded leopard densities of 0.4–1.3 individuals/100 km² (Sollmann et al., 2014). We conducted surveys that specifically focused on small to medium-sized felids and applied analyses that explore additional research questions. For example, we examined how detection probability, movement distribution and density of Sunda clouded leopards vary amongst different forest types along an altitudinal gradient.

Study area

Kerinci Seblat National Park is a UNESCO World Heritage Site on the island of Sumatra. The 16,194 km² Kerinci Seblat forest landscape stretches along c. 370 km of the Bukit Barisan mountain range and covers the provinces of Jambi, Bengkulu, South Sumatra and West Sumatra. The altitude is 150–3,805 m, with lowland forest < 300 m (20.2% of the landscape), hill forest at 300–800 m (26.6%), submontane forest at 800–1,200 m (30.9%), midmontane forest at 1,200–1,900 m (17.2%) and upper montane and sub-alpine forest $> 1,900$ m (5.1%). Our four study areas were Ipuh (lowland forest), Bungo and Sipurak (hill forest), and Renah Kayu Embun (submontane and midmontane forest; Fig. 1, Table 1, Supplementary Table 1).

Methods

Data collection

We conducted camera-trap surveys during June 2014–December 2016 in Kerinci Seblat National Park and adjacent forest areas. We designed the surveys to target the Sunda clouded leopard, golden cat, marbled cat and leopard cat, by placing cameras on ridge trails and animal paths, with the majority (60%) of camera traps placed where the forest canopy was disrupted and the semi-arboreal felids could be expected to descend. All camera stations in Bungo, Sipurak and Ipuh, and 70% of stations in Renah Kayu Embun, consisted of camera traps set up in pairs, to capture both flanks of passing animals. The camera traps within each study area covered 80 grid cells of 1 km². Prior to setting the cameras, we conducted reconnaissance surveys to determine the locations in a grid cell that were most likely to record clouded leopards and other small and medium-sized felids. We set up cameras within 100 m of the planned deployment points at a height of 30–40 cm off the ground. The paired traps were positioned at a distance of 2–3 m from the target trail, with a spacing of 0.7–1.3 km between camera stations (Supplementary Table 1). We used heat-motion sensor camera traps Cuddeback Ambush IR (Cuddeback, De Pere, USA) and Panthera IV (Panthera, New York, USA), without any bait or lure to attract felids. We set camera traps to operate continuously for 3 months and visited stations every 2 weeks for maintenance and data retrieval. We compiled all clouded leopard photographs, and at least three experienced project members then manually identified individual animals based on their unique pelage pattern. We used these data to develop daily detection matrices.

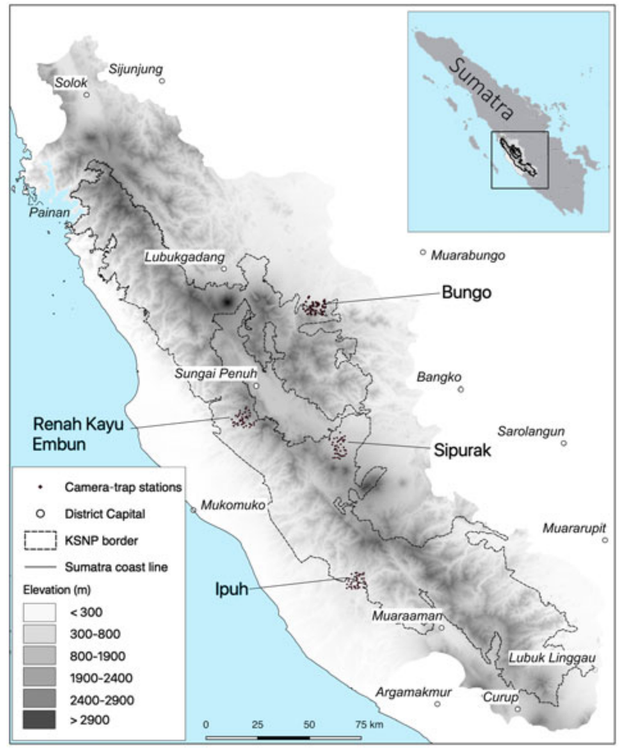

FIG. 1 Study areas in Kerinci Seblat National Park (KSNP), west-central Sumatra.

Clouded leopard density

Heterogeneity in the probability of detecting clouded leopards can be influenced by a variety of factors, including sex and camera trap site-specific covariates, although with limited data it is not possible to derive sex-based density estimates (Efford & Fewster, 2013). We estimated population abundance using a spatially explicit capture–recapture method, which assumes that each individual animal has a unique activity centre and that its probability of detection decreases with increasing distance from this centre. We constructed daily detection matrices, which included the spatial attributes of each individual, for each camera station. We analysed camera-trap data and developed detection matrices using the package *camtrapR* in *R 3.4.1* (Niedballa et al., 2016).

TABLE 1 Summary of camera-trap sampling effort and Sunda clouded leopard *Neofelis diardi* detections in the four study areas in Sumatra, from an earlier study (Sollmann et al., 2014; I) and this study (II).

Study area	No. of camera stations		Minimum convex polygon around camera traps (km^2)		Mean spacing of camera stations (km)		Total duration (days)		No. of trap nights		No. of independent photos		No. of individuals (M/F/Unknown)		No. of recaptures (M/F)	
	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Bungo[1]	34	76	322	64	2.00	0.87	238	147	2,486	8,399	8	25	6 (5/1/0)	6 (5/1/0)	M = 7/F = 1	M = 23/F = 1
Sipurak	20	77	94	63	1.90	0.94	91	135	1,258	7,053	6	18	2 (2/0/0)	3 (2/1/0)	M = 6/F = 0	M = 14/F = 3
Renah Kayu Embun	23	65	121	63	1.50	1.03	130	115	2,063	6,674	16	47	7 (6/1/0)	4 (3/1/0)	M = 11/F = 1	M = 45/F = 1
Ipuh[1]	38	75	706	61	3.50	0.79	222	110	3,563	6,278	17	24	7 (4/2/1)	5 (1/2/2)	M = 12/F = 4	M = 9/F = 15
Total	115	293	1243	251			681	507	9,370	28,404	47	114	22 (17/4/1)	18 (12/4/2)	M = 36/F = 6[2]	M = 91/F = 21[2]

[1]Earlier study (Sollmann et al., 2014) consisted of two trapping phases.
[2]Does not include photos of unidentified/unsexed individuals.

We used a Bayesian spatially explicit capture–recapture approach with the *R* package *SPACECAP 1.1.0* (Gopalaswamy et al., 2012) because it is more suitable for population estimations based on a small sample size (Wearn et al., 2013; Hearn et al., 2016b). We treated the study areas as independent sites because they are separated by at least 80 km, and a previous study recorded daily movements of clouded leopards of 2.3–2.4 km, with home ranges of 23–45 km^2 (Grassman et al., 2005). In addition, altitude and forest types vary between the study areas, and some are separated by settlements, towns and major roads that could act as barriers to clouded leopard movement (Grassman et al., 2005; Linkie et al., 2006). Using *QGIS 2.10.1* (QGIS, 2016), we created a state space or habitat mask that describes the potential home range centre of an individual based on their spatial movements and habitat suitability. A habitat mask limits the ranges of individual clouded leopard movement estimations to suitable (forested) areas (Gopalaswamy et al., 2012; Fig. 2).

We used a habitat mask with a 15 km buffer, based on movement patterns of clouded leopard studies from Malaysia and Bhutan that used a 12–30 and 25 km buffer, respectively (Hearn et al., 2017; Penjor et al., 2018). We applied the buffer around the minimum convex polygon containing all camera traps in a study area. Using a forest cover layer obtained from the Ministry of Environment and Forestry (KLHK, 2016), we then categorized the buffer area as habitat (forested area) or non-habitat (other areas), with a resolution of 0.5×0.5 km. Data augmentation was based on 10 times the number of identified individual animals. For the analysis, we ran 50,000 iterations with a burn-in of 20,000 and thinning of 10. We performed a Geweke test to investigate models convergence in the Markov chain Monte Carlo that should have values close to zero, as an indication that the data calculation has converged. The model also estimated the Bayesian P-value to assess model fit, whereby a value of 0.5 indicates a perfect fit, and values should not be close to 0.0 or 1.0 (Gopalaswamy et al., 2012).

We used the density values derived from *SPACECAP* to test for differences between the study areas, whereby non-overlapping upper and lower highest probability density estimates indicate a significant difference in density. However, overlapping highest probability densities could still be significantly different, so we performed a Tukey's honest significant difference test, with $P < 0.05$ as the significance level (i.e. $Pr(>|z|)$; Tukey, 1949).

Anthropogenic pressure

To understand the anthropogenic pressures in the study areas, we analysed camera-trap photographs of people. Where possible, we categorized them as fishers (groups of < 5 people with machetes and small backpacks, which are

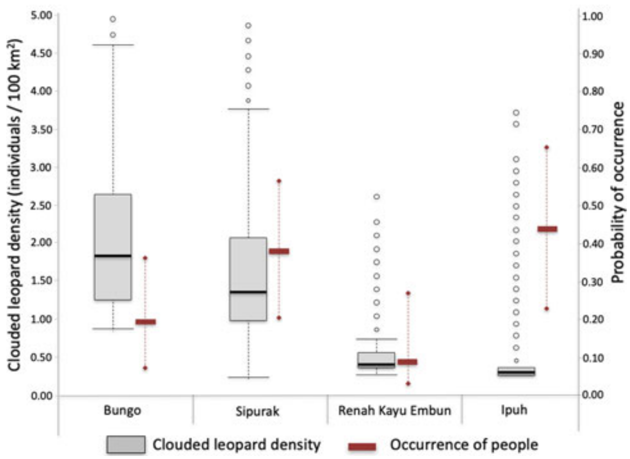

FIG. 2 Estimated Sunda clouded leopard *Neofelis diardi* density values derived from *SPACECAP* (box plots; black line in the box is the median, box is 50% distribution of the data, the whiskers represent minimum and maximum values, the circles represent outlier values) and associated occurrence of people (solid rectangles represent the median, whiskers represent minimum and maximum values) illegally entering each of the four study areas.

typically used to carry fishing nets), collectors of non-timber forest products (groups of 3–5 people without heavy equipment such as rifles or machetes), bird poachers (groups > 5 people carrying baskets/cages made from rattan, tree branches or sticks with glue on one end, and small blades < 40 cm length), armed tiger/ungulate poachers (groups < 5 people carrying hunting rifles and/or spears, accompanied by hunting dogs, or who were detected during dusk or at night carrying small rucksacks and torches) and forest patrol/monitoring team members (the latter being the only people who are permitted to enter the Park).

To investigate the spatial occurrence of people entering the Park illegally, we used an occupancy modelling framework approach. We aggregated human detections in each camera-trap station into 14-day detection/non-detection intervals, from which we constructed single species single season occupancy models that tested for associations between the presence of people and four landscape variables: study area, elevation, distance to forest and distance to river (MacKenzie et al., 2002). We performed a Tukey's honest significant difference test to determine whether the occurrence of people was significantly different between study areas (Tukey, 1949).

Results

Clouded leopard detections and abundance

The 293 camera-trap stations generated a combined sampling effort of 28,404 trap nights and captured 163 independent clouded leopard photographs, of which 114 were identified to an individual. There were 18 adult individuals

TABLE 2 Spatially explicit capture–recapture analyses run using *maximum likelihood SECR* and *SPACECAP* for the four study areas, with density measured as number of adult individuals/100 km² in this study and an earlier study (Sollmann et al., 2014).

Parameter[1]	This study Bayesian (95% HPD[2])	Earlier study Bayesian (95% HPD[2])
Bungo		
D	2.38 (1.11–4.26)	1.62 (0.58–3.38)
N	12.84 (6.00–23.00)	
σ (km)	3.35 (1.85–5.08)	2.59 (1.83–3.86)
λ_0	0.003 (0.001–0.005)	0.010 (0.004–0.021)
Ψ	0.20 (0.05–0.39)	
Sipurak		
D	2.05 (0.52–4.35)	0.77 (0.15–2.10)
N	11.79 (3.00–25.00)	
σ (km)	2.32 (1.08–4.75)	4.48 (2.84–8.10)
λ_0	0.005 (0.000–0.011)	0.006 (0.002–0.014)
Ψ	0.37 (0.05–0.77)	
Renah Kayu Embun		
D	0.81 (0.66–1.33)	1.57 (0.52–2.38)
N	4.86 (4.00–8.00)	
σ (km)	5.34 (3.50–7.35)	4.48 (2.84–8.10)
λ_0	0.005 (0.002–0.009)	0.006 (0.002–0.014)
Ψ	0.13 (0.03–0.24)	
Ipuh		
D	0.75 (0.73–0.88)	1.10 (0.42–2.24)
N	5.15 (5.00–6.00)	
σ (km)	32.98 (9.66–49.37)	2.59 (1.83–3.86)
λ_0	0.001 (0.000–0.001)	0.010 (0.004–0.021)
Ψ	0.18 (0.08–0.28)	

[1]*D*, density (number of animals/100 km²); N, number of individuals in the sampling area; σ, range parameter for an individual animal's activity centre (i.e. the average distance of an individual animal's activity centre to the lowest probability of detection of an individual at a certain distance from a camera trap); λ_0, expected encounter rate for any given individual whose home range centre is exactly at the camera-trap location; ψ, predicted ratio of the number of animals actually present in the study areas compared with the maximum numbers set in the augmented data.
[2]HPD, highest probability density.

(12 males, 4 females and 2 of unknown sex), with 76 captures and 38 recaptures (Table 1). The most frequently captured individual was a male that was recorded in 16 camera-trap stations in Renah Kayu Embun. Females were captured in fewer stations, with the highest capture count being of one female in five stations in Ipuh. We recorded no cubs (Table 1).

Clouded leopard density estimates varied amongst study areas, with Bungo having the highest density at 2.38 individuals/100 km² (highest probability density 1.11–4.26) and Ipuh the lowest at 0.75 (0.73–0.88; Table 2). Comparing the movement parameters ($\sigma \pm$ SE) between study areas showed that individual animals in Sipurak moved just over half (56.6%) as much those in Renah Kayu Embun, and those in Ipuh ranged more widely than in the other study areas. The Tukey honest significant difference test showed significant differences between all paired density

TABLE 3 Single season occupancy models for trespassers across the four study areas, showing occupancy ($\psi \pm$ SE), 95% confidence intervals (CI), detection probability (P), number of parameters (K), Akaike information criterion corrected for small sample size (AICc), difference in AICc between the model and the best-performing model (ΔAICc), likelihood of a model to be selected as the best model, and model weight.

No.	Model[1]	$\psi \pm$ SE	95% CI	P	K	AICc	ΔAICc	Model likelihood	Model weight
2.1	ψ(site), P(.)	0.277 ± 0.008	0.141–0.470	0.123	5	492.60	0.00	1.00	0.37
2.2	ψ(forest + river + elevation + site), P(.)	0.283 ± 0.006	0.141–0.479	0.122	8	493.10	0.51	0.78	0.29
2.3	ψ(site + elevation), P(.)	0.277 ± 0.008	0.135–0.493	0.123	6	494.68	2.08	0.35	0.13
2.4	ψ(river), P(.)	0.285 ± 0.005	0.162–0.435	0.121	3	496.71	4.12	0.13	0.05
2.5	ψ(.), P(.)	0.275 ± 0.004	0.166–0.424	0.124	3	497.05	4.46	0.11	0.04
2.6	ψ(river + elevation), P(.)	0.283 ± 0.006	0.152–0.456	0.122	4	497.49	4.90	0.09	0.03
2.7	ψ(.), P(.)	0.273 ± 0.000	0.178–0.394	0.126	2	498.49	5.90	0.05	0.02
2.8	ψ(site + river), P(.)	0.291 ± 0.010	0.098–0.555	0.134	9	498.76	6.16	0.05	0.02
2.9	ψ(forest + river), P(.)	0.284 ± 0.005	0.150–0.460	0.126	4	498.76	6.16	0.05	0.02
2.10	ψ(forest + elevation), P(.)	0.277 ± 0.004	0.155–0.450	0.124	4	498.90	6.31	0.04	0.02
2.11	ψ(forest), P(.)	0.277 ± 0.002	0.166–0.426	0.125	3	499.51	6.92	0.03	0.01
2.12	ψ(forest + river + elevation), P(.)	0.283 ± 0.006	0.141–0.479	0.122	5	499.56	6.97	0.03	0.01

[1]Model description: e.g. ψ(river), P(.) indicates occupancy with associated covariates distance to river and detection probability constant. Covariates are: site, study area; forest, Euclidean distance to forest edge; elevation, altitude above sea level; river, Euclidean distance to river (including medium and major rivers, i.e. order 1–3 according to BAKOSURTANAL, Indonesia's Coordinating Agency for Land Mapping).

estimates ($\Pr(>|z|) < 0.001$). The Geweke tests for the Markov chain Monte Carlo differed amongst study areas. In Ipuh, despite having a large number of iterations, the model exceeded the tolerated Markov chain Monte Carlo range value, meaning the population parameters from this study area need to be interpreted with caution. Nonetheless, the Bayesian P-value, which assesses model fit for each study area, was close to 0.5, except for Sipurak (0.7), indicating that all models across all study areas were adequate (Gopalaswamy et al., 2012; Supplementary Table 3).

Anthropogenic pressure

Camera traps recorded four independent photographs of national park rangers and field survey teams, and 137 of other people. The latter were bird poachers (68.8%), tiger and ungulate poachers (12.5%), collectors of non-timber forest products (12.5%) and fishers (1.4%; Supplementary Table 4). The highest number of camera stations recording human presence was in Ipuh (70 records, from 22 stations), followed by Bungo (35, 10), Sipurak (27, 17) and Renah Kayu Embun (5, 3). People carrying hunting rifles were photographed in Sipurak (n = 4) and Ipuh (n = 2).

Several covariates (study area, distance to forest edge and elevation) predicted human presence in the forest and were included in the top ranking models. We predicted higher occurrence of people in forests that were easier to access, i.e. those at lower elevations and closer to the forest edge, and those in the Ipuh and Sipurak study areas. The highest probability of occupancy (ψ) of trespassers was in Ipuh with 0.43 (highest probability density 0.23–0.66), followed by Sipurak with 0.37 (0.20–0.57), Bungo with 0.19 (0.09–035) and Renah Kayu Embun with 0.09 (0.03.0.27; Table 3). The Tukey's honest significant difference test found significant differences in human disturbance between Ipuh and Bungo (P < 0.001), Ipuh and Sipurak (P = 0.014), and Ipuh and Renah Kayu Embun (P < 0.001), but not between Bungo and Sipurak (P = 0.405).

Discussion

Here we present Sunda clouded leopard density estimates for the main habitat types in the Kerinci Seblat landscape, which advances the work conducted during 2004–2009 (Sollmann et al., 2014) and adds to the knowledge on this species. Our findings draw attention to the importance of Kerinci Seblat National Park and its surrounding forests, which provide critical habitat for this threatened carnivore. The protection of the forest outside the National Park falls under a different management authority and will therefore require engaging other government stakeholders (Wibisono et al., 2018).

Our density estimates of the Sunda clouded leopard were higher than those of the mainland clouded leopard *Neofelis nebulosa* in Bhutan (0.40 adult individuals/100 km^2; Penjor et al., 2018), but similar to two estimates from Peninsular Malaysia (1.98–6.04 and 0.97–3.48; Mohamad et al., 2015), and estimates from Sabah (1.39–3.10/100 km^2; Hearn et al., 2017) and central Kalimantan (0.72–4.41/100 km^2; Cheyne et al., 2013). Comparing our density estimates with the corresponding study areas surveyed by Sollmann et al. (2014), we found similarly high density estimates in Bungo and low density estimates in Ipuh. The results for Sipurak were difficult to compare because of the low number of captures: Sollmann et al. (2014) recorded two individual males and we recorded two males and one female.

There were notable differences between our study design and that used by Sollmann et al. (2014), which determined Sunda clouded leopard densities using bycatch data from tiger surveys. Sollmann et al. (2014) recorded a greater number of individual clouded leopards (n = 22) from a lower sampling effort (9,370 trap nights) over a larger area (1,243 km^2), but had fewer independent photographs (n = 47). We opted for a higher trapping intensity over a smaller area (28,404 trap nights, 251 km^2) to increase the number of clouded leopard records overall (n = 114), and captures of females in particular. We also had a shorter trapping period to ensure a demographically closed population. Nevertheless, both study designs had a low number of captured individuals (Table 1) and were subject to the male-biased sex ratio typical for camera-trap studies of solitary carnivores (Tobler & Powell, 2013; Wearn et al., 2013). Considering these factors, we decided not to use the same parameters as Sollmann et al. (2014), who categorized study areas into two primary forest and secondary forest. Instead, we performed analyses for each study area individually.

Many felids including tigers, jaguars, leopards and clouded leopards are solitary, with a social system characterized by a dominant male protecting a territory that encompasses the home ranges of 2–3 females (Sunquist & Sunquist, 2002; Macdonald & Loveridge, 2014). Within these territories and ranges, boundaries are demarcated through visual signs (e.g. scrapes), scent marks (especially urine) and vocalizations. Males tend to move across greater distances than females, probably resulting in higher detection rates and biased results when sex is not included as a covariate in density models. Male-biased sex ratios are thus common in camera-trap studies of these species (Mohamad et al., 2015; Anile & Devillard, 2018).

Interpreting camera-trap data thus requires caution, and we limit comparisons of our results to those of other studies with the same inherent sex bias. Future research should explore approaches that better detect females, which would also facilitate extrapolations to estimate population size at a landscape scale (Tobler & Powell, 2013), and should also consider the positioning of camera traps. Although we deployed many camera stations inside presumed female home ranges, setting cameras on ridge trails may have introduced a sex bias. Female clouded leopards in a Malaysian Borneo study area tended to avoid these types of trails, possibly to reduce infanticide by unknown adult males (Wearn et al., 2013). Setting cameras off trail would be logistically challenging in the rugged terrain of Kerinci Seblat National Park, but should be considered in future sampling designs. Future studies aiming to detect more females could also help determine whether males are at greater risk of falling victim to snare traps set along ridge trails.

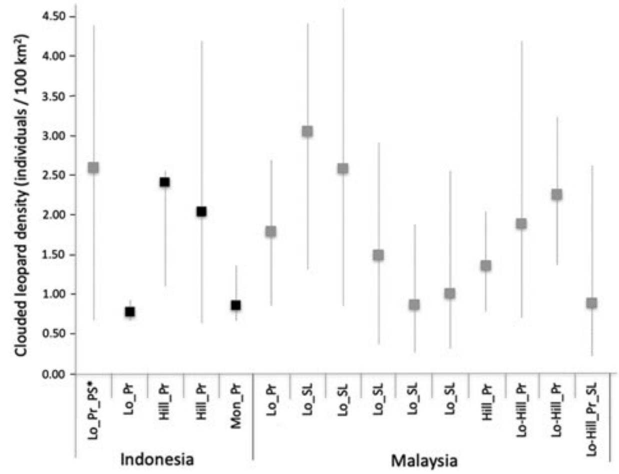

FIG. 3 Sunda clouded leopard densities across the Sunda region in Sumatra and Borneo, with results from the four study areas of this study in black, from other studies in grey. Whiskers represent density estimation ranges with minimum and maximum values. Abbreviations on the x-axis: Hill, hill forest; Lo, lowland forest; Lo-Hill, lowland to hill forest; Mon, montane and submontane forest; Pr, primary forest; PS, peat swamp; SL, selectively logged.

Studies have shown that the size of the trapping area affects sample size and parameter estimates, with a small trapping area potentially leading to underestimated Sunda clouded leopard movements and consequently overestimating density (Mohamad et al., 2015; Hearn et al., 2017). The movement parameter values derived from Sipurak, Renah Kayu Embun and Bungo were consistent with those found in other studies. However, the value derived from the Ipuh data set was large and probably a consequence of individual clouded leopards being recorded by the outermost camera traps, which potentially could have been avoided by designing a larger trapping area (Fig. 3).

Poaching of felids does occur in Kerinci Seblat National Park, but discussions with the Kerinci Seblat Tiger Protection and Conservation Units, which operate across all four study areas, indicated that clouded leopards are not a target species for poachers. These Units confiscated only one clouded leopard skin and one stuffed clouded leopard during 2001–2015, indicating that clouded leopard products are not in high demand in Kerinci Seblat (KS-TPCU, 2016). Nonetheless, the species is traded internationally and there may be an increase in the range-wide illegal trade of both live individuals and their body parts over the past decades, particularly during 1975–2013 (D'Cruze & Macdonald, 2015).

Our study cannot conclusively prove the direct impact of human disturbance on clouded leopard subpopulations because of the influence of other explanatory factors such as prey availability and topography of the landscape. However, the clouded leopard density pattern is similar to that found for tigers in the same study area 10 years prior to our study (Linkie et al., 2008). Compared to Bungo and Sipurak, Ipuh is more easily accessible, has a higher occurrence of people, has experienced higher forest conversion rates at its border and has lower levels of protection (Risdianto et al., 2016). This suggests an impact of anthropogenic disturbance. The lowland forests of Ipuh, which should be rich in prey and therefore present ideal habitat for both tigers and clouded leopards, had lower values for both densities than the hill–submontane forests of Bungo and Sipurak (Linkie et al., 2008).

Based on our findings, we recommend an island-wide assessment of clouded leopard densities and populations that utilizes the large volumes of bycatch data available from tiger population surveys, as was recently done for Peninsular Malaysia (Tan et al., 2017). A range-wide assessment could initiate a national dialogue on clouded leopard population status and conservation needs across Sumatran landscapes and Indonesian Borneo. It would also enable the clouded leopard to be considered by the Indonesian Ministry of Environment and Forestry for Priority Species status, thereby affording this Vulnerable felid greater conservation attention and targeted management actions.

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Author contributions Study design, data collection and analysis, writing: IAH; conception and direction of the wider project of which this study is a part, supervision, writing: DWM; assistance with study design, data analysis, writing: ML.

Conflict of interest None.

Ethical standards This study abided by the *Oryx* guidelines on ethical standards and did not involve human subjects and/or any animal experiments or collection of specimens.

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A photo of a few melanistic Asiatic golden cat individuals detected in a sub-montane – montane forest within KSNP

4

Small-medium sized felids population dynamics

RESEARCH ARTICLE

Population dynamics of threatened felids in response to forest cover change in Sumatra

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Abstract

Habitat loss caused by deforestation is a global driver of predator population declines. However, few studies have focussed on these effects for mesopredator populations, particularly the cryptic and elusive species inhabiting tropical rainforests. We conducted camera trapping from 2009–11 and 2014–16, and used occupancy modelling to understand trends of Sumatran mesopredator occupancy in response to forest loss and in the absence of threats from poaching. By comparing the two survey periods we quantify the trend of occupancy for three sympatric felid species in the tropical rainforest landscape of Kerinci Seblat National Park. Between 2000 and 2014, forest loss across four study sites ranged from 2.6% to 8.4%. Of three threatened felid species, overall occupancy by Sunda clouded leopard (*Neofelis diardi*) and Asiatic golden cat (*Catopuma temminckii*) remained stable across all four areas between the two survey periods, whilst marbled cat (*Pardofelis marmorata*) occupancy increased. In general occupancy estimates for the three species were: lower in lowland forest and increased to attain their highest values in hill forest, where they declined thereafter; increased further from the forest edge; positively correlated with distance to river, except for golden cat in the second survey where the relationship was negative; and, increased further from active deforestation, especially for clouded leopard in the second survey, but this was some 10-15km away. Our study offers fresh insights into these little known mesopredators in Sumatra and raises the practically important question of how far-reaching is the shadow of the encroachment and road development that typified this deforestation.

Introduction

A global review of felids and other large-bodied Carnivora revealed a general pattern of population decline that was primarily caused by habitat conversion to agriculture, poaching for trade, retaliatory killing from conflict with people, and stochastic events [1]. For example, the

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leopard (*Panthera pardus*), one of the world's most widely distributed felid species, has lost approximately 18–67% of its historic range in Africa, and 83–87% in Eurasia over the past 250 years [2]. Densities of jaguar (*Panthera onca*) across South America have been suppressed by human presence and their genetic diversity is threatened by habitat fragmentation, especially in critical habitat such as Brazilian Atlantic Forest [3–5]. Similarly, many felid populations in tropical Asia, such as clouded leopard (*Neofelis diardi* and *Neofelis nebulosa*) and tiger (*Panthera tigris*) in tropical Asia are declining due to inadequate protection, habitat loss, and/or the high demand for their body part [6, 7].

Monitoring trends in felid populations in tropical forests is technically challenging, because they tend to be elusive, to occur at low densities, and in dense vegetation. The effort and cost of surveying large-bodied felids has been high for tiger [8], leopard [9], and jaguar [10]. In contrast disproportionately small sums (<1% of global funding for felid conservation) have been allocated to field research and conservation of small felids, for which some 80% lack robust population assessments (J. Sanderson, unpublished data). This imbalance applies on the Indonesian island of Sumatra, where of the six resident felid species, only the Sumatran tiger (*P. t. sumatrae*) has been monitored effectively [11–16].

The smaller-bodied felid species in Sumatra include the Vulnerable Sunda clouded leopard (*Neofelis diardi*), the Endangered flat-headed cat (*Prionailurus planiceps*), the Near-Threatened Asiatic golden cat (*Pardofelis temminckii*), the Near-Threatened marbled cat (*Pardofelis marmorata*), and the Least Concern leopard cat (*Prionailurus bengalensis*). Of the limited research conducted on these species on Sumatra, only one study has established a baseline density estimate, which was for the clouded leopard [17]. Maximum entropy modelling, using presence-only data, has been used to predict the distributions of clouded leopard, Asiatic golden cat, leopard cat, and marbled cat using camera trap data [18]. That study provided baseline data for these species in southern Sumatra, where clouded leopard, golden cat and marbled cat, respectively, occurred more widely than the smallest cat, leopard cat. Haidir et al. [19] provided the first estimates of occupancy, habitat associations and niche overlap between the Sunda clouded leopard and Asiatic golden cat. A recent range-wide estimate of Sunda clouded leopard distribution suggested that this species occupied a third of the available forest blocks in Sumatra, particularly hill forest (300-800m above sea level and Dipterocarp dominated), whereas in Kalimantan they occurred at mid-elevation (600m+) protected areas [13].

Here, we assess occupancy as an indicator of population trends [20], of smaller-bodied felid species in the UNESCO World Heritage Site of Kerinci Seblat National Park, Sumatra, and the surrounding forests. We selected four study areas that have been systematically surveyed using camera traps set from 2009–2011 [21] and 2014–2016 [19]. More specifically, we use these temporal data to investigate: 1) the occupancy trends of the Sunda clouded leopard, Asiatic golden cat, and marbled cat using single-species, single season occupancy modelling; and, 2) patterns of deforestation and the accompanying response of these species to this type of habitat change.

Materials and methods

The study was conducted in Kerinci Seblat National Park and its adjacent forest that are under State land authority. A permit to conduct the fieldwork was provided by the Indonesian Ministry of Environment and Forestry (MoEF) technical unit Kerinci Seblat National Park (KSNP) Authority for Jambi, West Sumatra, South Sumatra and Bengkulu regions, of whom the first author is an employee of KSNP, MoEF. Our field teams had a permit from the national park head office and did not therefore require written permission from the village heads, but instead had their verbal permission.

Study area and sampling design

Our study area was the Kerinci Seblat Landscape that consists of national park forest, production forest, watershed forest, and wildlife and nature reserve forest that are designated for the protection of particular wild fauna and their natural habitats. The ~16,000 km^2 contiguous landscape lies on the Bukit Barisan mountain range that for the Kerinci Seblat section stretches ~370 km and encompasses forested areas in bordering provinces of West Sumatra, Jambi, Bengkulu and South Sumatra. We conducted two consecutive camera trap surveys in four study areas in this landscape for the years 2009–11 and 2014–15, hereafter respectively referred to as surveys I and II. The study areas were selected because they represented the main elevation classes for the landscape: lowland (ranges from 0–300 m above sea level), hill (300–800 m asl), sub-montane (800–1900 m asl), and montane (>1900 m asl).

We deployed a combination of passive infrared camera traps: 20 units of Bushnell (Bushnell Corporation, Overland Park, KS, USA), 10 units of Highlander Photoscout and Moultrie (Moultrie^{TM}, Alabaster, AL, USA) for survey I, and 160 units of Cuddeback Ambush IR (Non Typical Inc., WI, USA) and 36 units Panthera IV (Panthera Foundation, USA) particularly in Bungo, for survey II. No lures or attractants were used at any camera trap locations. Cameras were placed along the ridges and animal trails at a height of 40–60 cm above the ground and a distance of 2–3 metres from the target trail. Cameras were active 24 hr/day and set with a 5-minutes delay between exposures. Camera trap spacing ranged 1–4 km from one another. The cameras recorded time and date of each photographed animal. Every two weeks, two teams of 4–5 people visited camera locations for maintenance and data retrieval during ~100 days of camera trap operation.

Focal species occupancies

This study targets three focal felid species: Sunda clouded leopard, Asiatic golden cat, and marbled cat. Leopard cat is present but was excluded due to the low sample size. Flat-headed cat (*Prionailurus planiceps*) is strongly associated with peat swamp forest, a habitat that is absent from our study area. To estimate species occupancy, a single species, single season occupancy model was used, based on four main assumptions: i) occupancy state is closed, where species occupancy and detection probability at all sites remained constant over a survey period but may change between surveys; ii) trap locations (sites) and replicates are spatially and temporally independent, where detecting species of interest at a site is independent of detecting the species at other sites or other time interval, iii) site and survey covariates factors that influence occupancy are quantified and incorporated in the model calculation, and iv) factors that influence detection probability are explained through incorporating site covariates and survey covariates within the analyses [22], although in this study the latter assumption is considered constant across sites [23].

Focal species detection matrices of two series of surveys were constructed where '1' annotated a detection, '0' a non-detection, and '-' indicating a camera was not running during the time interval, where each sampling occasion (K) consisted of 14 trap days. The survey data used spanned 90–120 days that adhere to population closure assumption [24] and only adult individuals were included in our detection matrices.

Using the R package 'camtrapR' [25], camera trap data were extracted and converted from each survey into unique detection matrices (K = 14 days). We identified six site covariates that were potentially incorporated into the models: elevation and slope derived from SRTM [26]; distance to forest edge using global forest cover change data derived from Hansen et al. study [27]; distance to river, distance to road, and distance to village using rasterized data produced by the National Mapping and Survey Agency of Indonesia (BAKOSURTANAL, 2017); and, distance to deforestation polygons (>100 hectares/1km^2) in each survey, obtained from BAPLAN (Indonesian Ministry of Environment and Forestry's Planning and Mapping Centre).

We used the Euclidean distance to deforestation within a 15km radius from the outermost camera trap polygon associated with their respective surveys from the year 2010 or year 2014. We tested distance to forest edge and to deforestation, accepting these as proxies for habitat quality and degradation. Forest loss was calculated using data taken from the global forest dataset [27], which provides high resolution data on tree canopy cover at approximately 30 m resolution. Following Beaudrot et al., [28], we defined tree canopy for our tropical rainforest cover as being >75%. Deforestation was then defined as the complete conversion of a forest pixel to a non-forest pixel between survey periods. We measured forest cover and change for each study area including a 15-km buffer around the outermost camera trap locations, because deforestation can have wider reaching impacts. Using 'gfcanalysis', 'rgeos', 'raster', 'rgdal' in R software [29, 30], forest cover changes were calculated annually and clustered into two periods: i) 2005–2009 to correspond with camera trapping period I; and, ii) 2010–2014 to correspond with camera trapping period II.

We performed multicollinearity tests and, where correlated covariates were found, ensured that they were not included in the same occupancy model [31]. We used "layerStats" function in package raster [29] to compute correlation and (weighted) covariance for multi-layer raster objects in R version 3.5.3. Based on this test, we dropped variables that exhibited correlations >0.5. This resulted in a final data set consisting of scaled distance to deforestation, scaled elevation (quadratic function), scaled distance to rivers, and scaled distance to forest edge. We chose these variables because they are uncorrelated, and for comparability with earlier studies by Haidir et al. [19] that had found them to influence mammalian occupancy in the study areas [23, 32].

We performed single species single season occupancy analyses for each of the focal species for each study area and for each survey period. We then combined data from all study areas for each survey period and used study area as one of the covariates. We ranked the plausible models for small sample sizes using AICc (ΔAICc <2) and calculated model averages for each survey period, where possible, in each study area [15, 23, 33]. All calculations of model averaging, where each model was multiplied by its model weight, in order to get model rankings, were performed using 'wiqid' package [34].

The occupancy values derived from the model averaging procedure were used to test for significant differences of pairwise study areas over the study periods, where non-overlapping 95% confidence intervals, as a first step, indicate a significant difference. However, overlapping intervals may still be significantly different, and in such situations, a Tukey's Honest Significant Difference (HSD) test was subsequently performed, with $P < 0.05$ taken as the significance level (i.e. Pr(>|z|)) [1]. All model calculation, covariates analyses, raster analyses and statistical tests were performed in R Studio [35].

Results

Focal species detection

For both surveys, 246 camera trap locations generated 21,539 trap nights (Table 1) and detections of four small-medium sized cat species: Sunda clouded leopard (n = 163), Asiatic golden cat (116), and marbled cat (55), with two leopard cat detections and no flat-headed cat detections. Clouded leopard, golden cat and marbled cat were recorded in all four study areas and during both sampling periods (S1 Table).

Table 1. Summary of survey effort and characteristics of the study areas over two sampling periods: 2009–11 (I) and 2014–15 (II).

Feature	Bungo		Sipurak		RKE		Ipuh	
	I	II	I	II	I	II	I	II
Main forest type	Hill-submontane		Hill-submontane		Hill-montane		Low land-hill	
Mean elevation (min-max) in meter asl	753 (389–1355)	627 (307–1116)	883 (700–1253)	811 (575–1069)	1264 (593–1985)	1198 (489–1992)	512 (145–1032)	427 (263–649)
Annual deforestation 2004–2014 in 15 km buffer (percentage forest loss)	0.60% (6.38%)		0.88% (8.43%)		0.26% (2.59%)		0.61% (5.91%)	
# camera locations	21	40	21	40	23	40	21	40
Trapping area (km2)	76.5	63.9	71.8	62.5	91.9	63.2	140.8	60.6
Trapping dates (dd/mm/yy)	13/04/10 to 16/07/10	11/06/14 to 11/11/14	24/12/09 to 26/03/10	24/11/14 to 08/04/15	28/07/10 to 27/10/10	25/04/15 to 10/08/15	28/11/10 to 03/03/11	06/09/15 to 24/12/15
# Trap nights	1886	4247	1715	3504	2021	3090	1893	3183

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Occupancy changes

The constant model occupancy ($\hat{\psi}$) for clouded leopard in all study areas combined was 0.24 in survey I and 0.33 in survey II, while for the sympatric golden cat it was 0.27 and 0.36, and for marbled cat it was 0.13 and 0.27 (S2–S4 Tables). The top-ranked model predictions ($\hat{\psi}$)(±SE) for all study areas combined over the two survey periods were: clouded leopard = 0.24 (±0.05) and 0.33 (±0.04), with respective detection probabilities ($\hat{p}$) of 0.39 and 0.22; Asiatic golden cat = 0.27 (±0.06) and 0.36 (±0.05), with respective detection probabilities of ($\hat{p}$) 0.31 and 0.14; and, marbled cat = 0.13 (±0.04) and 0.28 (±0.04) with respective detection probabilities of ($\hat{p}$) 0.31 and 0.11 (Fig 1 and S2–S4 Tables). For clouded leopard and golden cat, distance to forest edge was the single most frequently occurring covariate in the top ranked model or candidate models within two ΔAICc units of the top model. The constant model remained the top candidate model for marbled cat in both surveys (S2–S4 Tables).

The general trends shared across the three cat species were: i) occupancy estimates were lower in lowland forest and increased to their highest values between 700 and 1000 m above sea level (mainly hill forest type), where they declined thereafter, except for clouded leopard in survey II; ii) occupancy increased further from the forest edge, except for clouded leopard and golden cat in survey II where there was a non-significant change, instead showing that they have slightly higher occupancy near forest edge; iii) occupancy was positively correlated with distance to river, exhibiting a linear relationship, except for golden cat in survey II where the relationship was negative; and, iv) occupancy increased further from active deforestation especially for clouded leopard in survey II (see Fig 2 for more details).

Comparing the occupancy estimates and their associated confidence intervals, Tukey's test indicated non-significant occupancy increases ($Pr(>|z|) > 0.05$) for clouded leopard and golden cat, whereas marbled cat had a significant increase of 77.2% ($Pr(>|z|) < 0.05$) from the first survey (S2 Table–S4 Table for details of changes of occupancy values).

Deforestation patterns

From 2005–2014, our remote sensing analysis recorded forest area baselines and annual rates of forest loss in Sipurak (baseline = 115,307 ha; mean annual forest loss of 0.93%; 1037 ha lost/year), Bungo (baseline = 112,876 ha; 0.67%; 739 ha/year), Ipuh (baseline = 115,721 ha; 0.61%; 693 ha/year) and RKE (baseline = 110,038 ha; 0.28%; 304 ha/year; Fig 3, Table 2). Forest loss trends from the different study areas showed wide year-over-year fluctuations, but the overall net value of forest change across all study areas combined from 2005–2014 was -24,970

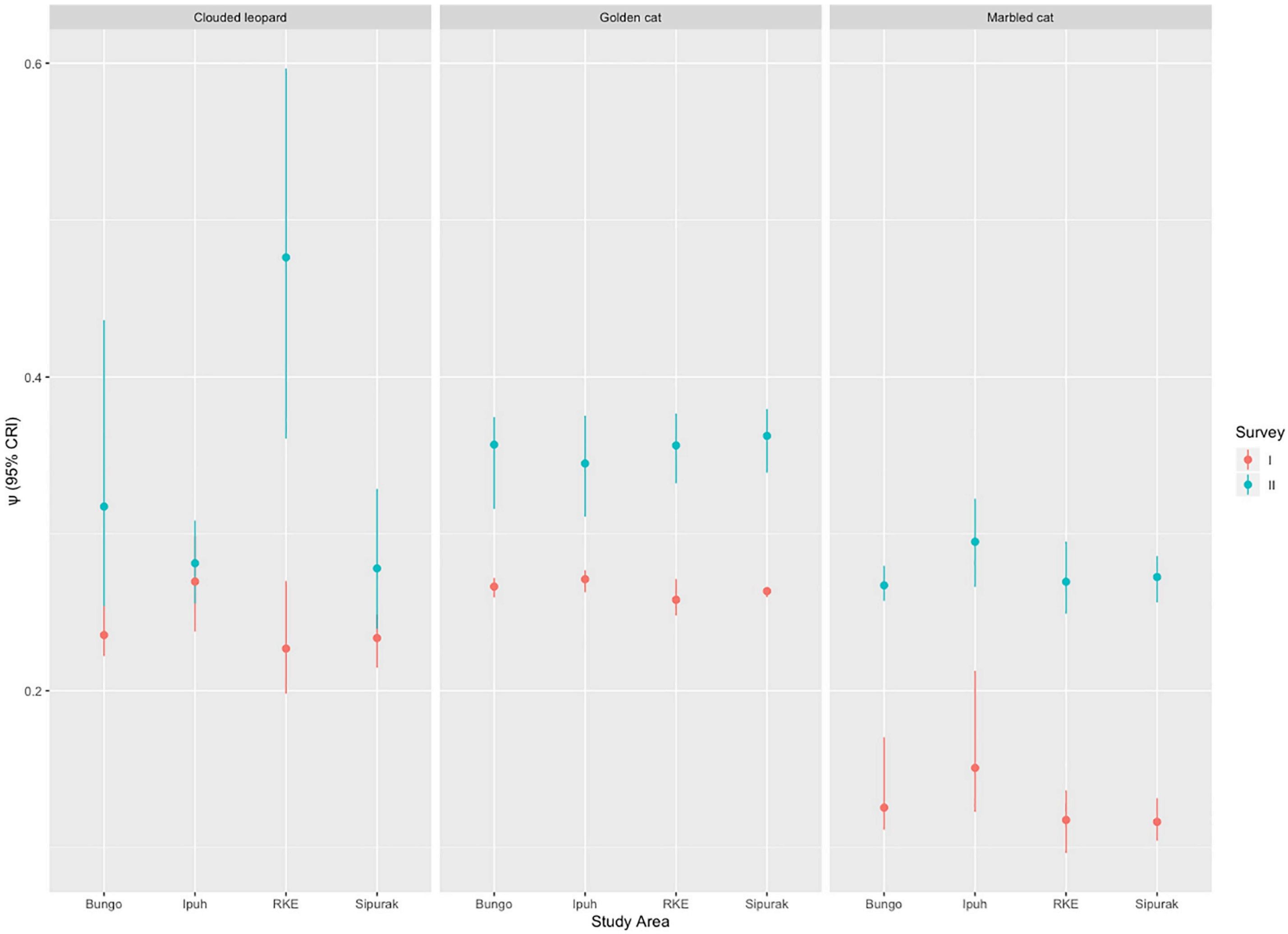

Fig 1. Focal species occupancy trends from survey periods I (2009–11) and II (2014–2016), points are mean of occupancy, bars indicate 95% credible interval.

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hectares, equivalent to 5.5% of the entire study areas. For the overall forest loss in the 15km buffered camera trap polygons in each study areas over two survey periods, see S2 Fig.

Discussion

This study is an important addition to the limited body of scientific knowledge on Southeast Asia's small-medium sized cat species, particularly from Sumatra [18, 36]. Our approach could usefully be applied widely [37]. Kerinci Seblat National Park, along with the national parks of Gunung Leuser and Bukit Barisan Selatan, form the Tropical Rainforest Heritage of Sumatra that have been placed on the UNESCO 'in danger' list since 2011. They must collectively demonstrate that the impact of their mitigating actions are assisting in the recovery of the priority species; we provide that evidence for the smaller bodied felids [38].

For example, occupancy studies have been used to assess the spatio-temporal distribution of herbivores in India [39], set population baselines and harvesting thresholds for fisher (*Pekania pennanti*) in the United States [40], and identify conservation priorities for multiple threatened species in production landscapes in Sumatra [15]. Nonetheless, the occupancy approach

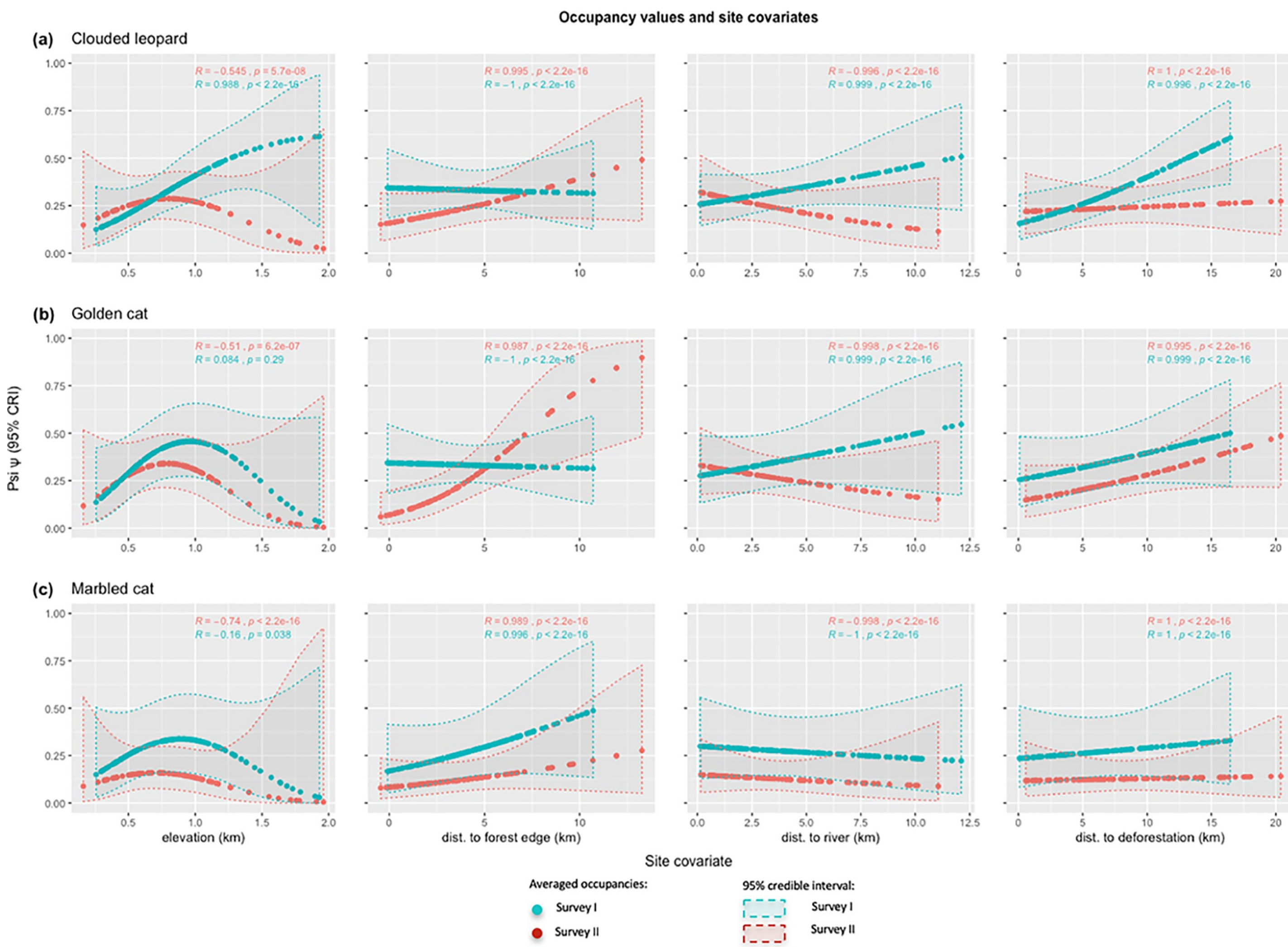

Fig 2. Relationships between occupancy values and covariates, where R is slope of relationships between psi and respective covariates and p is the significance value.

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has limitations with respect to monitoring difficult to detect and habitat specialist species for which data are sparse. The two leopard cat detections, and perhaps even the 55 marbled cat detections, are a case in point. For occupancy modelling to detect significant change in population indicators may require hundreds of camera traps for species with a low detection probability [41], of which in this study we did not test how types of camera trap unit affect detection probability. An additional consideration, relevant to our sampling design, is improving camera trap placement for semi-arboreal species–a factor that may apply to both clouded leopard and marbled cat. Nonetheless, and despite recognizing these possible limitations, we were able to record >100 independent records for both clouded leopard and golden cat. Our repeat surveys were conducted at times of year that overlapped by >60%. It is possible that more modern cameras, even of the same brand [42] may have increased detectability in the second survey.

A camera trap study conducted in the periphery of three Sumatran national parks—Gunung Leuser, Kerinci Seblat, and Bukit Barisan Selatan—found ongoing pressure from forest loss and habitat degradation outside of the protected areas might explain the higher,

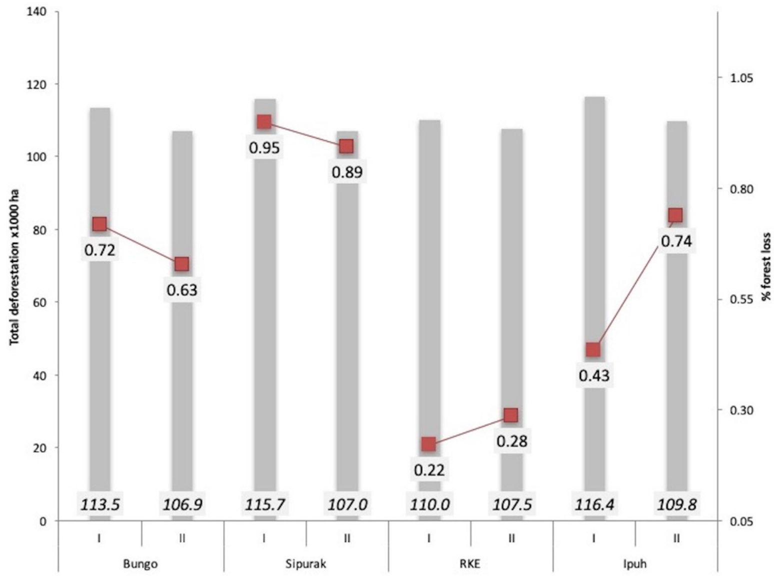

Fig 3. Forest cover change in four study areas over two sampling periods: 2005–2009; and, 2010–2014 (bars) and mean annual percentage of forest loss with red lines indicating the temporal trend.

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perhaps even inflated, tiger densities inside the park [43]. In Sabah, on the neighbouring island of Borneo, the carnivore community had ~28% higher relative abundance in previously logged forest compared to old growth forest [44]. These findings indicate the pernicious threat posed by active deforestation but also that populations of certain carnivore species can recover in degraded forests, if the threats are removed, in turn underscoring their conservation value. From our second survey period, clouded leopard and golden cat maintained higher occupancies in areas closer to the forest edge, nearby formerly selectively-logged or degraded forests. We speculate that prey, such as murid rodents, may be more abundant in these peripheral areas [44].

Table 2. Forest cover (in hectares) and forest loss (in hectares and as a percentage change) in four study areas prior to camera trap survey I in 2010–11 and survey II in 2014–16.

Year	Study area			
	Bungo	Sipurak	RKE	Ipuh
Forest cover (hectares)				
2005	112,876.2	115,307.4	109,931.2	115,721.4
2009	109,608.6	110,838.9	108,728.5	113,609.1
2010	109,182.3	110,270.4	108,506.1	113,142.2
2014	106,221.6	105,972.6	107,190.7	109,481.2
Forest loss, hectares (%)				
2005–2009 annual average	-817.9 (-0.7%)	-1,117.1 (-1.0%)	-301.7 (-0.3%)	-528.1 (-0.5%)
2005–2009 total area	-3,267.6 (-2.9%)	-4,468.5 (-3.9%)	-1,202.7 (-1.1%)	-2,112.3 (-1.8%)
2010–2014 annual average	-740.2 (-0.7%)	-1,074.4 (-1.0%)	-685.1 (-0.6%)	-1,560.1 (-1.4%)
2010–2014 total area	-2,960.7 (-2.7%)	-4,297.7 (-3.9%)	-2,740.5 (-2.5%)	-6,240.2 (-.5.5%)

Deforestation data from 2005 to 2009 were clustered as an initial deforestation rate in the first study period. Similarly, deforestation data between 2010 and 2014 were clustered for the deforestation calculation over study period II.

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Our forest cover analyses showed that the rate of deforestation fluctuated over the observed periods. It increased between 2005 and 2009 and then from 2010 onwards slowed down, following a nationwide pattern for Indonesia [45]. In our study area, we detected a subtle relationship between forest cover change and the presence of monitoring personnel: rates of forest loss were lower when research staff were active. We recorded that in 2010, forest loss in all study areas combined was 35–45% lower than the mean value, and forest loss in Bungo decreased by 52%. These periods coincided with the activity of monitoring teams in the vicinity from December 2009 to March 2011 [21]. This is in accord with a study on 98 protected areas in 15 tropical African countries that found non-protection activities such as research and tourism, when conducted on a regular basis, could reduce illegal activities in core areas, and hence improve habitat quality and support the recovery of wildlife populations [46].

Despite the levels of forest habitat loss we recorded, there was no evidence of reduced occupancy. One consideration is that the deforestation occurred some 10–15 km away from our camera-trapping grids, perhaps too far for a discernible effect to be felt by our study animals. Studies of a similar mesocarnivore, the African golden cat, reported that increased cultivation adjoining protected areas was associated with a six-fold density decrease on farmland compared to pristine forest [47]. In Madagascar, an increase in habitat degradation suppressed native carnivore occupancy, yet concentrated it in some areas, and with decreased encounter rates [48].

Considering our results more widely, assigning strict protection zones in the more accessible and therefore at-risk areas of the park with regular presence of law enforcement and monitoring personnel should reduce illegal activities [49]. Additionally, from Kerinci Seblat NP management point of view, an IUCN monitoring mission recommendation to the management authority was to implement an emergency action plan to withdraw the national park from the Tropical Rainforest Heritage Sites in danger list [38]. Key to this, as with other protected areas in Indonesia, is progressing from securing smaller core sites and expanding law enforcement and monitoring efforts to the wider landscape for ensuring the population viability of species such as golden cat, clouded leopard, marbled cat and other threatened species [14].

Supporting information

S1 Data.
(ZIP)

S1 Table. Small-medium sized wild cat detection encounter rate (#independent photo/100 trap days) and standard deviations in parentheses from the two survey periods and four study areas.
(DOCX)

S2 Table. Top occupancy models of clouded leopard from two periods of all study areas combined, of survey I and II.
(DOCX)

S3 Table. Top occupancy models of golden cat from two periods of all study areas combined, of survey I and II.
(DOCX)

S4 Table. Top occupancy models of marbled cat from two periods of all study areas combined, of survey I and II.
(DOCX)

S1 Fig. Map of study areas across Kerinci Seblat National Park and its adjacent forest in west-central Sumatra. *RKE: Renah Kayu Embun.
(TIFF)

S2 Fig. Forest cover changes over study period. Solid thin black line is KSNP border, bold solid black line is camera trap polygon of survey I, dashed bold black line is survey in period II, and thin dashed black line is 15 km buffer from the outer most camera trap polygon. Black shaded polygons are deforested area, grey polygons are the existing non-forested area, and light greens are: cultivated, plantation and settlement, white polygon is water body. Forest cover changes shown in this figure are a year ahead before the surveys were carried out.
(TIFF)

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Marbled cat is being the rarest small cat photographed inside KSNP forest

5

Identifying high conservation areas

Landscape Ecol
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RESEARCH ARTICLE

Felids, forest and farmland: identifying high priority conservation areas in Sumatra

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Abstract
Context Effective planning for protected areas and wildlife population management requires a firm understanding of the location of the species' core habitat patches, the dispersal corridors connecting them, and the risk they face from key threats, notably deforestation.
Objectives To quantify and map core habitat patches and dispersal corridors for Sunda clouded leopard (*Neofelis diardi diardi*), Asiatic golden cat (*Catopuma temminckii*) and marbled cat (*Pardofelis marmorata*) across the 16,000 km^2 tropical rainforest Kerinci Seblat landscape, Sumatra. Also, to model future forest loss and fragmentation and its effect on landscape connectivity for populations of these threatened species.
Methods Using data from camera trap (671 sites/ 55,856 trap nights), and occupancy modelling, we developed habitat use maps and converted these into species-specific landscape resistance layers. We applied cumulative resistant kernels to map core areas and we used factorial least-cost paths to define dispersal corridors. A 17-year deforestation dataset was used to predict deforestation risk towards the integrity of corridors and core areas.
Results The occupancy estimates of the three cats were similar (0.18–0.29), with preference shown for habitats with dense tree cover, medium elevation and low human disturbance. The overlap between core areas and corridors across the three species was moderate, 7–11% and 10%, respectively. We predicted future loss of 1052 km^2 of forest in the landscape, of which 2–4% and 5% in highly importance core areas and corridors.
Conclusions This study provides a valuable guidance for identifying priority areas in need of urgent protection within and outside the protected area network, and where infrastructure development planning can incorporate wildlife conservation goals.

Keywords Camera trap · Connectivity · Intact forest · Occupancy · Small-medium felids · Tropical deforestation · UNICOR · Wildlife corridors

Iding Achmad Haidir, Żaneta Kaszta, and Lara L. Sousa sharing the co-first authorship.

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Introduction

At a global scale, increasing deforestation rates and other anthropogenic drivers of landscape transformation cause habitat loss and fragmentation (Laurance et al. 2014). This imposes immense pressure on wildlife populations, especially for highly specialized species (Frank and Amarasekare 1998) or those with large home ranges and dispersal abilities, such as medium- or large-bodied felids (Sunquist and Sunquist 2019). Species adaptability to these changes, and populations' survival, often depends on how easily individuals can move through the landscape in search of food, better quality habitat and mates (Zeller et al. 2012). Small and isolated wildlife populations, without the possibility to disperse and increase their gene pool, are those most threatened by extinction risk (Smith 1993; Wikramanayake et al. 2011; Goossens et al. 2016). Therefore, it is crucial to identify and protect highly utilized habitats, as well as dispersal corridors linking population strongholds. Only well-connected landscapes with large enough core habitat can facilitate frequent gene flow, leading to genetically diverse and stable populations (Manel et al. 2003; Storfer et al. 2007; Thapa et al. 2018). Understanding and mapping population connectivity and species dispersal routes are further important in the current context of globally increasing human-wildlife conflict (Cushman et al. 2018). Habitat fragmentation and increased poaching pressure may push individuals to the periphery of protected areas or even to move out into human-dominated lands, elevating the likelihood of conflict (Nyhus and Tilson 2004; Macdonald et al. 2012).

When assessing local or regional landscape connectivity, either for human-conflict mitigation or conservation planning, it is crucial to base assessments on rigorous empirical data and reliable modelling methods. This is particularly important for Southeast Asia, which has one of the highest rates of biodiversity loss worldwide, primarily caused by forest conversion to smallholder farmland and large industrial monoculture plantations (Miettinen et al. 2011; Gaveau et al. 2016).

Due to challenging landscapes characteristics and thick canopy cover, movement data for target species are limited (Grassman et al. 2005; Mohamad et al. 2015; Hearn et al. 2019). Therefore, we need robust data for creating landscape resistance layers for defining corridors and core areas. Mateo-Sánchez et al. (2015) and Keeley et al. (2016) found that, in the absence of data on movement behaviour or population genetic structure, which is the case for our three study species in Sumatra, spatial information on habitat use can be a useful surrogate for deriving a resistance to movement layer. Mateo-Sánchez et al. (2015) and Keeley et al. (2016) showed that a negative exponential function best describes the relationship between habitat suitability and resistance values. Unlike many other connectivity modelling approaches, both cumulative resistant kernels and factorial least-cost paths, as implemented in UNICOR (Landguth et al. 2012), account for species dispersal abilities, which is crucial for accurately predicting landscape-scale connectivity patterns (Cushman et al. 2013a, b). Dispersal abilities are not well known for our focal species; however, some studies have defined relationships between maximum species dispersal distances and home range size (Bowman et al. 2002; Whitmee and Orme 2013).

Current understanding of wild cat ecology in the Kerinci Seblat (KS) landscape, and in Sumatra in general, is mostly limited to the critically endangered Sumatran tiger (*Panthera tigris sumatrae*). Several studies inform on the population status of mesopredators in Sumatra - clouded leopard (*Neofelis diardi diardi*) (Haidir et al. 2018, 2020), Asiatic golden cat (*Catopuma temminckii*) and marbled cat (*Pardofelis marmorata*) (McCarthy 2013; Pusparini et al. 2014; Sunarto et al. 2015). However, a recent study by Struebig et al. (2018), although focused on the Sumatran tiger, suggested that small-medium sized felids moving through the Kerinci Seblat landscape may encounter more interactions with humans than do tigers, again highlighting the knowledge gap on species dispersal patterns and meta-population connectivity. Therefore, applying a multi species approach focused especially on mesopredator species with diverse body sizes, ranges and habitat requirements (Schuette et al. 2013; Lesmeister et al. 2015; Moreira-Arce et al. 2016) can provide protected area managers with crucial information to prioritize management scenarios, leading to better assessments of particular interventions (Sauer et al. 2013).

Within Southeast Asia, Indonesia is reported to have lost six million hectares of primary lowland forest from 2000 to 2012, equivalent to 470,000 ha per year (Margono et al. 2014). The most recent report on national deforestation by the Indonesian Ministry of

Environment and Forestry recorded a loss of 223,000 ha in 2018 (KLHK 2019), with Sumatra accounting for 25% (59,000 ha) of this loss. In Sumatra, the Kerinci Seblat (KS) landscape is a biodiversity stronghold. Within the landscape, an intact area covering 1.39 million hectares, the Kerinci Seblat National Park (KSNP) is one of the largest protected areas in Southeast Asia, but its elongated shape makes it susceptible to deforestation pressures. These include complete forest clearance resulting from smallholder land conversion to agriculture, which is precipitated by the creation of logging roads and presence of a large-scale road network that increases access to remoter forest areas (Linkie et al. 2006; Gaveau et al. 2009; Margono et al. 2014). Thus, empirically-based detection of important core habitats and ecological corridors for felid species of conservation priority in tropical landscapes is urgent (Linkie et al. 2006).

This study surveyed the main forest habitat types in the Kerinci Seblat landscape aiming to: (1) spatially predict habitat use patterns of clouded leopard, Asiatic golden cat and marbled cat using single-species occupancy models; (2) model, map and quantify high-density movement and dispersal corridors for the three focal species; and, (3) model deforestation risk, a main driver of habitat loss and fragmentation in KS landscape, to determine its potential effects on population connectivity of the studied felids.

Methods

Study area

The study area encompasses 16,000 km^2 Kerinci Seblat landscape, which stretches across the west-central Sumatran section of the Bukit Barisan mountain range that runs the length of the island (Fig. 1). The landscape consists of 15 districts that are predominantly covered by Kerinci Seblat National Park (KSNP) and Batanghari Protection Forest, and other land-use types: dry agricultures, rubber, coffee, palm oil, and cocoa plantations, and paddy field across four provinces: Jambi, West Sumatra, South Sumatra and Bengkulu. The Kerinci Seblat landscape is listed as a National Strategic Area under Indonesian Government Act No. 26/2008 on National Spatial Planning because of its high environmental and biodiversity values (MoPWH 2017). The three national parks of Kerinci Seblat, Bukit Barisan Selatan and Gunung Leuser form the Tropical Rainforest Heritage Site, a natural UNESCO World Heritage Site (IUCN) (IUCN 2004).

Camera trap surveys

The camera trap surveys sampled seven study sites inside and adjacent to KSNP, spanning from the north to the southern-most extent of the KS landscape: Kambang (KM), Bungo (BG), Muara Hemat (MH), Sipurak (SP), Renah Kayu Embun (RKE), Ipuh (IP) and Karang Panggung (KP) - inside and adjacent to KSNP (Fig. 1 and Table S1). The four surveys in BG, SP, RKE and IP aimed at repeating camera trapping previously undertaken in 2004 and 2010 (see Linkie et al. 2008; and Wong et al. 2013). These sites cover the main forest and land-use types of the landscape. However, camera trap deployments in MH (n = 143 single camera placements), KM (130) and KP (106) aimed at sampling the forest-farmland interface, using a strip-shaped camera trap polygon (15–18 km long, 3–5 km wide and spanning 27–32 km^2). The distance between camera trap stations ranged from 0.4 to 0.7 km.

Surveys in BG, SP, RKE and IP covered the same areas studied by Haidir et al. (2018). A total of 292 camera trap stations, using a combination of Cuddeback Ambush IR (Non Typical Inc., WI, USA) and Panthera IV camera trap units (Panthera Foundation, NY, USA), were set with gaps ranging from 0.8 to 1.4 km, covering a roughly circular area of 60–70 km^2. At each trap station, paired cameras were set except for RKE where only $\sim$ 75% were in pairs. Each camera was placed on a pole/tree next to forest trails at a height of 40–60 cm above the ground, c.a. 2–2.5 m from the centre of the trails. No bait or lure was applied at trap sites. Two field teams of five to six personnel, checked the units fortnightly to clean the cameras and replace memory cards and batteries. In total, camera polygons covered 18 villages and represented a mosaic of forest-farmland-forest or forest-farmland-settlement. All surveys took place between June 2014 and April 2016 (Table S1).

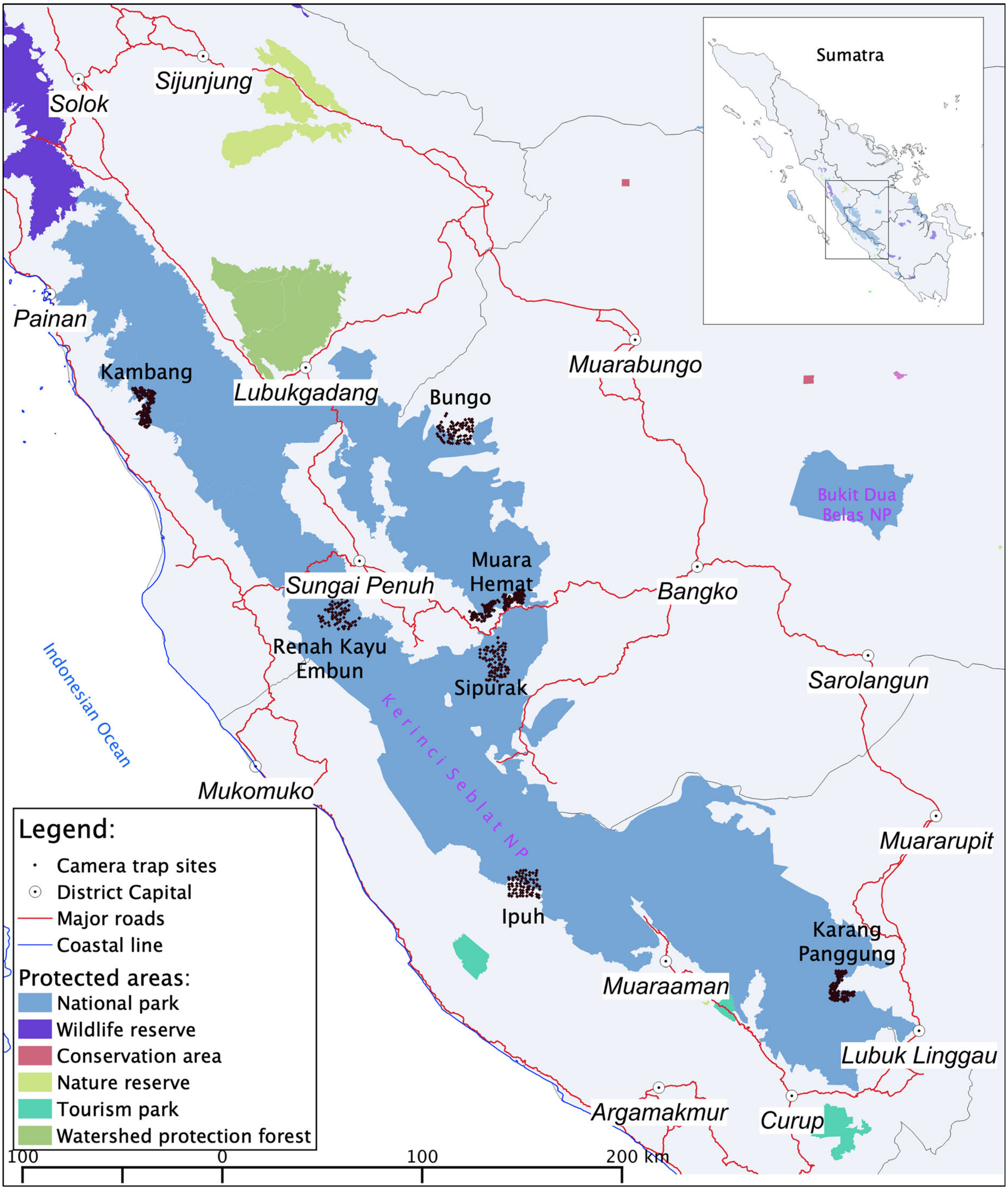


Fig. 1 Study areas in Kerinci Seblat landscape, black dots indicate camera trap locations with study area names and district capitals

Species habitat use

In order to estimate species occupancy (habitat use), a single species single season occupancy model was used, based on four main assumptions: (i) occupancy state is closed, where species occupancy and detection probability at all sites (camera trap locations) remained constant over a survey period but may change between surveys; (ii) sites and replicates are spatially and temporally independent, where detecting species of interest at a site is independent of detecting the species at other sites or during other time intervals, (iii) site and survey covariates that influence occupancy are quantified and incorporated in the model calculation, and (iv) factors that influence detection probability are explained through incorporating site covariates and survey covariates within the analyses (MacKenzie et al. 2002), although in this study the (iv) assumption is considered constant across sites (Linkie et al. 2007).

Our large-scale spatial study did not consider certain finer-scale temporal covariates. Camera traps were active for 24 h/day over several months and all data were used, so we did not consider either daily activity budget or date as a covariate. It is possible that our study animals adjusted their daily activity based on weather, which for our study area would be rainy or dry, as the temperature is fairly constant throughout the year being an equatorial rainforest. However, reviewing the scientific literature for similar studies, we decided to follow an occupancy modelling approach that is typically used studies covering large spatial scales (Brodie et al. 2015a; Espinosa et al. 2018; Penjor et al. 2019). Therefore, during model development, we tested eight landscape covariates that were considered likely to influence the spatial behaviour of the marbled cat, golden cat and clouded leopard (McCarthy 2013; Haidir et al. 2018). We included elevation (elev) and slope (slope) using data obtained at 30 m resolution from the Shuttle Radar Topographic Mission (SRTM) (Rabus et al. 2003). We obtained NDVI (Normalized Difference Vegetation Index) (vegcov) data using Global Forest Change data version 1.6 for year 2018. Combination of cloud free Landsat 8 OLI composite images over the year 2018 was used to generate NDVI as a ratio between the red and near infrared values. This dataset was first published in 2013 (version 1.0, see Hansen et al. 2013) and then updated each year (currently version 1.7 which provides data from 2000 to 2019). During the study period, there might have been some changes in vegetation cover, but these would have been minor. This dataset was first published in 2013 (version 1.0, see Hansen et al. 2013) and then updated each year (currently version 1.7 which provides data from 2000 to 2019). Euclidean distance to forest edge (fordist) was calculated based on official forest cover data from BAPLAN (Indonesia Ministry of Environment and Forestry's Planning and Mapping Centre), data obtained from year 2014. Euclidean distances to villages (vildist), distance to major roads (national and provincial roads; roadist) and distance to rivers (rivdist) were calculated based on spatial layers from BAKOSURTANAL (Indonesia Land Survey and Mapping Agency) for the year 2018. All layers were projected to UTM 47 Mercator Southern Hemisphere Projection and re-sampled to 250 m resolution following Macdonald et al. (2018b) study on clouded leopard in Borneo.

We used photographic evidence from camera trap surveys, sorted into two-week sampling occasions adopting the approach of previous studies by (Linkie et al. 2007; Haidir et al. 2018), these detection data were then converted into detection matrices for four species: clouded leopard, golden cat, marbled cat and leopard cat. Detection matrices were developed through 'camtrapR' package in R (Niedballa et al. 2016). However, due to low detection of the leopard cat (< 5 photographs), that species was excluded from the analysis.

For the three focal species: clouded leopard, golden cat and marbled cat, we applied a single-species, single-season occupancy approach, psi ($\hat{\psi}$), which incorporates a function of detection probability (Mackenzie 2006; Kéry et al. 2013). All variables were extracted at the camera trap station location and, before the analysis, these were inspected for collinearity by calculating Pearson's correlation (Dormann et al. 2013). From the pair of highly correlated variables ($|r|>0.7$; Booth et al. 1994), we excluded the one with higher AICc value (Akaike's Information Criterion corrected for small sample sizes; Burnham et al. 2002) in a univariate model.

We assembled and tested a set of 10 candidate and biologically realistic models per species (Table S2). Expecting a parabolic relationship between occupancy and elevation, this covariate was tested in its quadratic term, while for the others, non-correlated covariates, we used normal (non-quadratic) relationships (Penjor et al. 2019). The 10 candidate models were then compared using the AICc and all models with ΔAICc $\leq$ 4 were averaged using model weights (Burnham et al. 2002) in the 'wiqid' package (Meredith 2018). We used ΔAICc $\leq$ 4 so that we could consider the influence of a greater number of models and their covariates for the final species 'model averaging'(see Richards 2005; and Symonds and Moussalli 2011). To generate predictive maps of habitat use for each species, we applied the averaged model coefficients to the raster representing each of the final model covariates (Rhodes et al. 2009; Banner and Higgs 2017).

To test the performance of the predicted habitat use models based on occupancy following Gould et al. (2019), higher quality data are required, which would substantially increase the cost of the surveys. Due to lack of sufficient data, instead we validated the final models using a Bayesian five-fold cross-validation with 80% of the data used for training and 20% used for validation (Petracca et al. 2018; Penjor et al. 2019). We decided to use Bayesian fivefold, over 10-fold which has high computational demands. To assess model accuracy, we calculated the proportion of expected detection $\hat{y_i}$ to observed detection y_i. (proportion of true positive and negative observations), sensitivity (proportion of true positive observations correctly identified) and specificity (proportion of true negatives correctly identified).

Landscape connectivity models

Species occupancy modelling generated predicted probabilities for habitat use that reflect the likelihood of each cell being used by a focal species (Gould et al. 2019; Penjor et al. 2019). To model landscape connectivity for each species, we transformed the habitat use layers into 'resistance to movement' values. Mateo-Sánchez et al. (2015) and Zeller et al. (2012) found that, in the absence of data on movement behaviour or population genetic structure, which is the case for our three species in Sumatra, spatial information on habitat use can be a useful surrogate for deriving a resistance to movement layer. Mateo-Sánchez et al. (2015) and Keeley et al. (2016) showed that a negative exponential function best describes the relationship between habitat suitability and resistance values. Therefore, we transformed habitat use (H) into resistance (R) ranging from 1 (low landscape resistance to movement) to 100 (high resistance to movement) using the following equation:

$$R = (\exp\left(-1 \times \frac{H}{C}\right) \times 100 + Y \tag{1}$$

Equation 1 transformation of habitat use layer (predictive habitat use) into resistance layer, where R is the resistance (cost) value, H is habitat use (occupancy, ψ), C is the factor used to determine the shape of the curve (0.15), and Y is the value used to convert minimum resistance to 1 (Y for clouded leopard = + 0.67, golden cat = + 0.42 and marbled cat − 0.07).

Landscape features such as settlements, water bodies and roads, likely constituting a barrier to the movement and dispersal of the three felid species, were not included in the habitat use model. Therefore, we 'burnt in' these features to the final resistance layers (reclassifying the pixels). For this, we considered large water bodies, settlements and major roads to be impermeable to felid movement and, therefore, assigned them a resistance of 100. Field observations have shown that these species can occasionally cross rivers (Haidir 2016) and, so, major rivers were given a medium resistance value of 50, unless the base resistance value was higher, in which case the higher value was retained.

Landscape connectivity models, which predict patterns of population connectivity, require animal source locations, reflecting the actual distribution and density of the target population (Cushman et al. 2018). The number of source points corresponding to the number of individuals in our study area was informed by the most recent published literature on density estimates of the three focal species in Southeast Asian countries. In summary, we generated a total of 206 source locations for clouded leopard (Haidir et al. 2020), 260 for golden cat and 346 for the marbled cat (Hearn et al. 2016; Rustam et al. 2016; Naing et al. 2017). We then distributed these sets of source points in the landscape, retaining 2 km minimum distance between the points, probabilistically to the habitat use of each species. This was done in three steps: (i) we first created a uniform random raster with values between 0 and 1 with identical extent and cell size to the area of interest; (ii) the random raster was then subtracted by the predicted occupancy layer, so that the positive values of the resulting layers reflect areas with higher than the random probability of species occurrence; and lastly; and, (iii) from the positive values of the resulting layer we randomly selected a set of cells with minimum gap between the pixels of 3 km for clouded leopard and 2 km for both golden cat and marbled cat. The number of the selected cells representing individuals source locations followed the estimated number of individuals (see Fig. S1 for illustration).

To map and quantify core movement areas and dispersal corridors for each of the focal species we applied cumulative resistant kernel (Compton et al. 2007) and factorial least-cost path approaches to the source points and resistance surface layers described above (Cushman et al. 2009). For both methods, we used the UNICOR program (Landguth et al. 2012). The cumulative resistant kernel identifies the main pattern of synoptic connectivity and core habitat areas (Kaszta et al. 2018) by predicting the total movement density across the landscape. This is calculated by summing all individual least-cost kernels from all dispersal source points (Compton et al. 2007). The factorial least-cost path approach complements the cumulative resistant kernels by defining narrow linkages in the landscape where the movement pattern is constrained. Therefore, the least-cost paths set up with larger dispersal thresholds can be applied to define dispersal corridors. The final network of paths is computed by summing the least-cost paths between all possible pairs of points (Cushman et al. 2013b). Therefore, combinations of the factorial least-cost path and cumulative resistant kernel has the advantage over other methods, such as circuit theory, by explicitly including dispersal thresholds that enable the method to realistically reflect the limited distances that can be traversed by real organisms and to explore scale dependent relationships with varying dispersal ability (Cushman and Landguth 2012; Cushman et al. 2013b; Kaszta et al. 2020).

Empirical dispersal abilities of the three felids are unknown. Therefore, to estimate the dispersal thresholds for connectivity analyses we applied Bowman equation where dispersal is calculated as 40 × (home range size$^{0.5}$) in highly suitable habitat (Bowman et al. 2002). With the average home range of clouded leopard varying from 23 to 45 km^2, the golden cat from 33 to 48 km^2 and marbled cat from 2 to 29 km^2 (Grassman 2004), such estimated dispersal thresholds vary between 57 and 277 km. Based on these estimates, and for the purpose of this study, we chose a lower threshold for cumulative resistant kernels of 125,000 cost units (CU) and an upper threshold of 250,000, reflecting distances of 125 km and 250 km respectively, in a uniform landscape of resistance equal to 1 (Hearn et al. 2019; Kaszta et al. 2020). To model long-distance movement and dispersal, beyond the extent of locally connected populations, we defined the threshold to 1,250,000 CU, which is five times higher than the upper threshold defined for the cumulative resistance kernels (Kaszta et al. 2019; Kaszta et al. 2020). This allows prioritization of linkage areas beyond the dispersal ability of most individuals, which are important for long-term connectivity of meta-populations (Elliot et al. 2014; Cushman et al. 2018; Kaszta et al. in press). To better reflect local gradients of movement density, the final three least-cost paths density layers (further referred to as LCP) were smoothed by calculating the focal mean of a 5 km radius.

To compare the landscape connectivity of the three felids we calculated Pearson's correlation and the averaged absolute difference between the cumulative resistance kernels layers (across both dispersal thresholds for sensitivity analysis) and between the three least-cost paths layers.

To identify the areas of high conservation priority defined by zones of high core areas overlap between the three felids, we followed three different approaches. First, we used a threshold to define core areas of high-density movement for all three felid species (Cushman et al. 2018; Kaszta et al. 2019; Kaszta et al. 2020). For that, we selected the value of the 55th percentile of the cumulative resistant kernel raster with the lowest maximum value across all three species (i.e. the golden cat at a dispersal threshold of 250,000 CU and threshold value of 1.64). We reclassified the cumulative resistant kernel rasters into binary layers ('0'/'1'), with areas equal or above the threshold were reclassified as 1, and below that value as 0. We then summed up all the binary layers ('0'/'1') representing core areas of each felid to delineate the inter-species core areas overlap. Second, to avoid the arbitrary selection of a threshold for defining core areas, we normalized the values of cumulative resistant kernel surfaces across all species by rescaling the original cumulative resistance layers to continuous values ranging between 0 and 1. We then summed up the three rescaled layers. The third approach of calculating core areas overlap across species was through to multiplying the three rescaled cumulative resistance kernels layers from the previous steps.

We also identified the most important corridors predicted to be jointly used by all three species. To maintain only significant connections, we used the 20th percentile value of the species with the lowest maximum LCP (i.e. 0.24 for marbled cat) (Cushman et al. 2018; Kaszta et al. 2020) and converted the LCP layers into binary layers with 1 assigned to the values equal or above the threshold. These binary LCPs were then summed up and overlapped with a layer of the protected area network to calculate the proportion of the most important corridors that is legally protected.

To assess how much of the core areas and corridors are contained within the protected area network in the study area, we calculated for each species the proportion of the resistant kernels for each species being officially protected. Lastly, we further calculated for all three species the proportion of the joined connectivity for all three species (sum and multiplication of the rescaled resistant kernels layers) that lie within the protected area network.

Deforestation risk

To estimate rates of deforestation and model forest loss, we performed a time-series forest cover analysis using ArcGIS 10.1. The forest cover maps were obtained from BAPLAN (Indonesia Ministry of Environment and Forestry's Planning and Mapping Centre) between the years 2000 and 2017. We calculated the extent of forest cover in 2000 as the landscape baseline and mapped the amount of forest cleared for the years 2003, 2006, 2009, 2011, 2014 and 2017, to determine the rates and locations of loss.

To model forest loss risk, we created two layers that depict the historical record of deforestation in the study area. The first layer was the deforestation data (binary, deforested = 1; forest = 0) for 2003–2014 that was used to train the deforestation model. The second layer contained information on deforestation (also binary) occurring from 2014 to 2017 and was used to validate the predicted deforestation model. To sample the landscape, we created 10,000 random points with a minimum distance of 3 km between each point to avoid spatial autocorrelation. We used Moran's I test in 'spdep' (Bivand and Wong 2018) package in R to test for spatial autocorrelation in the best model's residuals'. To maintain the proportion between forested and deforested regions in the study area (Kaszta et al. 2017), a total of 89 points were selected from deforested areas and another 717 points from forested areas (from 2003 to 2014). For consistency, we selected 30 points from deforested areas in 2017 and 688 points from forested areas, in 2017, to validate the predictive model. All calculations were performed in R (R Core Team 2017).

To investigate the landscape factors driving deforestation, and to predict future forest loss and fragmentation patterns, we developed 10 candidate generalized linear models (GLMs) with a binary response variable (1: deforested, 0: forest). We used the same GIS covariate layers as for the small felid species' habitat use analysis, testing for collinearity prior to model inclusion. We, therefore, used the following non-correlated variables: elevation, slope, distance from roads, and distance from villages (see Table 2).

Model parsimony was assessed using AIC corrected for small sample size (AICc). Beta coefficient values of the final model with the lowest AICc were used to predict future deforestation risk. Based on the deforestation model coefficients we generated a predictive map of probability of deforestation for the period between 2015 and 2026 by using a percentage tree cover layer updated by the deforestation from 2003 to 2014.

To assess the predictive strength of the models, we calculated the area under the ROC curve (AUC), sensitivity and specificity by comparing the observed values (deforested areas in 2017) with predicted deforestation values (generated from the best deforestation model using data from 2003 to 2014).

To assess which core habitats of the three focal felids might be most affected by future deforestation risk, we summed the probability of deforestation within core habitats of each species and in the areas of high core areas and corridors overlap amongst the three cats. We then compared these values to the deforestation probability predicted for the entire study area. The same procedure was applied to calculate the percentage of deforestation predicted to occur in the protected area network.

The whole processes and workflow that indicate steps taken in this study starting from field data collection to final results are visually shown in Fig. 2.

Results

Focal species habitat use

From the 55,856 combined camera trap nights recorded, there were 211 clouded leopard detections, 137 golden cat detections and 50 marbled cat detections. The model-averaged ($\hat{\psi}$) estimate with the highest density interval (HDI) was 0.18 (0.12–0.27) for clouded leopard, 0.29 (0.19–0.42) for golden cat and 0.21 (0.06–0.36) for marbled cat with top candidate models of respective species presented in Table 1. The southwest quadrant (Ipuh) had the highest predicted habitat use for all species at $\hat{\psi} > 0.50$, followed by BG, SP, RKE and MH at $\hat{\psi} \sim 0.40$, and BG and KM ($\hat{\psi} \sim 0.30$), with Batanghari (north-eastern) at $\hat{\psi} \sim 0.57$.

Clouded leopard habitat-use was found to be explained by two top models within ΔAICc ≤ 4 (Table S2) that included elevation, slope, distance to villages, vegetation cover, tree cover and distance to forest edge (Table 1). Our results showed that the species responded negatively to higher elevation and positively to the increased tree cover and vegetation cover. Higher distances to both forest edge and villages were also found to have a strong positive impact on clouded leopard habitat use.

Golden cat habitat use was explained by seven plausible models (ΔAICc ≤ 4, Table S2) and the averaged model showed a significant negative relationship with elevation (Table 1). This species was found to prefer areas closer to the forest edge and with gentler slopes.

Marbled cat habitat use was explained by six plausible models (Table S2) and the averaged model (ΔAICc ≤ 4, Table 1) revealed a negative species response to higher elevation and a positive response to slope, distance to villages and forest edge, vegetation cover and tree cover.

Model validation indicated that model accuracy for each species was above 0.75 (95% CRI 0.73–0.91) and the AUC above 0.66. The specificity values varied from 0.86–0.94 and sensitivity from 0.10 to 0.28 (Table S3).

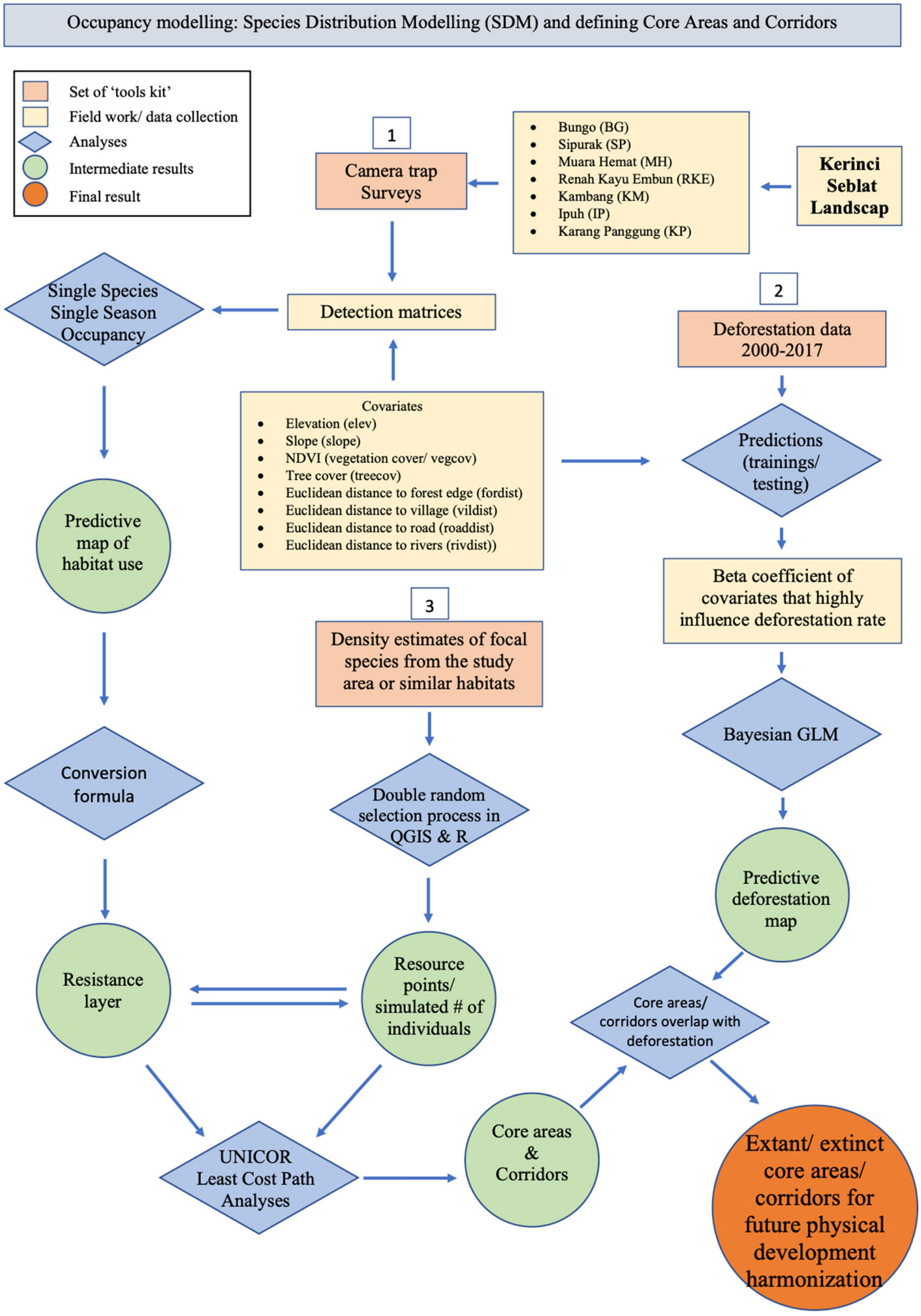
Populations connectivity: core areas and dispersal corridors

The overlap for all three species is shown in Fig. 3, while the cumulative resistant kernels layers for the tested dispersal threshold of 125 kCU and 250 kCU, as well as LCP (corridors) layers for clouded leopard, golden cat and marbled cat, are presented in Fig. S1.

The total value of connectivity (sum of kernel density pixels) for both dispersal thresholds was higher for golden cat and double that of clouded leopard, with the marbled cat having the lowest total predicted density of movement (Table 2). The mean value of kernel density was also highest for the golden cat (2.8 and 1.8 for dispersal thresholds 125 kCU and 250 kCU, respectively) and lowest for the marbled cat (1.4 and 0.7; Table S4).

The sensitivity analysis between the two tested dispersal thresholds showed a high correlation between cumulative resistant kernels (r $\geq$ 0.94) and the averaged absolute difference was low (AAD < 0.75), indicating that the resistant kernels correspond to each other well in the two thresholds (Table S5).

The individual population connectivity patterns of the three species showed that generally clouded leopard and golden cat had substantially larger core areas in comparison to marbled cat, despite the dispersal threshold (Fig. S1). A binary core areas map, based on 55th percentile threshold applied over the resistant kernels at lower dispersal threshold of 125 k CU, showed that clouded leopard had one predominant core area (4000 km^2) and several smaller core habitats (< 1000 km^2; Fig. 3). Golden cat core areas were substantially larger with two main cores (8500 km^2 and 3400 km^2) and several smaller core habitats (< 1500 km^2). Marbled cat, with the smallest and most fragmented core areas amongst the three cats, was predicted to have one larger core area (1500 km^2), with several much smaller cores (50–300 km^2) all distributed far (> 20 km) from each other. LCPs of the three felids revealed that all these core areas are potentially still connected by long-distance dispersal corridors, but some of those linkages are weak, especially for the marbled cat (Fig. 3 and Fig. S1). Clouded leopard corridors were the strongest of those predicted amongst the three species.


Occupancy modelling: Species Distribution Modelling (SDM) and defining Core Areas and Corridors
Set of 'tools kit'
Field work/ data collection
Analyses
Intermediate results
Final result
1
Camera trap Surveys
Bungo (BG)
Sipurak (SP)
Muara Hemat (MH)
Renah Kayu Embun (RKE)
Kambang (KM)
Ipuh (IP)
Karang Panggung (KP)
Kerinci Seblat Landscap
Single Species Single Season Occupancy
Detection matrices
2
Deforestation data 2000-2017
Covariates
Elevation (elev)
Slope (slope)
NDVI (vegetation cover/ vegcov)
Tree cover (treecov)
Euclidean distance to forest edge (fordist)
Euclidean distance to village (vildist)
Euclidean distance to road (roaddist)
Euclidean distance to rivers (rivdist))
Predictions (trainings/ testing)
Predictive map of habitat use
Beta coefficient of covariates that highly influence deforestation rate
3
Density estimates of focal species from the study area or similar habitats
Bayesian GLM
Conversion formula
Double random selection process in QGIS & R
Predictive deforestation map
Resistance layer
Resource points/ simulated # of individuals
Core areas/ corridors overlap with deforestation
UNICOR Least Cost Path Analyses
Core areas & Corridors
Extant/ extinct core areas/ corridors for future physical development harmonization

◀**Fig. 2** Workflow of the whole process in defining core areas and corridors from occupancy approach

Patterns of connectivity and species overlap

The AAD between kernel density surfaces (Table S5) was generally small across all species and both dispersal thresholds (AAD < 2). However, the largest difference between kernel densities reflect by high AAD and low correlation was found between kernel densities of marbled cat and golden cat (AAD = 1.92 and 1.33, r = 0.29 and 0.37 for dispersal thresholds 125 kCU and 250 kCU, respectively; Table S5). The lowest difference in connectivity patterns, as shown by the lowest AAD and highest correlation between kernel densities, was found between the clouded leopard and marbled cat (AAD = 0.69 and 0.45, r = 0.72 and 0.76 for dispersal thresholds 125 kCU and 250 kCU, respectively). Dispersal corridors (LCPs) showed much lower correlation (< 0.03) and higher AAD (6.6–17.7) than kernel density layers (Table S6). However, similarly to kernel density surfaces the highest correlation and smallest AAD was reported between the clouded leopard and marbled cat (AAD = 6.64, r = 0.03) and the highest difference was found between golden cat and marbled cat (AAD = 17.75, r = 0.03).

Table 1 Standardized coefficient (β) for predicted habitat use of clouded leopard, golden cat, and marbled cat based on the top ranked and averaged occupancy models

	β coefficient	SE	Low CI	Upp CI
Clouded leopard				
Intercept	− 3.357	0.503	− 4.343	− 2.371
Elevation	1.497	0.241	1.025	1.969
Elevation^2	− 0.200	0.087	− 0.371	− 0.030
Slope	0.485	0.149	0.194	0.777
Distance to villages	0.127	0.093	− 0.055	0.309
Distance to forest	0.036	0.048	− 0.058	0.129
NDVI	0.465	0.201	0.071	0.859
Percent tree cover	4.106	0.968	2.209	6.003
p intercept	− 1.975	0.081	− 2.133	− 1.817
Golden cat				
Intercept	− 0.577	0.218	− 1.004	− 0.149
Elevation	1.267	0.225	0.827	1.708
Elevation^2	− 0.507	0.127	− 0.757	− 0.257
Slope	− 0.046	0.050	− 0.144	0.053
Distance to villages	0.088	0.083	− 0.075	0.251
Distance to forest	− 0.002	0.040	− 0.080	0.077
NDVI	0.220	0.121	− 0.017	0.457
Tree cover	0.004	0.018	− 0.032	0.039
p Intercept	− 2.798	0.134	− 3.062	− 2.535
Marbled cat				
Intercept	− 1.659	0.441	− 2.523	− 0.794
Elevation	0.383	0.184	0.023	0.743
Elevation^2	− 0.112	0.106	− 0.320	0.097
Slope	0.143	0.098	− 0.050	0.336
Distance to villages	0.429	0.146	0.142	0.716
Distance to forest	0.302	0.161	− 0.013	0.617
NDVI	0.196	0.117	− 0.034	0.426
Percent tree cover	0.216	0.157	− 0.091	0.523
p Intercept	− 3.490	0.348	− 4.173	− 2.807

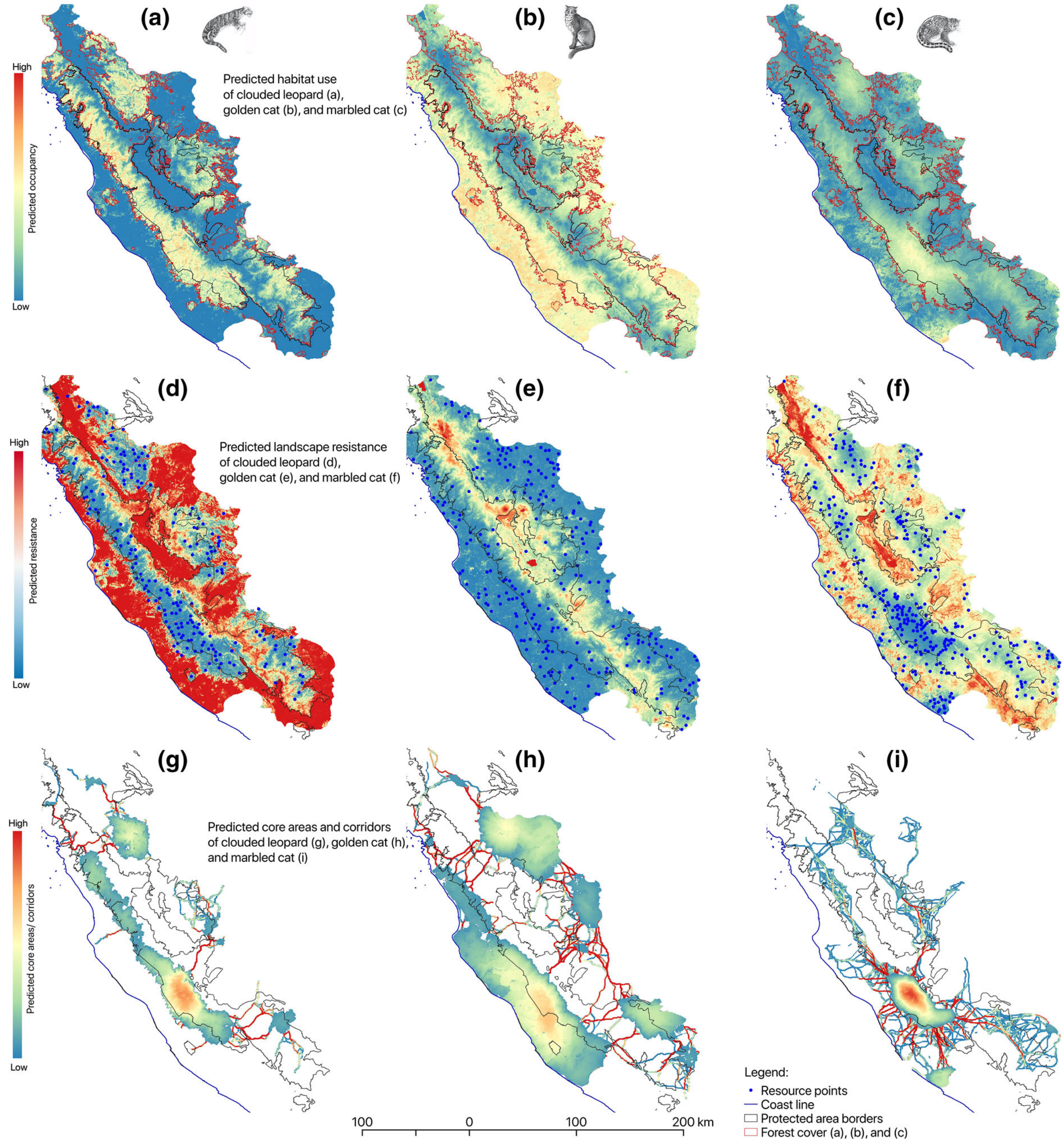


Fig. 3 Predicted species occupancy (top), resistance layer (middle), and core areas and corridors (bottom). First row indicates species-wise occupancy values from low (blue) to high (red) for clouded leopard (**a**), golden cat (**b**) and marbled cat (**c**). Second row is landscape resistance, same respective species, with darker colour indicating lower resistance. The third row is predicted core areas and corridors from low density (blue) to high (red), both core areas and corridors are based on a lower dispersal threshold of 125 k cost units for the three species

The analysis of spatial overlap between the core areas defined by the threshold of 55th percentile revealed that 7–11% (approximately 1250–1650 km^2, depending on the tested dispersal thresholds) of the total core areas were potentially utilized by all three species (Fig. 3). These habitats were mostly (88%) located inside the protected area network. Core habitat overlap of two species only was much larger and

Table 2 Standardized coefficients (β) for the final deforestation model with the lowest AICc

Variable	Standardized β-coefficient	Standard error	p-value
Elevation	− 2.6101	0.2455	< 0.001
Slope	− 1.2439	0.2528	< 0.001
Distance to roads	− 1.1001	0.2813	< 0.001
Distance to villages	− 0.6040	0.2009	< 0.005
Elevation	− 2.6101	0.2455	< 0.001

represents 18–22% of all core areas. However, only 30–44% (depending on the dispersal threshold) of this habitat was inside the protected area network. The majority of the core areas (71% for both dispersal thresholds) were inhabited by only one species and approximately 21% of it was located in the protected area network (Fig. 3). The core areas defined by the binary overlap of all three species covered 4924 km^2, with the majority (54%) of all three species core areas encompassed inside Kerinci Seblat National Park. The remaining 46% of the three species overlapped located outside KSNP was found to lie within Batanghari Protection Forest (north-eastern of the landscape; 23%), along the border in the western KSNP 15%, in south-western KSNP (further from KSNP forest, > 10 km) 6%, and the remaining (2%) were scattered in forested areas in the north western of the landscape.

The sum and multiplication of rescaled resistant kernel layers of the three felids indicated similar areas of the highest importance for joint conservation of the three felids, when comparing to the results of binary core areas overlap (Fig. 3). The proportion of the total value of the summed-up kernel density layers within the protected area network was 41–42%, depending on the dispersal threshold. The proportion of the multiplied kernel density layers, indicating the potential presence of all three species, being located within the protected area network, was 87–94%.

Overlap in dispersal corridors (LCPs) revealed that only 10% of predicted corridors were used in common by all three felid species, and 68% of all corridors, whether shared or not, lay within the protected area network (Fig. 3) and 46% of these two-species corridors were within the protected area network.. The single species corridors represented the vast majority of the corridors network (63%), with 32% of these single-species corridors lay within the protected area network (Fig. 3).

Deforestation risk

The most parsimonious deforestation model showed high accuracy in its predictive power (AUC = 0.80; Table S7) and model validation indicated that the model had a sensitivity of 0.11 and specificity of 0.97 (using threshold of 0.5). The final deforestation model was not affected by spatial autocorrelation (Moran's I = 0.17, p > 0.06).

The top model, which ranked much higher than the second top model (ΔAICc = 8.1; Table S7), included four of the five tested variables: elevation, slope, distance from roads and distance from villages (Table 1). The model predicted a lower probability of deforestation in areas that were higher elevation, of steeper slope and greater distance to roads and villages (Fig. 4).

The deforestation risk model predicted that 1052 km^2 of the landscape was at risk of clearance with 32% of the total deforestation probability predicted to occur within protected areas (Fig. 5).

The layer of future deforestation risk predicted that approximately 4% of the total deforestation will occur within both the clouded leopard and golden cat core habitats and, 1.6–2.8% within marbled cat core areas (calculations were based on the binary core areas and for two dispersal thresholds; Table S8). Furthermore, 2.7–3.7% of the total predicted deforestation will affect the joint core areas and 4.5% was predicted to occur within corridors jointly utilized by the three species. Additionally, 5–6% of the deforestation was predicted to affect core areas and 5% to occur in corridors jointly utilized by two felids (Fig. 5; Table S8).

Discussion

This study presents a quantitative framework to assess landscape connectivity for populations of small- and

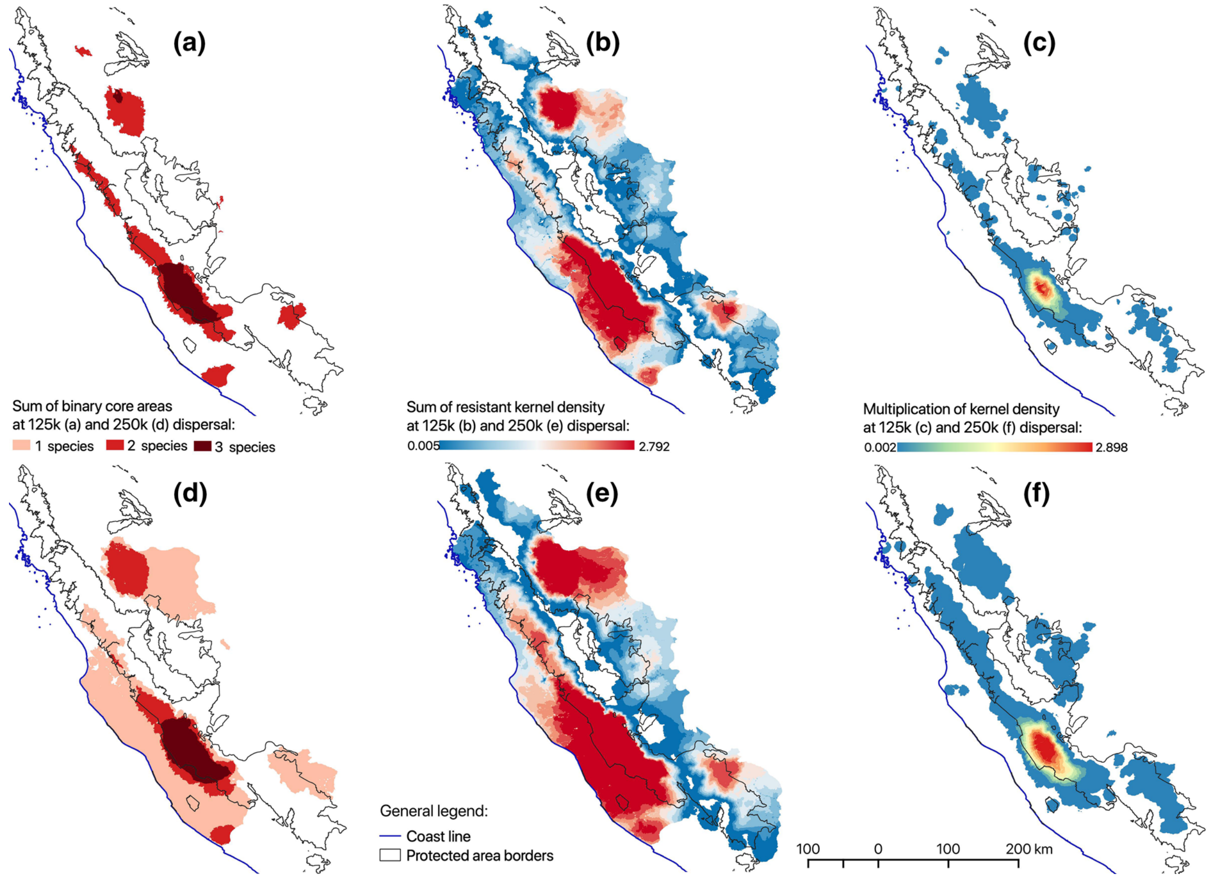


Fig. 4 Core areas and dispersal corridors overlap between the three felids for dispersal threshold of 125 k cost units (**a**), and prediction map of future probability of deforestation (**b**)

medium-size felid species, and the effects of future habitat loss, in Sumatra. However, the methodology proposed here can also be applied to other areas and other species, and can ultimately assist efficient management of practical, on-the-ground and multi-species conservation efforts. Based on an extensive camera trap surveys we identified habitat use and landscape connectivity for populations of clouded leopard, golden cat and marbled cat. We identified the most important core habitats and dispersal corridors for each of them, as well as key habitats for joint conservation of these felids. Using six intervals (data from year 2000 as baseline: 2003, 2006, 2009, 2012, 2015, and 2017) to sample the deforestation throughout the 17 years' overall (2000–2017) period of deforestation data, we have also modelled the probability of future deforestation risk as a major threat to these species in the landscape. Hence, we detected key habitats, the loss of which might, in the longer-term, affect the stability not only of populations of the three felids but also of other species ecologically linked to them.

Focal species habitat use

All three felids showed a significant and non-linear relationship with increasing elevation, avoiding lowland areas but also disfavouring high altitude areas. Similar findings were reported by McCarthy et al. (2015) on golden cat, and Sunarto et al. (2015) for all three species in Sumatra, and Hearn et al. (2018) for clouded leopard and marbled cat in Borneo.

The results of our occupancy models support several assessments of Southeast Asian small- and medium-sized wild cats that indicate the sensitivity of these cats to habitat disturbances (Rayan and Mohamad 2009; Sunarto et al. 2015; Brodie et al. 2015b; Granados et al. 2016). In line with findings of previous

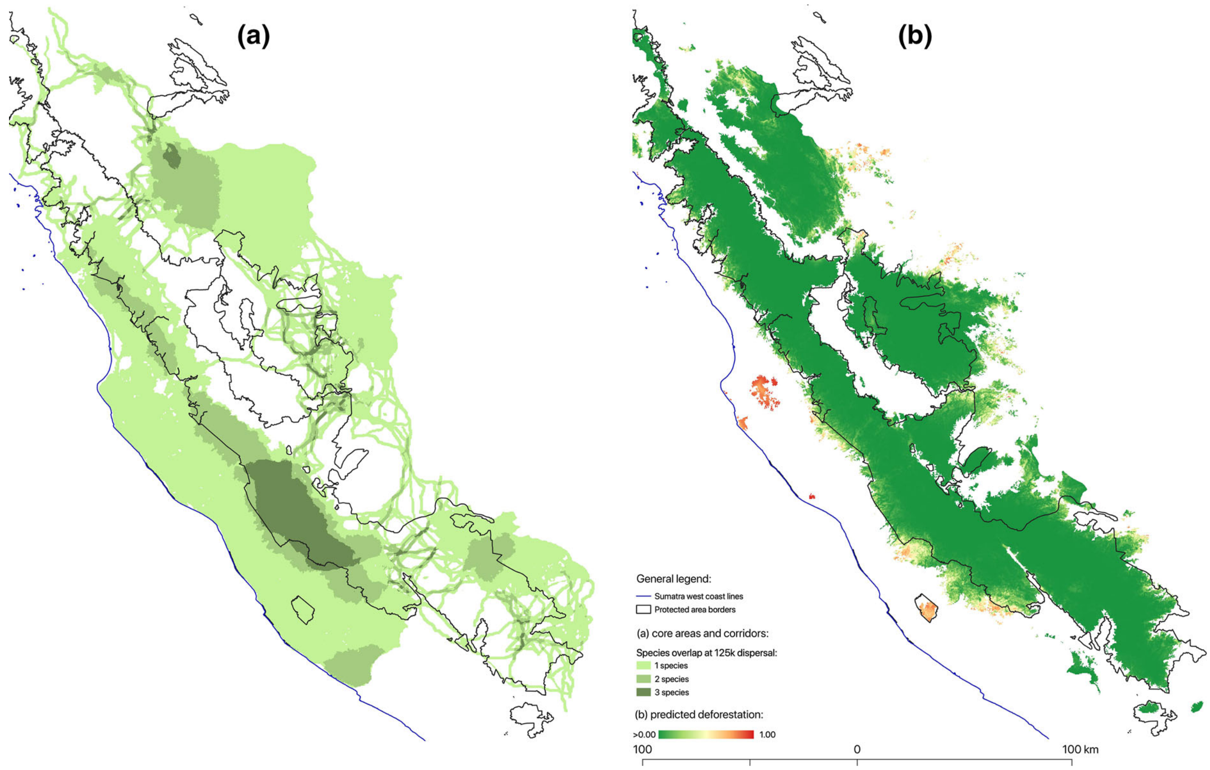


Fig. 5 Multi-species connectivity. Core areas overlap for the three species for dispersal threshold 125 k CU (panels **a**, **b** and **c**) and 250 k (panels **d**, **e** and **f**). Overlap of the binary core areas defined by a resistant kernels threshold value (panels **a** and **d**), sum of the 0–1 rescaled resistant kernels for the three species (panels **b** and **e**), multiplication of the 0–1 rescaled resistant kernels (panels **c** and **f**)

studies (Brodie et al. 2015a; Tan et al. 2017; Macdonald et al. 2018a; Penjor et al. 2018; Hearn et al. 2019; Haidir et al. 2020), our analysis revealed that predicted habitat use for all three felids is confined to densely forested areas and further from human disturbances. Similarly, golden cat and marbled cat, although found to be less sensitive to forest cover changes, and not specifically confined to old-growth forest, were highly associated with areas that have increased tree/canopy cover, including agroforestry land, forest plantations and selectively logged forest (Wearn et al. 2013; McCarthy et al. 2015).

Population connectivity

The connectivity analysis revealed that the golden cat population in our landscape was the most connected of the three felid species, with large and strong core areas representing meta-population strongholds, linked by a diffused network of dispersal corridors (Fig. 4). The largest golden cat core habitat stretches across the western KSNP, with more than half of it being located outside of the park boundary. The second core area covers Batanghari Protection Forest. These two main core areas are connected through a network of corridors that are partially located in the northern KSNP.

The clouded leopard population, although predicted to be much less connected than that of the golden cat, was also predicted to have two well-defined and relatively robust core population strongholds (Fig. 3). The largest one was located almost entirely inside KSNP and the other in the Batanghari Protection Forest. They are linked by a network of dispersal corridors in northern KSNP, with the strongest (highest LCP values) corridor overlapping one of the golden cat's dispersal corridors, highlighting its high importance for conservation.

Clouded leopard landscape connectivity patterns were spatially and quantitatively most similar to those of the marbled cat. The main marbled cat core area, located in central KSNP, although much smaller than that of the clouded leopard, overlapped with the largest core area of the latter (Fig. 3). Our analysis predicted the marbled cat population to be the least connected amongst the three species, with small patchy core habitats, which makes this species the most susceptible to landscape disturbance.

Conservation effectiveness and future habitat loss

Our results showed that large parts of predicted core areas are inside state forests but some are not legally protected by any of the protection categories defined by the IUCN, from 12% of the core habitats jointly utilized by the three felids, up to 70% used by only two species, and 79% used exclusively by one of the species. This is similar for dispersal corridors, where 47% of corridors are jointly suitable for the three species, 54% of corridors jointly suitable for two species, and 68% of corridors used by only one of the species, are located outside of the protected area network. The analysis of overlap for core areas and corridors identified areas of high conservation importance where core habitats of all three species overlap—one of them is central KSNP and the second is Batanghari Protection Forest.

Batanghari Protection Forest and its surrounding area also have a resident population of Sumatran tigers (Dinata 2008). It is partly categorized under Indonesian law as 'limited production forest' and watershed protection forest. However, the protection status of this area is not recognized by the IUCN classification scheme and, in practice, this status and limited conservation attention have resulted in forest clearance and the development of a local road network (Sloan et al. 2019), which impacts the predicted core habitats and corridors. The area between KSNP and Batanghari was identified in our analysis as a network of key corridors used by all three felid species and connecting the most important core habitats. We recommend, for future infrastructure development in this area, the implementation of strategic environmental assessments be conducted that take into account the importance of this key area for population connectivity of the three species.

Our deforestation risk model indicated that areas of lower elevation and gentler slope, located close to roads and villages were most susceptible to deforestation. This trend is similar to findings from deforestation modelling in Borneo (Cushman et al. 2017). Most importantly, our model showed that, over the 10 years covered by our predictions, 335 km^2 (equivalent to $\sim$ 2% of the overall landscape) of high deforestation risk in the 16,000 km^2 Kerinci Seblat landscape is predicted to take place within protected areas, although the areas of the highest probability of deforestation are mostly located outside the protected areas network. Furthermore, up to 10% of the predicted deforestation may occur within core habitats and up to 5% of the deforestation is likely to be in the dispersal corridors utilized by the three or two felid species, which are the areas of the highest conservation priority.

Scope and limitations

The validation of the occupancy models showed high accuracy and high AUC and specificity values. However, the sensitivity of these models was low, indicating the good ability of our models to predict non-occurrence of the three species but relatively low capacity to predict their presence. This is most probably due to the low detectability rate of these three rare felids during our surveys, with marbled cat probability of detection being the lowest. The low detectability might constitute a potential limitation to the habitat use predictions made by our models, and further surveys with increased trapping effort and improved sampling design should be carried out in the Kerinci Seblat landscape.

Management implications

The current status of the Kerinci Seblat landscape as one of 73 National Strategic Areas of importance to regional sustainability should promote the integration of a landscape-based development approach for wildlife conservation (MoPWH 2017). The role of remnant forests adjacent to KSNP in facilitating population connectivity shows the need for such an approach in maintaining viable populations of small- and medium-sized felid species. Our multi-species models offer suggestions on further designation of core areas and both physical and functional corridors within the national park and other protected area management units. The results and maps produced in this study provide information for national park managers in identifying priority areas for conservation, i.e. forest patrols and other support to areas that are likely used for felid movement. The KSNP authority, as the main government institution, is the epicentre of future collaborations with local government agencies and stakeholders in managing the landscape.

Although, a relatively large portion of the predicted small-and medium-sized cat dispersal corridors and some of the most important core habitats, are located in the protected area network, this conservation status does not guarantee prevention of deforestation risks. The majority of the remaining forest is currently within the protected area network (67%) and an additional ~ 30% is within state-owned forest areas, therefore relatively little additional forest remains outside of the protected forest network. Consequently, our deforestation risk model predicts that one third of the predicted deforestation may occur within the boundaries of the protected area network. Poor et al. (2019) found that the role of protected areas in effectively curbing deforestation should be strengthened, although protected areas in Sumatra already have the advantage of practical protection afforded by its location at rather high elevation typified by rugged slopes that discourage deforestation through the expense of access.

With the current pace of infrastructure development, managers of conservation areas face two substantial challenges in (1) mitigating the impacts of accelerated deforestation rates in central Sumatra; and, (2) ensuring national policies and conservation programs are well-communicated and integrated into provincial and district government plans (Poor et al. 2019; Sloan et al. 2019). In the meantime, national government restrictions on new road developments and/or expansion of existing roads that transect national park forests, e.g. those listed in the UNESCO Tropical Rainforest Heritage of Sumatra sites (GoRI 2019), should be well-communicated to the local authorities and stakeholders.

We propose that both the results and methodological framework of this study serve as a guideline for future development planning to achieve a smart and scientifically-guided compromise between development and wildlife conservation goals (Rayan and Linkie 2015). The methodology applied here, and our results, may be transferable to identify connectivity corridors for other sensitive species of concern and/or other areas where major infrastructure developments are taking place (MoPWH 2017), e.g. where the trans-Sumatra highway and major road upgrade projects are being planned or have already begun (CMoEA 2011).

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Two individuals of Asiatic wild dog, another species of mesocarnivores presence in the KS landscape, a potential competitor for small-medium sized wild felids in the landscape

6

General Discussion and Conclusion

Summary of results

In this chapter, I briefly summarised the main results from preceding chapters. Here, I identify some general results and points that emerge from each data chapter, and provide brief discussions and future directions.

Chapter 2, Sumatra's mesopredators and their putative prey spatiotemporal interactions.

In this chapter, I presented results from the first-intensive camera trapping surveys in Sumatra that mainly targeted sympatric small-medium sized wild felids, namely clouded leopard and golden cat, and their putative prey species. These target species occupied c.a. 25% of the study areas I surveyed. While the five putative prey species - pig-tailed macaque, muntjac, argus pheasant, porcupine, and mouse deer - varied in their occupancy, ranging from 73% to 19%. Multi-species spatial correlation occupancy models adopted from Cusack et al. (2016), revealed that both clouded leopard and golden cat were more likely to use sites at which muntjac and macaque were present, with weak evidence of golden cat occupancy being influenced by clouded leopard presence. The predator-predator and predator-prey temporal patterns (Ridout and Linkie 2009, Linkie and Ridout 2011), revealed that clouded leopard and golden cat had obvious temporal segregation, with a tendency to be more nocturnal and diurnal, respectively. Despite variations across study areas, clouded leopard had the highest temporal overlap with muntjac and mouse deer, followed by the more diurnal macaque and great argus pheasant. Similarly, golden cat had the highest temporal overlap with muntjac, followed by the more diurnal macaque and great argus pheasant, and finally the more nocturnal mouse deer.

The intensive camera trapping survey I completed in KSNP's humid evergreen rainforest yielded several positive results: (i) detection of mesocarnivore species in an area with very low or zero previous detections; (ii) sufficient data for spatial and temporal analyses, and thus robust results, by using a high number of camera units, covering a wide range and broad variety of habitats; (iii) supplementary information on keystone species to help protected area managers create appropriate conservation interventions; and (iv) key data to fill knowledge gaps on mesocarnivore ecology and behaviour and contribute to updating their conservation status's globally.

Chapter 3, Sunda clouded leopard densities and human encounters in the humid, evergreen, tropical rainforest of Sumatra.

This chapter is dedicated to the analysis of clouded leopard densities across study areas. I aimed to unveil a sex-based density estimate developed upon previous work by Sollmann et al. (2014). I was unable to analyse clouded leopard density based on sex despite colossal camera trap work: a total of >28,000 trapping nights, which captured 163 independent photographs of 18 adults (12 males, 4 females, and 2 unknowns). Nonetheless, my study successfully updated clouded leopard densities across study areas to a range of 0.8 to 2.4 individuals/100km^2. As the study area with the highest detection of illegal activities showed the lowest clouded leopard density, this study supports previous research that indicates anthropogenic pressures from illegal human activities, including ungulate and tiger poaching, bird hunting, illegal fishing, and non-timber collectors, negatively affect clouded leopard density (Risdianto et al. (2016).

I suggest future directions and recommendations for maintaining clouded leopard populations in Sumatra at two levels: scientific research and management interventions. Based on this study, future mesocarnivore conservation and research should include four aspects: i) conducting intensive, periodical, and standardized surveys to assess species population states across the landscape; ii) utilizing study designs that allow multi-taxa data collection using non-invasive methods (e.g. camera traps) to facilitate multi-species analyses; iii) supporting management authorities to improve frontline staff presence through regular patrols, in order to curb direct and indirect threats to wildlife; and iv) providing capacity building training for protected area staff through collaborations with relevant stakeholders: national and international universities, NGOs, and research institutions.

Chapter 4, Small-medium sized felid population dynamics

Quantifying population trends of small-medium sized felids and threats to their populations over time is crucial for understanding mesocarnivore population dynamics in the tropics (Wong et al. 2013). In Chapter 4, I combined two surveys from 2009 to 2011 (Wong and Linkie 2013) and 2014 to 2016 (Haidir et al. 2018) so that all study areas are ~85% spatially overlapped. The 5-year interval between these surveys will likely provide a sufficient temporal break for two generations, whilst the data is robust enough for scientific analyses and financially feasible from a management perspective. My analyses strongly suggest the importance of hill forest: forests at elevations between 700 and 1000 m above sea level, where they are further from active deforestation and have a relatively higher abundance of prey species. Deforestation analyses between 2005 and 2014 showed that 5.5% of forest loss occurred within a 15km buffer from study areas. Years with active monitoring activities had lower annual deforestation rates, suggesting non-protection interventions may halt the illegal activities that cause habitat degradation.

From this study, I highlighted three important points: i) the importance of continuing previous research as part of long-term population monitoring efforts; ii) the use of occupancy modelling for effectively assessing population dynamics, potentially making this method, with many of its advanced developments, a new standard, cost-effective mechanism for landscape-scale population monitoring in the tropics; and iii) deforestation and degradation, although occurring outside the national park forest and further from my camera trap study areas, very likely have negative effects on mesopredator populations, and a more collective effort should be made to combat these threats in the future.

Chapter 5, Identifying high value conservation areas: core areas and corridor networks using a multi-species approach as a proxy

In this chapter, I analysed perhaps the largest camera trap data set ever conducted in West-central Sumatra, and possibly Indonesia. A total of 55,856 camera trap-nights, of 671 camera trap sites in seven study areas, successfully logged clouded leopard 211 times at 5-day independent interval detections, while golden and marbled cats were found 137 and 50 times, respectively. This chapter combines camera trap works and occupancy modelling (Cove et al. 2013) with analyses that successfully identified important core areas and corridors in the landscape (Cushman et al. 2018). This was achieved through the following analyses: creating detection/non-detection matrices for species distribution modelling (habitat use prediction) (Kéry et al. 2013); converting habitat use into habitat resistance; and creating least cost path analyses and kernel density estimates for defining core areas and corridor networks, using the highest density estimate for the probability of path used by respective species. I simulated two scenarios of dispersal abilities - 125 km and 250 km - to predict maximum potential core areas and corridors connecting their habitats. Fortunately, both scenarios predicted >80% of all species' core areas were located inside protected forest: KSNP. Nonetheless, deforestation in neighbouring areas is threatening core areas and the existence and connectivity of key corridors.

In this chapter, I successfully used small-medium sized felids as focal species for defining core areas and corridors in the KS landscape. As a result of this study, I have three recommendations: i) use a multi-species conservation approach, specifically on species with high disturbance sensitivities, when identifying areas of high conservation importance; ii) replicate steps and processes in identifying core areas and corridors in other landscapes, while providing space for further improvements; and iii) for future studies, focus on integrating regional-spatial planning to direct conservation and development efforts.

Implications for future wildlife management in Sumatra and Indonesia

Technologies in wildlife population monitoring in the developing world are still being adopted from more developed countries (Cobb et al. 2008, Sintov et al. 2019). Therefore, in order to support wildlife conservation advancements in the tropics, where most biodiversity is found but less developed countries are located, skills and knowledge must be transferred from, and collaborations must be made with, more developed countries (Cobb et al. 2008, Quinn et al. 2012). Collaborative efforts should be respectful, bring benefits to both parties, anticipate the direct advantages for wildlife conservation and management, and develop in-country capacity.

In this thesis, the context of science-driven wildlife conservation, management, and policy, should be initiated by filling information gaps on the bio-ecology and behaviour of priority species (Macdonald 1980, Macdonald 1983, Elwood et al. 2008). For example, Sumatran mesocarnivores from the felid family require further studies to unveil their ecologies, behaviours, population trends, and important areas to be conserved for the long-term viability of their populations (Haidir et al. 2013, Linkie et al. 2013, Pusparini et al. 2014, McCarthy et al. 2015, Sunarto et al. 2015, Risdianto et al. 2016, Haidir et al. 2018). Therefore, future conservation and research efforts in Sumatra should target species within and outside protected areas to avoid population fragmentation and isolation in so called 'conservation area islands' (Shi et al. 2005, Haidir et al. 2020 (in press)).

Using advanced technologies (software and hardware) for wildlife population monitoring can help to effectively manage and protect wildlife in various habitats (O'Connell et al. 2011, Linkie et al. 2013); this would be particularly true for wildlife monitoring in Sumatra, where dense vegetation limits direct observation and remote devices (i.e. camera traps) are used to support non-invasive population monitoring (Nichols et al. 2011, O'Connell et al. 2011). There are quite a few conservation technologies available that require knowledge and skills in adopting, but would make wildlife research and management easier (Elwood et al. 2008), including camera traps, geolocators (GPS collars), SMART software, and conservation drones (Karanth et al. 2006, Koh and Wilcove 2009, Walston et al. 2010)

Frontline wildlife conservation staff in protected areas throughout Southeast Asia should have been assisted by regular capacity building, as this is a compulsory mandate of Aichi Biodiversity Targets under Strategic Goal E, 'Enhance implementation through participatory planning, knowledge management, and capacity building' (Böhm and Collen 2015). Improving human resources in wildlife monitoring and conservation, through supportive government policies and programmes, should be able to maintain 'the wheels' (front line staff) of wildlife conservation, in form trainings, workshops, and knowledge exchanges to disseminating publications (Schmeller et al. 2017). Hence, the importance of long-term wildlife conservation and the monitoring of key/priority species in providing a means to transfer resources from developed countries to biodiversity-rich developing regions (Pereira et al. 2010). Through this study, my overarching goal is to find the best mechanisms for improving existing and potential collaborative efforts beyond my thesis that support knowledge-skill transfer to frontline staff, not only in KSNP, but also across the nation.

Concluding remarks

Through this thesis, I identified three emerging issues regarding mesocarnivore conservation and research: (i) mesocarnivores are more diverse than a single top predator, meaning their associated population indicators are very likely to provide broader and more specific proxies of tropical forest ecosystem health; (ii) mesocarnivores are effective focal species for several study types: ecology and behaviour; core areas and corridors; and proxies for measuring protected area management effectiveness and threats towards wildlife communities within protected areas and surrounding landscapes; and (iii) mesocarnivores are potential ambassador species that could attract finances for conservation efforts across the tropics.

Small-medium sized felids, especially clouded leopard, are inspirational and beautiful animals. Their continued existence in Sumatra's rainforests and across the Sunda plateau is under great threat; a burden which our generation's shoulders must hold. Protecting their habitats, studying their behaviours, and assuring the viability of their populations, is a task of honour for wildlife conservationists, and of human kind. Therefore, it's a worthwhile duty for wildlife conservationists, and mankind, to become adept in showing our gratitude to Mother Nature, The Creator, the God All Mighty.

The references listed here are for Chapters 1 and 7 only, as Chapters 2-5 each contain their own reference lists.

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The majestic yet critically endangered Sumatran tiger,
a flagship species for wildlife conservation in their range countries and global scale

Appendices

Appendix 1

Spikes and pattern in wildlife poaching in Kerinci Seblat

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Examining the shifting patterns of poaching from a long-term law enforcement intervention in Sumatra

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A B S T R A C T

Current levels of illegal wildlife trade for many in-demand species are unsustainable and place them at a heightened risk of extinction. While several Asian protected areas standout for their remarkable successes in tackling poaching, the threat continues nonetheless. We analyse a decade of law enforcement data from a Sumatran protected area to investigate tiger and prey poaching trends, the arrests and subsequent prosecution of those involved. Some 3882 snare traps were destroyed, but a recent spike in tiger poaching revealed that twice the number of snares were annually encountered in 2013 and 2014 than the eight preceding years. We detected a change in the techniques employed for poaching tigers from 2011 onwards, with more frequent encounters of snare trap clusters that contained six or more tiger traps set in a single location. Comparing monthly patterns of poaching within years revealed an increase in deer, but not tiger, poaching during the month of Ramadan. This result confirmed long-held views by the ranger teams that local demand for meat increases in the build up to Idul Fitri, a main Islamic holiday. Finally, from 24 law enforcement operations conducted, 40 tiger poachers/traders were arrested with >90% being prosecuted. However, the fines and prison sentences issued were much lower than the maximum available, and the highest sentence was for firearms possession and not illegal activities towards wildlife. Our site-based study demonstrates what can be achieved, but also identifies areas for strengthening the sub-national and national law enforcement response to an escalating tiger poaching trend.

1. Introduction

Overexploitation by humans threatens about one-third of the endangered species of vertebrates (Rosser & Mainka, 2002), with one of the most serious threats being poaching, which relates to the illegal sale, harvest, transport, possession, purchase and use of wildlife and their parts (Lawson and Vines, 2014). After drugs, weapons and counterfeiting, wildlife and their products represent the greatest illegal traffic. Currently the world is dealing with an unprecedented rise in wildlife poaching that could overturn decades of conservation gains (Dutton et al., 2013). For instance rhino poaching, feeding the unsustainable demand for rhino horn in China and Vietnam, has sharply risen over the past few years, with 1175 rhinos poached in 2015 in South Africa alone (TRAFFIC, 2016). Likewise, the recent extirpation of tigers from flagship protected areas or entire countries has been driven by the high demand created from a rising Asian middle class with a greater disposable income and new found taste for luxury goods that includes wildlife products (Bennett, 2011).

To prevent threatened wildlife from entering into the market, robust site-based tiger protection that involves ranger patrols to dismantle snare traps and deter poachers is essential. Likewise, outside of the forest local informants and law enforcement operations to dismantle trade networks is essential. A recent tiger study from Kerinci Seblat National Park, a global priority Tiger Conservation Landscape in Sumatra, investigated the effectiveness of forest ranger patrols in mitigating the poaching of tiger and their prey (Linkie et al., 2015). While this study

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did not find an overall decline in poaching, it did identify localised declines in response to sustained law enforcement intervention at key patrol sites. The study also raised several previously unaddressed research questions that warrant investigation for potentially enhancing conservation strategies. These include, for example, i) how methods employed by tiger and/or poachers have changed over time and whether this is in response to law enforcement interventions; and, ii) how the number of arrests and the subsequent prosecutions rates have changed and, if so, the reasons for this?

Next, a question arises over which timescale to analyse poaching trends is most revealing. For example, monthly statistics might provide richer information than coarser annual figures that are commonly used. In this regard, insights accumulated from our long-term experiences (10–20 years) of working in Sumatra include ranger team comments on a change in deer poaching intensity during the Islamic holy month Ramadan, when venison is in high demand for the forthcoming Idul Fitri celebratory feast. This is a time when food prices, particularly meat from reared animals, increases by 10–30% in local markets. So, the motivations for hunting may be driven by consumer preference, such as cost or taste, and therefore require specific seasonal responses (Luskin et al., 2014).

The purpose of this study is to assess whether the nature of tiger and prey poaching is changing. We select Kerinci Seblat because it is, we argue, representative of other forest tiger landscapes and protected areas in Southeast Asia and has a long-term law enforcement dataset. Thus, from 2005 to 2014, we aim to assess: i) annual poaching patterns of tigers and their ungulate prey base; ii) monthly poaching patterns within the study years; and, iii) fines and prosecutions for trading tiger body parts. The first aim primarily sets out to determine whether poaching intensity and the methods employed by poachers towards targeting either tiger or its prey species has changed over time. The second aim sets out to test whether there is change in poaching intensity for either tiger or deer during specific times, such as Ramadan. The third aim is intended to answer whether the number of arrests and prosecutions has changed over time. Finally, we discuss the reasons for these changes and how the law enforcement response should be modified to tackle an evolving threat.

2. Materials and methods

2.1. Study area

The 13,800 km^2 Kerinci Seblat National Park spans the Indonesian provinces of West Sumatra, Jambi, Bengkulu and South Sumatra. Its forests and wildlife comprise a single management unit that is under the Ministry of Environment and Forestry. The National Park has an elevation that ranges from 175 m asl to 3805 m, but its forest ranger teams primarily conduct patrols from 175 m asl (lowland forest) to 1500 m (montane forest). The park has an elongated shape that is 375 km long and typically <35 km wide, with an enclave in the central section which is not part of the protected area. In combination, these features create a long boundary and make the forest highly accessible to poachers. Kerinci Seblat National Park is a UNESCO World Heritage Site and a Level 1 Tiger Conservation Landscape, in recognition of its abundant and widespread tiger population (Dinerstein et al., 2007; Linkie et al., 2006; Wibisono et al., 2011).

In the year 2000, two Tiger Protection and Conservation Units (referred to as ‘patrol teams’ hereafter) were established by the National Park management authority and the international NGO Fauna & Flora International (FFI). These patrol teams steadily increased until 2005–2006 when five units were established, all of which continue to the present day. A sixth team was active in 2006–2007 and then 2013 onwards. A team typically consists of four rangers, but may on occasion be five rangers. To select these rangers, there is an initial 1–3 month training phase that is used to evaluate candidates, with the best performing ones recruited full-time to the TPCU programme. This is followed by formal training that includes SMART-based patrolling, species sign recognition, sourcing information on threat and wildlife crime and navigation (map reading and GPS use). However, much of the training is on-the-job to enable learning from experienced peers. The TPCU leaders have between six and eight years' experience and within teams the amount of experience ranges from newly graduated rangers to those who have been working since the beginning of the programme in 2000 (*i.e.* >15 years'). Annual evaluations on individual team and ranger performance are conducted, which may result in rangers being moved between teams to ensure each has similarly high levels of field experience and high performing staff.

We selected 2005 to 2014 as the focal period for this study because it coincides with when most of the patrol teams were active. The primary aim of the patrol teams is to secure the population of wild tigers inside the National Park and its adjacent forests through reducing the threats from poaching, domestic trade of tiger and prey, and conflict with forest-edge communities.

2.2. Field data and analysis

Two main types of data are used in this study: i) patrol team data on the location and number of active snare traps set for tigers and their prey (typically sambar deer (*Rusa unicolor*), muntjac (*Muntiacus* sp) and sometimes serow (*Capricornis sumatrensis*)), for which data were aggregated by month and year; and, ii) records of law enforcement operations that set out to arrest tiger poachers and traders and which included information on the outcome of these arrests.

Field data were compiled using information recorded in patrol team logbooks and data sheets collected by five teams covering eight districts. On patrol, a team of four rangers would record its route, using a GPS unit and compass, on a 1:50,000 paper topographic map. Key signs of encounters were also recorded in logbooks and these included indications of snaring or other forms of poaching (whether for mammals or birds) and the presence of threats to habitats, such as illegal logging. Two types of snare trap were recognized and these were primarily differentiated by the construction of the snare anchor, its strength and the material used. A metal cable indicated a snare trap set for a tiger, whereas a nylon rope would conventionally be set for ungulate prey.

From 2005 to 2014, data from patrol team logbooks were used to calculate the number of patrols conducted during each year. Patrol effort was measured as the number of patrol kilometers walked, team days expended and number of patrol trips. The inter-dependency of these three metrics was measured using a Spearman's rho test to identify a single metric for patrol effort to be used in the subsequent analyses. For each study year, the absolute abundance of snare traps set for tigers and for their prey was determined, from which the catch-per-unit effort of the ranger teams was calculated by dividing by patrol effort. To determine whether and how the number of patrols detecting signs of tigers and prey poaching changed over time, a Spearman's rho test was performed. The temporal pattern of tiger snare trap clusters was measured by calculating the number of snare traps set within a 1 km radius for each year from 2005 to 2014. Cluster categories were 1–2 traps, 3–5 traps and >6 traps. These category sizes were determined through consultations with the patrol teams on the snaring patterns that they had observed over the study period. In the earlier study years, the teams consistently noted that one or two traps were most frequently encountered, but more recently larger clusters of snares were being encountered. We sought to test this using a Fisher's exact test on whether there were non-random associations between the occurrences of these cluster types across years.

To investigate changes in poaching intensity across the months for each of the years, we separately calculated year-wise circular means and associated 95% confidence intervals (CIs) for the number of tiger and prey snare traps removed by anti-poaching patrols. A Rayleigh's test was performed using the ‘circular’ package in R (Agostinelli & Lund, 2013) to test whether there was significant clustering in the monthly snare removal data, including during the Ramadan period (Batschelet, 1981). During the fasting month of Ramadan, a time when field activities generally slow down, a financial incentive is provided by the project to maintain forest patrolling intensities that are similar to those in other months. Thus, to compare between months we used the catch per unit effort from patrolling.

Next, information on the suspected number of tigers poached in the forest was compiled. These estimates were derived from the evidence found at snare traps that had been triggered and had either a tiger carcass still present in the trap or its body parts, such as flesh and skin for recent kills or hair for older kills. The patrol team did not formally record tiger poaching incidents reported by its well-established and trusted local informant network unless these could be verified, first-hand, by team personnel. However, these reports were used as guidance for assessing levels of threat to support appropriate strategic responses including patrols or law enforcement where evidence might be secured. We also recorded information on the number of live tigers caught in snare traps that were handled by the patrol teams.

For each study year, the number of active investigations into tiger poaching, law enforcement operations arising from these investigations, and then arrests and prosecutions was quantified. For arrests, information on the number of suspects, the type of suspect (poacher or trader), and the goods confiscated was recorded. For prosecution, the court outcome (released, fine and/or prison sentence) was recorded. These cases were tracked and data on the court verdicts compiled by the Tiger Protection and Conservation Unit programme for Kerinci Seblat National Park.

3. Results

3.1. Patrol effort

From 2005 to 2014, 757 anti-poaching patrols were conducted on foot totalling 3713 patrol team days and 13,947 km walked. The annual average patrol effort was 75.7 ($\pm$13.93, SD) trips, 371.3 ($\pm$60.95) team days and 1394 km ($\pm$353.85) walked. There was no significant change in patrol effort between years, as measured by the number of kilometers walked ($\rho_8 = -0.018$, $P = 0.960$) or team days patrolled ($\rho_8 = 0.515$, $P = 0.128$). However, the number of anti-poaching patrol trips ($\rho_8 = 0.661$, $P = 0.038$) significantly increased because of an intensified patrol effort in 2013 and 2014. The annual number of patrols was significantly and positively correlated to the annual distance patrolled ($\rho_8 = 0.661$, $P = 0.038$) and the number of patrol days ($\rho_8 = 0.781$, $P = 0.008$). Therefore, only patrol effort, as measured by the number of field days, was used in the subsequent analyses.

Comparing monthly patrol effort allocation within each year revealed no significant clustering of the number of patrol days per month (Rayleigh's test for all datasets; $P > 0.05$; Fig. 1). Monthly patrol effort remained constant throughout each year.

3.2. Annual poaching trends

Across the 10 year study, the patrol teams detected and destroyed 231 tiger snare traps and 3652 prey snare traps. During this period, there was no significant change in the number of patrols that encountered poaching of tigers ($\rho_8 = 0.2$, $P = 0.580$). However, in 2013 and 2014, patrols detected twice the number of tiger snare traps on average than the preceding years, revealing an increase in tiger poaching (Fig. 2). The average annual encounter rates of tiger snare traps removed greatly increased from one per 33.45 ($\pm$16.3, SD) patrol days (2005–2012) to one per 7.32 ($\pm$0.106) patrols days (2013–2014). In absolute terms, the ranger teams destroyed more tiger snare traps in 2013 and 2014 (n = 124) combined than the eight preceding years (n = 107). For tiger prey, there was no change in the number of snare traps encountered over time ($\rho_8 = -0.15$, $P = 0.676$). The mean annual encounter rate of prey snare traps was one in 1.57 ($\pm$1.065) patrol days.

There was an apparent change in the techniques employed for poaching tigers during the study period (Fisher's exact test, $P = 0.007$). From 2011 to 2014, a higher percentage of snare trap clusters with more than six tiger traps set per location being recorded, despite the search tactics of the patrol teams remaining unchanged (Fig. 3). In the preceding years this technique was only ever encountered once, in 2006.

Accurately quantifying the number of tigers lost to poaching was difficult because the number of snare traps destroyed in the forest indicated poaching pressure rather than the number of individuals killed. The ranger team separately recorded skeletal remains of two individual tigers that had been caught in a snare trap. In these cases, only the skin had been taken because at that time (before 2012) tiger pelts were the primary demand for the illegal domestic trade, whereas bones were not in high demand. The teams suspected that an additional 22 Sumatran tigers had been snared and killed, based on evidence gathered in the field (such as dismantled snare trap placements with tiger hair) and other crime scene evidence including, in the more recent incidents, decaying flesh and skin fragments from the on-site butchering process. This total represents only the detected incidents where a patrol unit was certain that it was a tiger. From these field records of 24 individuals, four

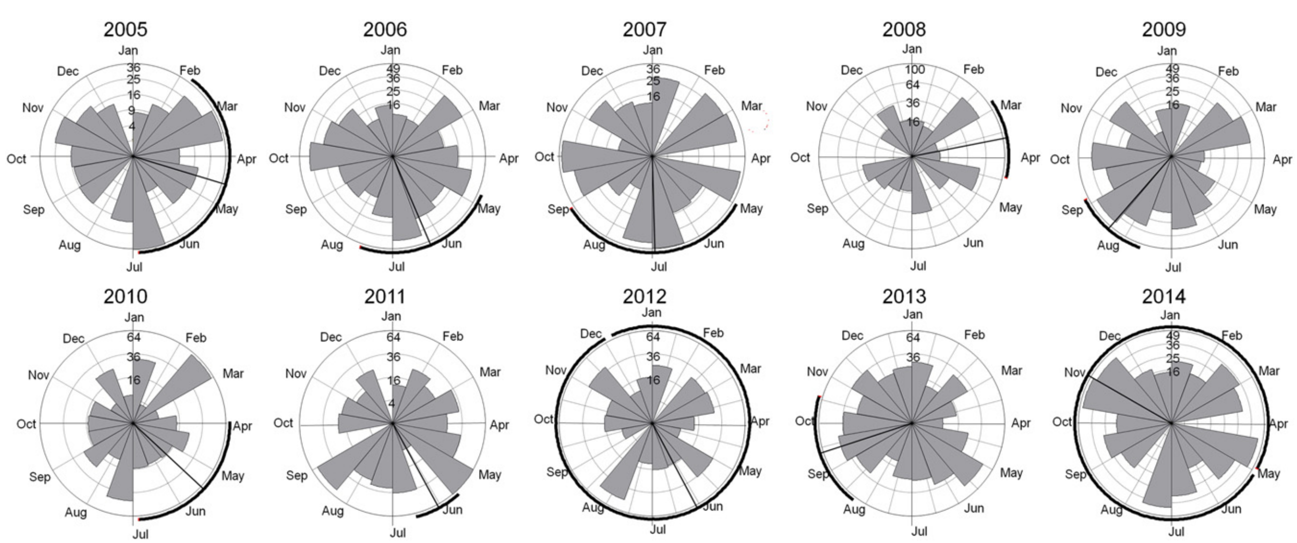

Fig. 1. Annual comparison of patrol effort (days) between months with associated circular means (black line), 95% confidence intervals (black arc).

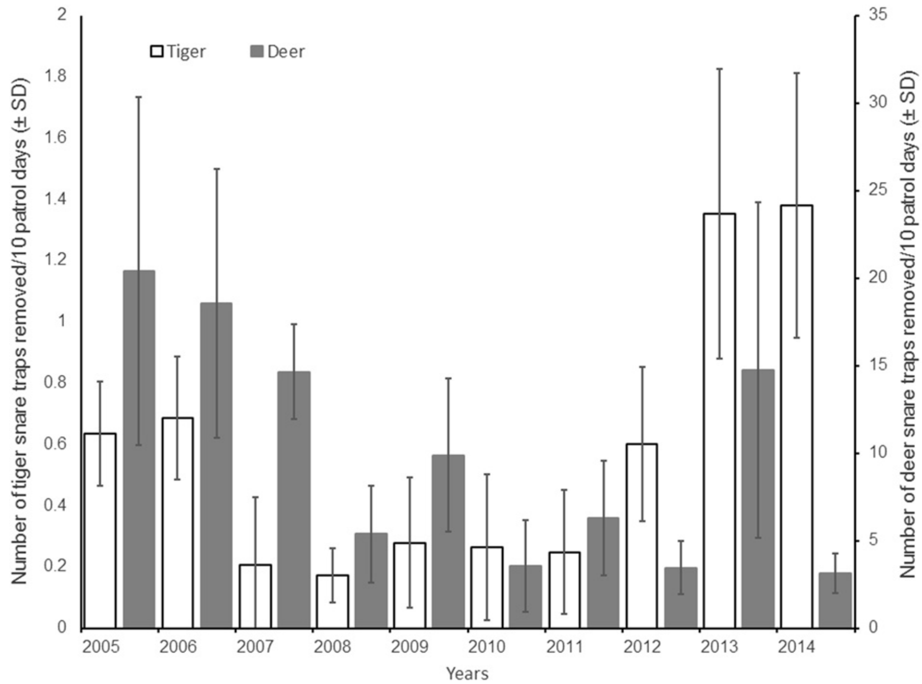

Fig. 2. Change in the mean number of tiger and prey snare traps annually removed from 2005 to 2014 in the Kerinci Seblat landscape.

tigers were suspected to have died from 2005 to 2010, whereas there were 20 snare-related tiger deaths from 2011 to 2014.

Records on other large-bodied mammal species accidentally caught in tiger snare traps were routinely kept from 2011 onwards. Here, the patrol teams discovered 12 sun bears (one of which escaped from a snare but left behind a severed foot) and eight dead Asian tapirs (there is no local demand for this animal's meat), with an additional two tapirs in separate incidents being successfully released from a snare trap by a different patrol team. The capture of these species is due to their ranging patterns that, like the tiger, include traversing ridge trails in the mountainous landscape of the National Park.

During the study period, there were three cases where patrol units, with veterinary backup, rescued a live tiger from a snare trap and evacuated the animals for *ex-situ* veterinary treatment. Only one of these animals could subsequently be released, one died from snare-related gangrene and the third was unable to be released back into the wild due to the severity of the snare injury. Next, in a fourth case, a snared tiger was rescued from the trap, treated on-site by a ranger-veterinary team and then released. In a fifth case, a tiger involved in a low-grade but potentially dangerous human-tiger conflict situation was caught with the purpose of relocation but was removed from the wild because its foot was found to have been almost completely severed in a poacher's snare, while in a sixth case, a tiger rescued after roaming in farmland far from the park-edge was found to have suffered serious gunshot injuries to its abdomen. Both these animals subsequently died while undergoing emergency veterinary treatment.

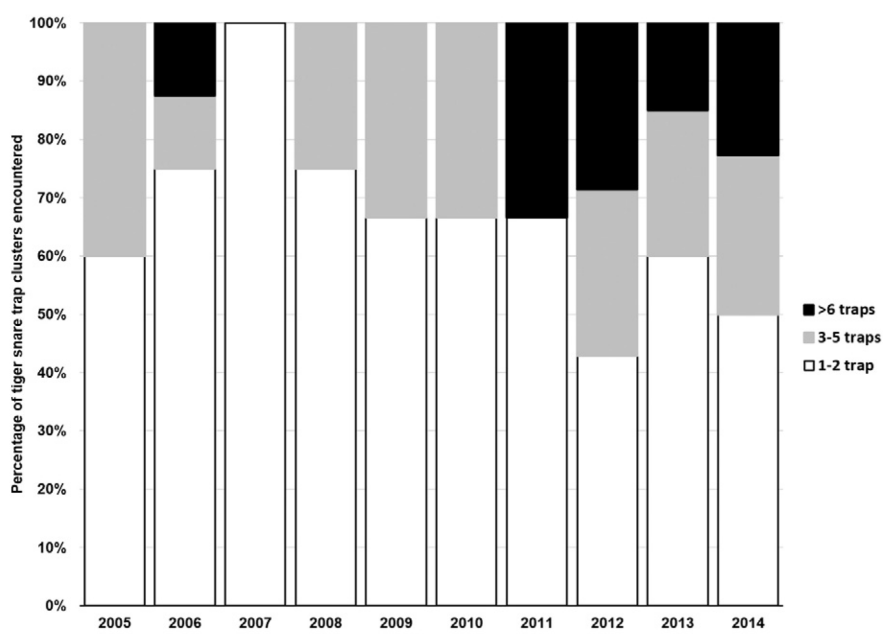

Fig. 3. Percentage of tiger snare trap clusters encountered from 2005 to 2014 in the Kerinci Seblat landscape.

3.3. Monthly patterns

During the study, there was no significant clustering in the removal of tiger snares between months for each the different study years (Rayleigh's test for all datasets; $P > 0.05$; Annex 1). For the number of prey snares removed, there was significant clustering within certain months (Rayleigh's test for all datasets; $P < 0.001$; Fig. 4 and Annex 1). Comparing within years, and controlling for patrol effort, most (47–85%) prey snare traps were removed 4.87 ± 0.46 weeks before Idul Fitri, with the exception of the year 2008 where this relationship was not found.

3.4. Arrests and prosecutions

From 2005 to 2014, 619 active investigations into tiger poaching and trade were conducted, with an average of 62 investigation reports per year being logged ($\pm$15.6, SD). These investigations led to 24 law enforcement operations that resulted in 40 suspected tiger poachers (n = 19) and traders (n = 21) being arrested (Fig. 5). Of these, 37 suspects were found guilty and prosecuted, while one received a formal warning (for trading in fake rhino horn), one outcome was unknown and one case was handled by the military because the suspect in question was one of its own personnel. Here, the military officer was sentenced to three months corrective custody by a military court.

Outside of the forest in the districts and provinces that include Kerinci Seblat National Park, law enforcement agencies recovered no <22 tiger skins or stuffed tigers, but also tiger bones and body parts of other protected wildlife (two clouded leopard *Neofelis diardi* pelts, one stuffed sun bear *Helarctos malayanus*, one live Sunda pangolin *Manis javanica* and numerous dead sambar and muntjac body parts (flesh, heads and antlers)). Of the 37 people prosecuted, all received a prison sentence and some (43.2%) were also fined. These prosecutions amassed 442.5 prison months (mean/person = 12.0 months, min.–max. = 3.0–36.0) and IDR21.9 million in fines (approximately USD 1683, mean = USD106/person, min.–max. = USD 8–383).

The average prison sentence for a trader (11.6 ± 9.5 months, SD) was not significantly different to that issued for a poacher (12.3 ± 10.9 months; Mann-Whitney *U* test: $P = 0.642$). There was no significant difference between prison sentences for being caught with a tiger skin or a skin and skeleton ($P = 0.935$). The highest prison sentence was for three poachers/traders who were caught with a tiger skin and three pistols (32.0 months in prison and a US$37 fine per person). In two court cases, six people were prosecuted for handling clouded leopard body parts, for which the prison sentences were 3.5 and 5 months.

4. Discussion

Poaching pressures and techniques used by poachers vary between species, countries and even protected areas within the same country. Differences in terrain, accessibility and population abundance between protected areas and landscapes have a strong influence on the distance travelled by poachers and therefore the location and distance required to be patrolled. In formulating an effective anti-poaching response, lessons must be collectively drawn from the strategies employed by other law enforcement projects (Hotte et al., 2015; TDNPWPC, 2012). Here, our study adds to this particular conservation science knowledge base. We recorded an escalation in tiger poaching and an apparent change in poaching tactics employed over the 10 year study. We also recorded relatively high levels of success in being able to apprehend and prosecute tiger poachers and traders year after year and over a decade. Yet, the sentences issued fell far below the maximum fine or prison term available and indicates where the law enforcement should be strengthened.

4.1. Study limitations

Our study has several possible limitations. First, it is focussed at a macro-level and although our intention was to treat the protected area as a whole, the analyses would not have detected subtle changes occurring at a finer scale, such as within patrol team sites (Linkie et al., 2015). Secondly, we used snare trap encounter rates to monitor poaching pressures and this did not control for varying snare trap detection probability either between patrol months or years (Keane et al., 2011). However, unlike in a previous Kerinci Seblat analysis where detection probability was accounted for, our study was not intended to evaluate the law enforcement intervention *per se*, which would have also required controlling for the influence of confounding variables (Linkie et al., 2015). Here, we argue that if a bias existed then it should generally be consistent across all years because poachers still set snare traps in where there were natural channellings in the forest, such as ridge trails. Thirdly, our temporal analysis of monthly poaching patterns tested for the relationship with one variable, the occurrence of Ramadan. It may have been possible that pattern is explained by other untested seasonal factors, although we are unsure of what these might be.

4.2. Poaching patterns

Linkie et al. (2015) demonstrated the effectiveness of the Kerinci Seblat ranger teams' approach in mitigating poaching in areas most

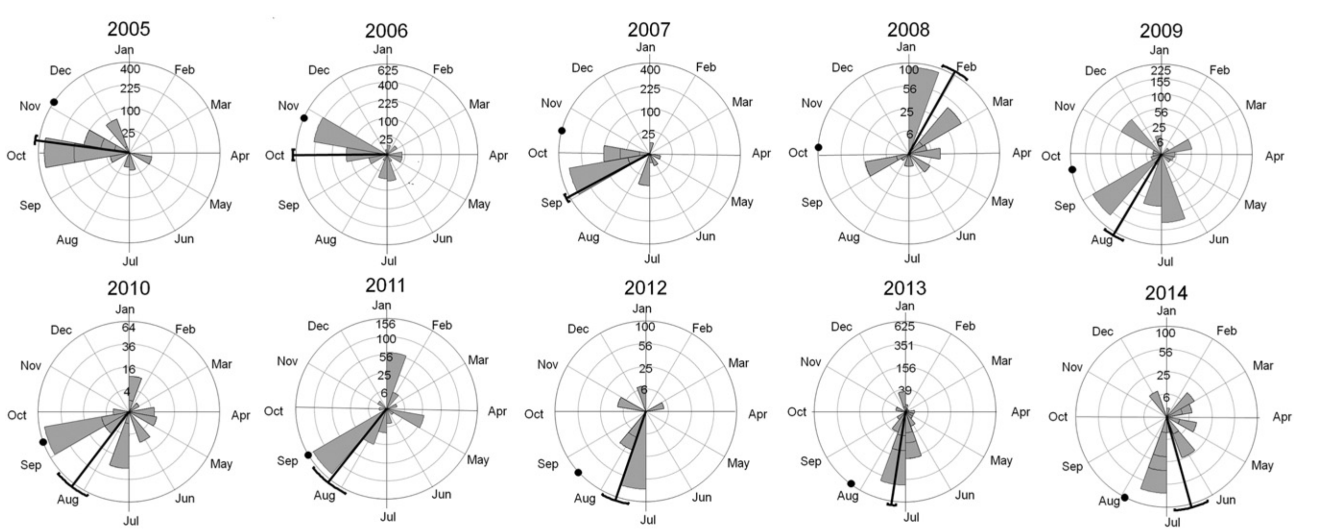

Fig. 4. Comparison of deer snare removal between months with associated circular means (black line), 95% confidence intervals (black arc) and the 1st day of Idul Fitri (black dot).

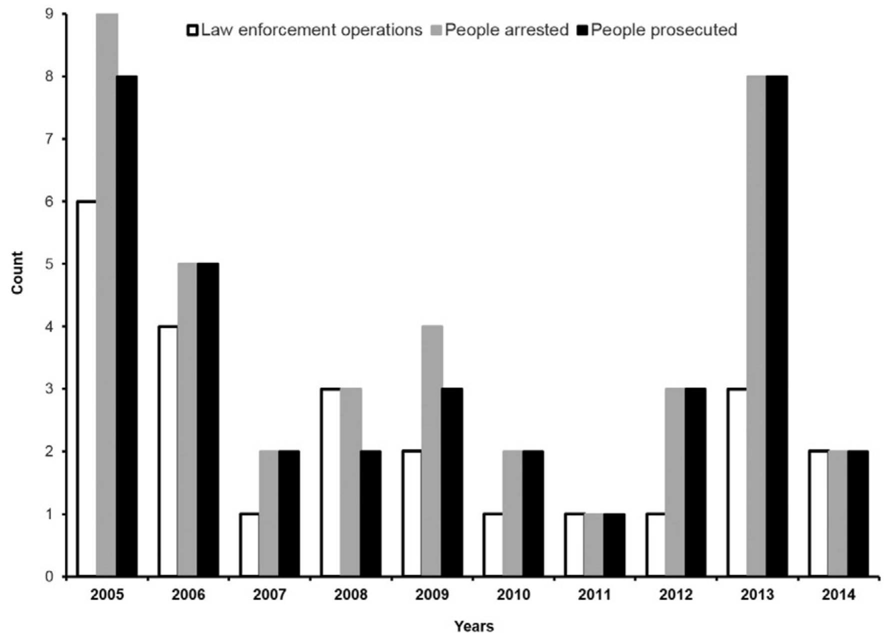

Fig. 5. Law enforcement operations, arrests and prosecutions from 2005 to 2014 in the Kerinci Seblat landscape.

frequently patrolled from 2000 to 2010. Our analysis of patrol results from similar areas in more recent years clearly shows how since 2013 poaching activity has dramatically increased for tigers and with a tendency to now set tiger snare clusters with more than six traps per location. Our unpublished informant data indicates that this increase in tiger poaching is facilitated by a revival of old tiger poachers who are bringing in younger family members in response to the higher demand and prices now offered for tigers. The majority of snares recorded since 2012 are thought to have been set by < 12 poaching gangs and < 40 individuals on the basis of long-term informant monitoring and investigations. To put this number into context, there are approximately 3.5 million people living in 14 park-edge districts (BPS 2016). Further, a recent and deeply worrying example of a spike in opportunistic poaching is provided by the helmeted hornbill (*Rhinoplax vigil*). A sudden spike in demand from east Asian countries for the bird's 'red ivory' casque has resulted in its near extinction from the jungles of Sumatra and Borneo over five years, as witnessed by its Red List status being upgraded from Least Concern directly to Critically Endangered (Collar, 2015).

Over our 10 year study period, the remote island of Sumatra has undergone a dramatic transformation. The infrequent and poorly coordinated illegal wildlife trade from 2005 has been replaced by sophisticated organized criminal networks that operate island-wide and are capable of, for example, storing and shipping five tons of frozen pangolin or importing ivory and lion canines from Africa (WCS, 2015; Williams et al., 2015). New networks and trade routes are continually formed and the law enforcement tactics must respond to dismantling them. As an example, from 2011 to 2014 investigations from Kerinci Seblat advised of strong links between organized poaching and trade in Sumatran tigers and the trade in agarwood (*Aquiliaria* sp) for onward sale to cities in Riau province, eastern Sumatra, but from 2015 to 2016 this had changed to sales in West Sumatra and Medan (D. Martyr pers ob).

Our fine scale temporal analysis confirmed a long-held view of the ranger teams that demand for deer meat increases during Ramadan. This is not surprising because a parallel example exists in the Christian parts of the Indonesian island of Sulawesi where bushmeat hunting significantly increases during the build up to Christmas (Milner-Gulland and Clayton, 2002). While there is an important role for faith-based approaches to play in Indonesia (McKay et al., 2014), it is still essential to ensure that ranger patrols continue to detect and remove snare traps to maintain a healthy tiger prey base. Further, Ramadan can be a gruelling month for rangers who fast, meaning that they abstain from consuming food and drink during daylight hours. Here, the Kerinci Seblat programme offers an innovative management solution to maintain patrol effort through the 'Kerinci Great Snare Sweep' competition. Teams score varying points for the number and type of active snare traps destroyed, with the winning team receiving half a month's salary as a bonus. As our analysis showed, patrol productivity for the six teams did not lessen during the Ramadan period.

4.3. Law enforcement

The arrest of tiger poachers and traders is dangerous and requires meticulous planning. Thus, the 37 people arrested through the Kerinci Seblat Programme represent some of the hardest fought conservation achievements. Further, there was an almost 100% prosecution success rate for those arrested. The involvement of select patrol team members in the arrests and initial interrogation of poacher/traders also enabled them to gain valuable insights into the changing poaching dynamics that is used to continually adapt the law enforcement patrols. For example, in all of the high-intensity poaching cases (>6 snare traps per cluster), an examination of the snares and subsequent information collected, strongly suggested that the poachers had been supplied with the expensive snare cables by traders and buyers. Unfortunately, with illegal wildlife traders now frequently facilitating tiger poacher activities through the provision of snare cables and even guns, the loss of a capital outlay through a patrol team's effort—which may amount to USD30 or more per tiger snare—detection and destruction of snares alone is no longer a significant deterrent to some of the most active poaching gangs (Keane et al., 2011).

The maximum fine and sentence for illegally handling a protected Indonesian species is five years and/or IDR100 million (approximately USD 7685). Yet, our analysis of the fines and prison sentences revealed that the average fine issued (USD 106) was equivalent to a month's income for a poacher and therefore not a strong deterrent. This is clearly an aspect of the law enforcement approach that needs to be strengthened. Similarly, the average prison sentence issued was one year in our study, with a maximum sentence of only three years. This higher sentence was actually influenced by the defendant being in possession of an illegal firearm and not the confiscated tiger body parts. Under the current Indonesian species conservation law (UU No 5/1990), there is often a misperception that possession of snares is not a criminal offence and species law enforcement action can only be launched if a protected species falls victim to snare poaching and the poacher is arrested in possession of the carcass or specific body parts. As a consequence, where people were encountered in the forest, even when suspected to be connected to active snare poaching being detected, the patrol teams were not confident that such cases would be accepted by state or police investigators, who are responsible for case development, or subsequently by court prosecutors. Thus in certain districts and provinces around Kerinci Seblat these cases were unlikely to proceed smoothly through the legal process and so the patrol teams would only search the suspects and issue a formal legal warning for entering the National Park without a permit. We recommend specialized training for prosecutors and judges to ensure that the different types of wildlife crimes are prosecuted and to the full extent of the law.

5. Conclusions

Sumatran tigers, like tigers from elsewhere in Southeast Asia, occur at naturally low population densities making them vulnerable to the effects of poaching that can depress these densities to critically low levels. It is therefore essential that preventive law enforcement actions are in place and effective. A recent study has shown that even with a long-term and robust ranger patrol strategy in operation, a well-protected but low density tiger population may still take a long time to recover (Duangchantrasiri et al., 2015). Site-based protection efforts must therefore be sustained or, as found in Kerinci, increased in response to the escalating tiger poaching (Walston et al., 2010).

Acknowledgements

We dedicate this paper to Suhardi, a longserving and highly active tiger team member who passed away recently. We are grateful to the Indonesian Ministry of Environment and Forestry for its lead role in this programme, especially the management and staff of Kerinci Seblat National Park; Ir Wandoyo, Ir. Listya Kusumawardhani, Ir. Soewartono, Ir Suyanto, Ir Luhut Sihombing and Ir Arief Toengkagie. FFI gratefully acknowledges the long-term support and commitment of the US Fish and Wildlife Service, Save the Tiger Fund, 21st Century Tiger, Dreamworld, Australia Zoo and Panthera. The write up of this study was partially funded by a World Animal Protection grant to WildCRU.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.10.029.

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Appendix 2

Multi scale habitat analyses for species distribution modelling

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Multi-scale habitat selection modeling identifies threats and conservation opportunities for the Sunda clouded leopard (*Neofelis diardi*)

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ABSTRACT

Clouded leopards are among Asia's most widely distributed felids, but also among its least known and most vulnerable. Clouded leopards occur in some of the most rapidly disappearing forests in the world, yet a comprehensive assessment of their status and habitat use is lacking, which in turn limits identification of their priority conservation needs and capacity to act as umbrella species for conserving associated forest biodiversity. To address this need for the Sunda species (*Neofelis diardi*), we applied multi-scale modeling to identify both key environmental variables influencing habitat use and optimal scales of relationship with these variables. We detected clouded leopards at 18.3% of 1544 camera stations and 17 of 22 sampling locations on the islands of Borneo and Sumatra. Multi-scale GLMM revealed that recent forest loss and large-scale plantations strongly and negatively influence clouded leopard detection. Our findings also suggest that higher elevations and ridges are important components of *N. diardi* habitat use. We illustrate how scale optimization of habitat use can provide critical information for characterizing the requirements of protected areas, and identify core habitat patches and connectivity gaps in need of future protection. Our findings indicate greater challenges facing clouded leopards on Sumatra, including higher poaching pressure, greater fragmentation, and roughly half the habitat area available to *N. diardi* on Borneo. This research contributes vital insights to assist in prioritizing habitat conservation networks for the protection of this vulnerable felid and the forest biodiversity for which it is an ambassador species.

1. Introduction

Accelerating rates of deforestation, fire, and land conversion (e.g., to large-scale oil palm plantations and *Acacia* monocultures), have rapidly transformed the natural landscapes of Southeast Asia, with dire consequences for native fauna (Tacconi, 2003; Cushman et al., 2017). Clouded leopards are among Asia's most broadly ranging and charismatic felids, but also among its rarest, least understood, and most vulnerable (Ross et al., 2013; Hearn et al., 2016). Clouded leopards occur throughout Southeast Asia, from the Himalayan foothills in the west to southern China in the north and east, and extend south, in the form of the Sunda species, into the islands of Borneo and Sumatra. In 2006, genetic and morphological analyses led to splitting the species, with *Neofelis nebulosa* occupying mainland Southeast Asia, and Sunda clouded leopards (*N. diardi*) occurring on Borneo and Sumatra (Buckley-Beason et al., 2006; Kitchener et al., 2006; Wilting et al., 2007). The elusive nature of these two species poses a research challenge, and there remains sparse information on the ecologies of either species.

Both the mainland and the Sunda clouded leopard occur across

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broad geographical ranges, prompting questions of how their habitat uses, population densities, and intra-guild interactions vary between regions. Considering that clouded leopards occur in the most rapidly disappearing forests in the world (Miettinen et al., 2011; Gaveau et al., 2016), understanding the habitat preferences of these threatened felids is critical for mitigating their likely deteriorating conservation status. Clouded leopards are listed as Vulnerable on the IUCN Red List of Threatened Species in accordance with their high extinction risk (Hearn et al., 2015; Grassman et al., 2016; Hearn et al., 2016). While at least mainland clouded leopards are threatened by direct exploitation of pelts and bones for medicine (D'Cruze and Macdonald, 2015; Min et al., 2018), both species face grave indirect threats from habitat loss and poaching of their prey. In particular, very high rates of deforestation across their range drive loss, fragmentation and degradation of habitat quality (Cushman et al., 2017; Macdonald et al., in press). In this paper we aim to identify the primary habitat requirements as well as limiting factors and sources of threat for the Sunda clouded leopard across its range. Furthermore, the iconic charisma of these cats combined with their forest-dwelling habits make them ambassador species (Macdonald et al., 2017) whose conservation provides an influential co-benefit to broader forest conservation programmes (Collins et al., 2011).

There have been several local estimates of the abundance of Sunda clouded leopards based on camera trapping (Wilting et al., 2012; Cheyne et al., 2013; Sollmann et al., 2014), and we recently published the first robust estimate of their population size for the Malaysian state of Sabah (Hearn et al., 2017). Low detection rates observed in a recent survey of Indonesian Borneo (Cheyne et al., 2016) suggest *N. diardi* may be less abundant in south and eastern Kalimantan compared to Sabah in the north. Additionally, Hearn et al. (2018a) conducted a multi-scale path level analysis of *N. diardi* movement in an anthropogenically disturbed landscape in Sabah, which showed that clouded leopard movements are closely associated with forest habitats with closed canopies and resisted by plantation habitats with open canopies. Yet a comprehensive, range-wide assessment is lacking.

To address this need, we developed a multi-scale habitat model that encompasses the full range of *N. diardi* across Borneo and Sumatra. Multi-scale habitat modeling is critical to correctly identify the drivers and meaningful scales of relationship with patterns of species distribution (Levin, 1992; Thompson and McGarigal, 2002; Grand and Mello, 2004), yet a recent review showed that < 5% of all recent habitat modeling papers used robust approaches that optimize multivariate scale relationships (McGarigal et al., 2016). Given *N. diardi's* relatively large home range estimates (Hearn et al., 2013, 2018a), we expected to find that clouded leopards are utilizing key habitat components (e.g., closed canopy forest) at the broadest scales included in our study (8–10 km). The primary goals of this paper were therefore to (1) identify key environmental and anthropogenic variables contributing to Sunda clouded leopard habitat use, (2) determine the spatial scale at which each variable most strongly influences clouded leopard detection, and (3) investigate differences between clouded leopard presence and habitat associations on Sumatra and Borneo. These findings provide critical information to assist in prioritizing habitat conservation networks for the protection of this vulnerable felid, and more broadly demonstrate the value of multi-scale modeling for characterizing the requirements of protected areas.

2. Methods

2.1. Data collection

From 2007 to 2016, our field teams conducted intensive and systematic camera trap surveys of *N. diardi* in 22 sampling locations across the islands of Borneo and Sumatra (Fig. 1, Tables 1 & S1). Sampling locations include sites previously selected for intensive autecological research focused on clouded leopards and their associated guild. Additional sites were chosen to encompass a representative sample of the spectrum of forest types, elevations, and anthropogenic disturbances present throughout their range. Across the 22 sampling locations, camera arrays comprised an average area of 91.63 km^2 (± SE 14.97). Within Borneo, sampling effort was focused within the Indonesian provinces of Kalimantan in the south and southeast and the Malaysian state of Sabah in the north. Throughout the remainder of this paper, 'regions' is used in reference to Sumatra, Sabah, and Kalimantan. To improve rates of detection in densely forested landscapes, camera traps were primarily deployed where breaks in the forest allowed for greater visibility, for example along forest trails cut by people (either well-established or newly cut), natural ridgelines, or disused logging roads, where available. Furthermore, evidence from our preliminary model of habitat use in Sabah suggests *N. diardi* select for these habitat types (Hearn et al., in review). Camera stations were spaced approximately 1.0–2.0 km apart, with paired camera units positioned approximately 40 cm above the ground. Grid size, camera spacing, and study duration were based on the home range size of clouded leopards, consensus views on the closure assumption, and attaining the largest grid feasible within logistical and financial constraints (Penjor et al., 2018), The field surveys deployed 1544 camera stations, with 801 in Borneo (317 in Kalimantan and 484 in Sabah) and 743 in Sumatra (Kerinci Seblat) (Table 1).

2.2. Predictor variable compilation

Based on previous studies of Sunda clouded leopard ecology, a suite of 12 predictor variables associated with *N. diardi* habitat use, behaviour and sources of threat were selected (Table S2; Hearn et al., 2016, 2017, in review; Penjor et al., 2018; Sollmann et al., 2014; Macdonald et al., in review). These primary variables were further transformed into a total of 60 more biologically informative predictor variables using class and landscape level spatial statistics (Table S2). A SRTM (Shuttle Radar Topographic Mission) digital elevation model (Jarvis et al., 2008) was transformed into several variables that account for topographic heterogeneity (roughness, slope position, and compound topographic index (CTI)) using the Geomorphometry & Gradient Metrics Toolbox (Evans et al., 2014) in ArcGIS 10.2.2 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011). CTI, also referred to as topographic wetness index (TWI), is a measure of flow accumulation (Beven and Kirkby, 1979). Lowlands with large drainage areas have high CTI, whereas mountaintops and ridgelines are associated with lower CTI values. To account for anthropogenic impacts, we included human footprint (WCS and CIESIN, 2005) and human population density layers (CIESIN and CIAT, 2016). Percent forest cover (Hansen et al., 2013) was reclassified into non-forest (0–20%), open forest (20–40%), and closed forest (> 40%). Similarly, land cover was classified into 13 categories (Miettinen et al., 2012). For reclassified forest cover layers, land cover classes, forest loss, and protected areas, we calculated several landscape metrics using FRAGSTATS (McGarigal et al., 2012). Class level statistics included percentage of the landscape occupied by each variable class (PLAND) and the correlation length of each class (GYRATE_AM; i.e., average distance an individual can travel within habitat patches from a random starting point moving in a random direction). Five landscape level statistics (McGarigal et al., 2012) were generated to investigate how the spatial composition and configuration of the landscape influenced clouded leopards at each spatial scale, including aggregation index (AI), edge density (ED), contrast weighted edge density (CWED), patch density (PD), and largest patch index (LPI). All raster layers were re-sampled to 250 m resolution. Finally, poaching risk was estimated as the total number of hunters or poachers detected at each camera station, standardized by camera effort. Hunting of any bird or mammal species is prohibited by law in our sampling locations, and no human residences occurred in or near our sites. Therefore, we assumed that people photographed carrying shotguns, spears, and/or traveling with dogs were poachers; unarmed park staff, field researchers, and tourists were clearly distinguished and

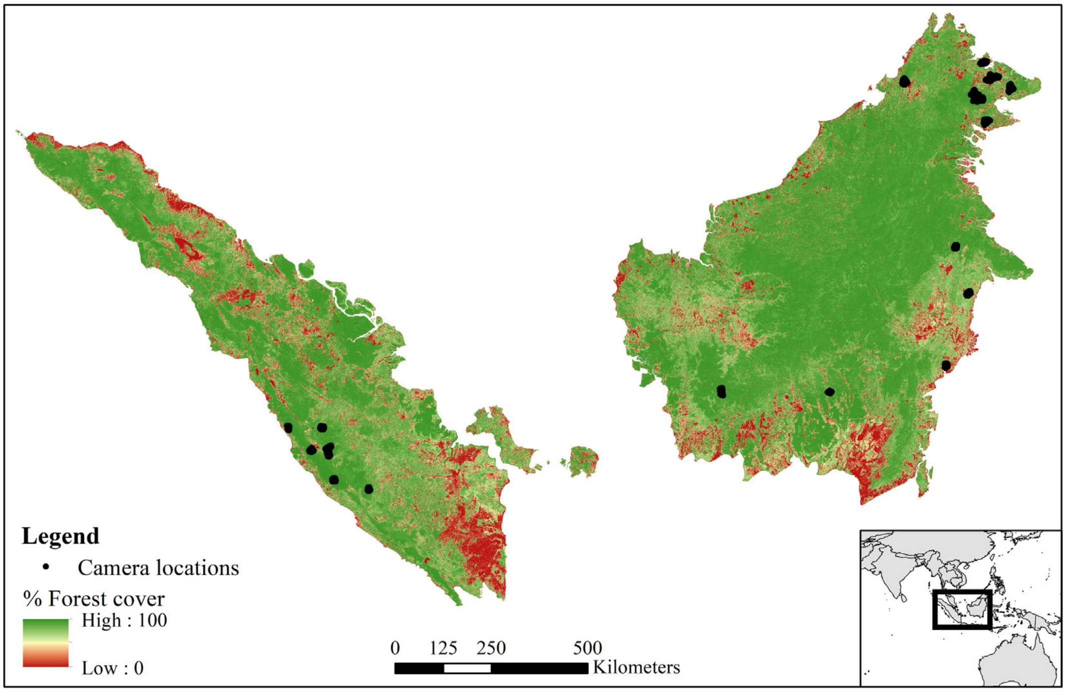

Fig. 1. Camera trap locations deployed in Sumatra and Borneo (n = 1544).

excluded (Hearn et al., 2017).

2.3. Data analysis

Species habitat preferences vary in a scale-dependent manner, and different components of the environment may influence habitat use at different spatial scales (Thompson and McGarigal, 2002; Timm et al., 2016; Wan et al., 2017). Multi-scale optimization has been shown to substantially improve model predictive power compared with single scale, non-scale-optimized models (e.g., McGarigal et al., 2016; Timm et al., 2016; Wan et al., 2017). We used the two-step scale optimization approach recommended by McGarigal et al. (2016). First, we transformed GIS layers into multi-scale predictor variables using neighborhood statistics (Table S2). For all continuous variables, the focal mean and standard deviation were calculated in ArcGIS by applying a circular window around each camera location across eight spatial scales (window radius = 250 m, 500 m, 1 km, 2 km, 4 km, 6 km, 8 km, and 10 km). The minimum spatial scale was selected based on input variable spatial grain size and computational modeling constraints. The largest scale coincides with previously reported home range estimates from radio-collared tracking studies (Grassman et al., 2005; Hearn et al., 2013, 2018a). Categorical variables were transformed using moving window analyses in FRAGSTATS (McGarigal et al., 2002). To identify the spatial scale most strongly correlated with

Table 1
Sampling information, including sampling locations within each region, number of camera stations (n), total number of trap nights and mean trap nights per camera station, total detections, detection rate, and camera model.

Region	Sampling location	n	Total # trap nights (mean)	Total detections	Detection rate	Camera model
Kalimantan (n = 317)	Sungai Wain	78	4729 (60.63)	12	0.12 (9/78)	Cuddeback Ambush IR
	Bawan	63	4070 (64.60)	0	0	Cuddeback Ambush IR
	Kutai	52	3269 (62.87)	1	0.02 (1/52)	Cuddeback Ambush IR
	Lesan	73	10,057 (137.77)	2	0.01 (1/73)	Cuddeback Ambush IR
	Belantikan	51	3846 (75.41)	3	0.04 (2/51)	Cuddeback Ambush IR
Sabah (n = 484)	Ulu Segama	22	2847 (129.41)	83	0.82 (18/22)	Snapshot Sniper
	Malua	38	3867 (101.76)	11	0.18 (7/38)	Snapshot Sniper
	Danum2012	79	5880 (74.43)	88	0.38 (30/79)	Panthera V3, Reconyx HC 500, Reconyx PC 800
	Danum Palm	23	2214 (96.26)	0	0	Snapshot Sniper
	Tabin	74	6877 (92.93)	41	0.34 (25/74)	Snapshot Sniper, Cuddeback Ambush IR
	Kinabatangan	68	4450 (65.44)	15	0.15 (10/68)	Snapshot Sniper, Cuddeback Ambush IR, Bushnell
	Sepilok	35	2067 (59.06)	0	0	Panthera V3, Snapshot sniper, Reconyx HC 500, Bushnell
	IJM	33	1855 (56.21)	0	0	Panthera V3, Snapshot sniper, Reconyx HC 500, Bushnell
	Crocker	35	4059 (115.97)	51	0.37 (13/35)	Panthera V3, Snapshot sniper, Reconyx HC 500, Bushnell
	Tawau	77	17,600 (228.57)	239	0.49 (38/77)	Reconyx PC 800, Reconyx HC 500
Sumatra (n = 743)	Bungo	79	8405 (106.39)	29	0.23 (18/79)	Panthera V4, Cuddeback Ambush IR
	Sipurak	80	7227 (90.34)	23	0.16 (13/80)	Cuddeback Ambush IR
	RKE	72	5586 (77.58)	62	0.38 (27/72)	Cuddeback Ambush IR
	Ipuh	79	6277 (79.46)	31	0.16 (13/79)	Cuddeback Ambush IR
	Muara Hemat	164	13,466 (82.11)	72	0.11 (18/164)	Cuddeback Ambush IR
	Kambang	149	12,599 (84.56)	20	0.08 (12/149)	Cuddeback Ambush IR
	Linggau	120	7269 (60.58)	0	0	Cuddeback Ambush IR
Total		1544	138,516 (89.70)	933		

N. diardi detection for each predictor variable, univariate generalized linear mixed-effects models (GLMMs) were fitted using a Poisson function with the total number of detections as the response variable (*glmer* function in the *lme4* package; Bates et al., 2015) in R 3.3.2 (R Core Team, 2016). Because we were interested in range-wide relationships between the Sunda clouded leopard and its environment rather than site-level comparisons, we included region (Sabah, Kalimantan, Sumatra) as a random effect and retained among site variation as a component of critical interest within fixed effects. The best-supported scale for each variable was selected based on Akaike's Information Criterion, adjusted for small sample size (AICc; Burnham and Anderson, 2002).

Prior to analysis, four steps were taken to reduce the number of variables included in the final model. (1) We removed 16 variables that occurred in association with < 10% of camera locations, and therefore lacked sufficient coverage across the data set to be informative; (2) six variables were removed for which univariate models exhibited $p > 0.01$; and (3) 27 highly correlated variables ($|r| > 0.7$) were removed, with the predictor variable exhibiting the higher univariate GLMM AICc value being omitted (Table S3). Of the remaining variables, (4) only those with variance inflation factors (VIFs) ≤ 3 were retained (Zuur et al., 2009), resulting in the removal of two additional variables. Following this screening, nine variables were retained for the final model (Table 2). GIS maps of all final covariates are available in Supporting Information II.

In the second step of the two-step spatial optimization, we fit a multivariate GLMM of clouded leopard detections as a function of scale-optimized predictor variables. The assumption of independence among detection locations was tested by assessing spatial autocorrelation with Moran's I (*moran.test* function in the *spdep* R package; Bivand et al., 2013; Bivand and Piras, 2015). The most parsimonious combination of variables for describing *N. diardi* detection was identified by testing all variable combinations, using the *dredge* function in the *MuMIn* R package (Barton, 2016). Final candidate GLMMs were ranked according to their ΔAIC value and Akaike's model weight (w_i). Only models with ΔAIC ≤ 2 were considered for model averaging based on weights (Burnham and Anderson, 2002). Final parameter estimates were then used to map predicted clouded leopard detection across the islands of Borneo and Sumatra. To assess variation in amount, extent, and configuration of predicted habitat among regions, we reclassified the final model into low to high, medium to high, and high quality habitat based on percentiles (> 50th, > 70th, > 90th). Low includes the sum of habitat area encompassed by low, medium, and high quality habitat; similarly, Mid includes both the extent of medium and high quality habitat. These inclusive categories facilitate comparison of total habitat amount and configuration across the landscape for full models based on different levels of stringency. We then used FRAGSTATS to assess the percentage of the landscape occupied by each habitat quality class (PLAND), the total number of habitat patches, correlation length (extent) within habitat patches (GYRATE_AM), and largest patch index (LPI). We further tested for significant differences in available habitat among regions within our sampling sites using Kruskal-Wallis rank sum tests in R (Wallis, 1952), followed by non-parametric Steel-Dwass All Pairs tests (Hollander and Wolfe, 1999) in JMP Pro 12.0.1 (JMP, 1989–2007).

3. Results

We obtained a combined sampling effort of 138,516 trap nights from 1544 camera stations, with number of trap nights per station averaging 89.7 ± 1.17 SE (Table 1). Records of *N. diardi* were obtained from 17 of the 22 sampling locations, and at 283 (or 18.3%) of the camera stations, with station-level detection rates of 13/317 (or 4.1%) in Kalimantan, 169/484 (or 34.9%) in Sabah and 101/743 (or 13.6%) in Sumatra. Average detection rates per camera station varied across regions, with 0.04 (± 0.02) in Kalimantan, 0.30 (± 0.08) in Sabah, and 0.16 (± 0.05) in Sumatra.

3.1. Scale optimization

Univariate GLMMs revealed that clouded leopards were affected by most predictor variables at either the finest or broadest spatial scales included in our analysis. Clouded leopard detections were sensitive to human population density at broad spatial scales, with detection rate decreasing as human population density increased within a 10 km-radius focal landscape. As expected, given *N. diardi's* semi-arboreal nature and relatively large home ranges, variables associated with forested habitat were also most important at the largest spatial scales, with clouded leopard detection increasing with higher extent of closed canopy forest within a 10 km-radius focal landscape, and also increasing with higher correlation length (extent) of connected forest within an 8 km-radius focal landscape. In contrast to the other forest variables, percent lower montane forest (750–1500 m asl) was positively associated with clouded leopard detections at the 500 m scale. Variables most significant at the finest scales were those quantifying topography, including slope position (250 m) and compound topographic index (1 km); clouded leopard detections were higher near ridgetops with low topographical convergence.

3.2. Multi-scale model

To model clouded leopard detection as a function of scale-optimized predictor variables, we first tested for and determined that spatial autocorrelation was non-significant. AIC model selection produced four top models, for which ΔAICc ≤ 2. Model averaging estimated coefficients for a final model including six predictor variables (Table 2). Two variables related to anthropogenic disturbance were strongly and negatively associated with clouded leopard detection - percent forest loss

Table 2
Generalized linear mixed effects model predicting Sunda clouded leopard detections, including the optimal scale for each covariate, AIC importance (weighted average of models that include each predictor variable, weighted by AIC model weight), standardized regression coefficients (β), adjusted standard error, z-scores, and significance.

Fixed effects	Optimal scale (m)	AIC imp.	β	Adjusted SE β	z	p
(Intercept)			−1.6914	0.2247	7.526	< 0.001***
Camera effort (# trap days)		1	0.2375	0.0234	10.155	< 0.001***
Compound topographic index focal mean	1000	1	−0.454	0.075	6.06	< 0.001***
Lowland forest correlation length	8000	1	0.1456	0.0553	2.635	0.008**
% Lower montane forest	500	1	0.1701	0.0326	5.216	< 0.001***
% Forest loss	10,000	1	−0.4289	0.079	5.432	< 0.001***
Plantations & regrowth correlation length	1000	1	−0.5191	0.0746	6.961	< 0.001***
Slope position focal mean	250	1	0.4204	0.0354	11.886	< 0.001***
Non-forest correlation length	2000	0.22	0.0113	0.0343	0.329	0.742
Human population density focal mean	10,000	0.18	−0.0086	0.0393	0.219	0.826
% Protected areas	10,000	0.17	0.006	0.0344	0.174	0.862

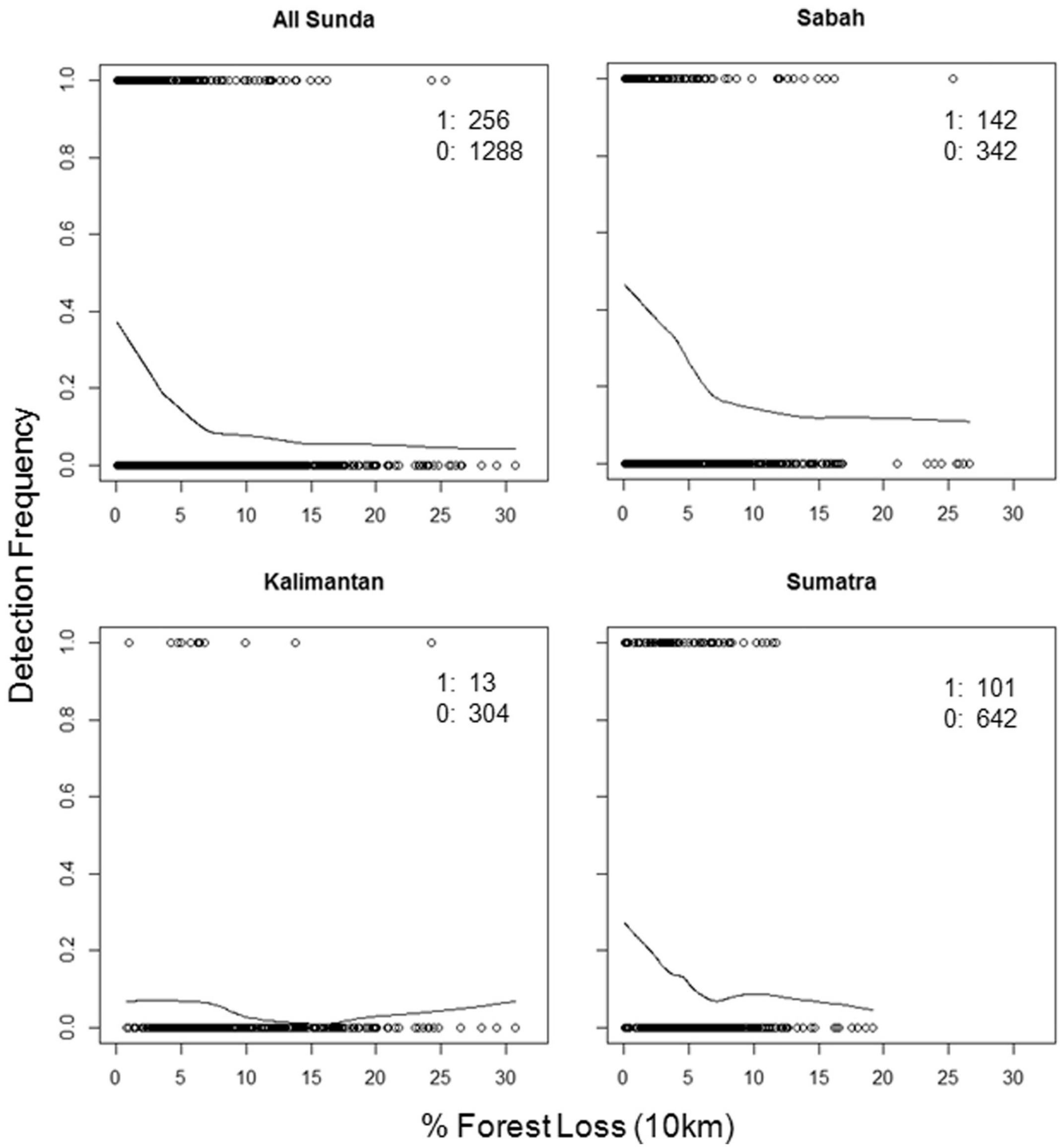

Fig. 2. Clouded leopard detection frequency declined sharply as deforestation increased. Considering the whole Sunda region, we detected clouded leopards at ~40% of camera stations in closed canopy forests; conversely, detection frequency decreased to 0.1 when percent forest loss within a 10 km-radius focal window increased to just 8%. 1 = number of camera stations that detected clouded leopard; 0 = number of camera stations where no clouded leopards were detected.

(10 km scale; Fig. 2; $\beta = -0.4289 \pm 0.0790$) and extensiveness (correlation length) of plantations and regrowth (1 km scale; Fig. S5; $\beta = -0.5191 \pm 0.0746$). Number of detections was also negatively associated with increasing mean CTI (1 km scale; $\beta = -0.4540 \pm 0.0750$). We observed low detections for CTI values above 9.5 and a sharp rise in detections for CTI values below 9.5, suggesting a potential threshold response in preference for higher elevation ridgelines and avoidance of lower elevation drainages (Fig. 3). Similarly, we detected a positive association between mean slope position (250 m scale; Fig. S1; $\beta = 0.4204 \pm 0.0354$) and *N. diardi* detections, reiterating ridgelines as an important component of clouded leopard habitat. We also found forested landscapes to be critical components of the habitat model. Clouded leopard detections were positively related to the extensiveness (correlation length) of lowland forest at an 8 km scale (Fig. S2; $\beta = 0.1456 \pm 0.0553$), and percent lower montane forest (500 m scale; Fig. S3; $\beta = 0.1701 \pm 0.0326$).

3.3. Regional variation

Comparing differences in habitat availability at our sampling sites, we detected important differences among regions. We note that comparisons are strictly based on our sampling sites and may not necessarily represent the broader island-wide landscape. Generally, our sampling locations in Sabah and Sumatra more closely resembled each other than those in Kalimantan. Our sampling locations in both Sabah and Sumatra exhibited lower CTI and higher slope position compared to our sites in Kalimantan (Figs. S7–S8; $p < 0.0001$), indicating significantly more available habitat in higher elevation areas and ridgelines in our sites in the former two regions and a greater proportion of lower elevation drainages and flatter landscapes characterizing sampling locations in Kalimantan.

There were also substantial differences in forest landscape structure, protected areas, and poacher detections between our three study regions that vary in accordance with different levels of clouded leopard detections. The average distance clouded leopards could travel without leaving lowland forest patches (correlation length) was significantly lower in Kalimantan than the other regions (Fig. S9; $p < 0.0001$; Kalimantan: $\bar{x} = 2957.80\,m \pm 89.13$, Sabah: $\bar{x} = 3873.62\,m \pm 72.13$, Sumatra: $\bar{x} = 3609.83\,m \pm 58.22$), and mirrored the low, high, and moderate *N. diardi* detections in these regions, respectively.

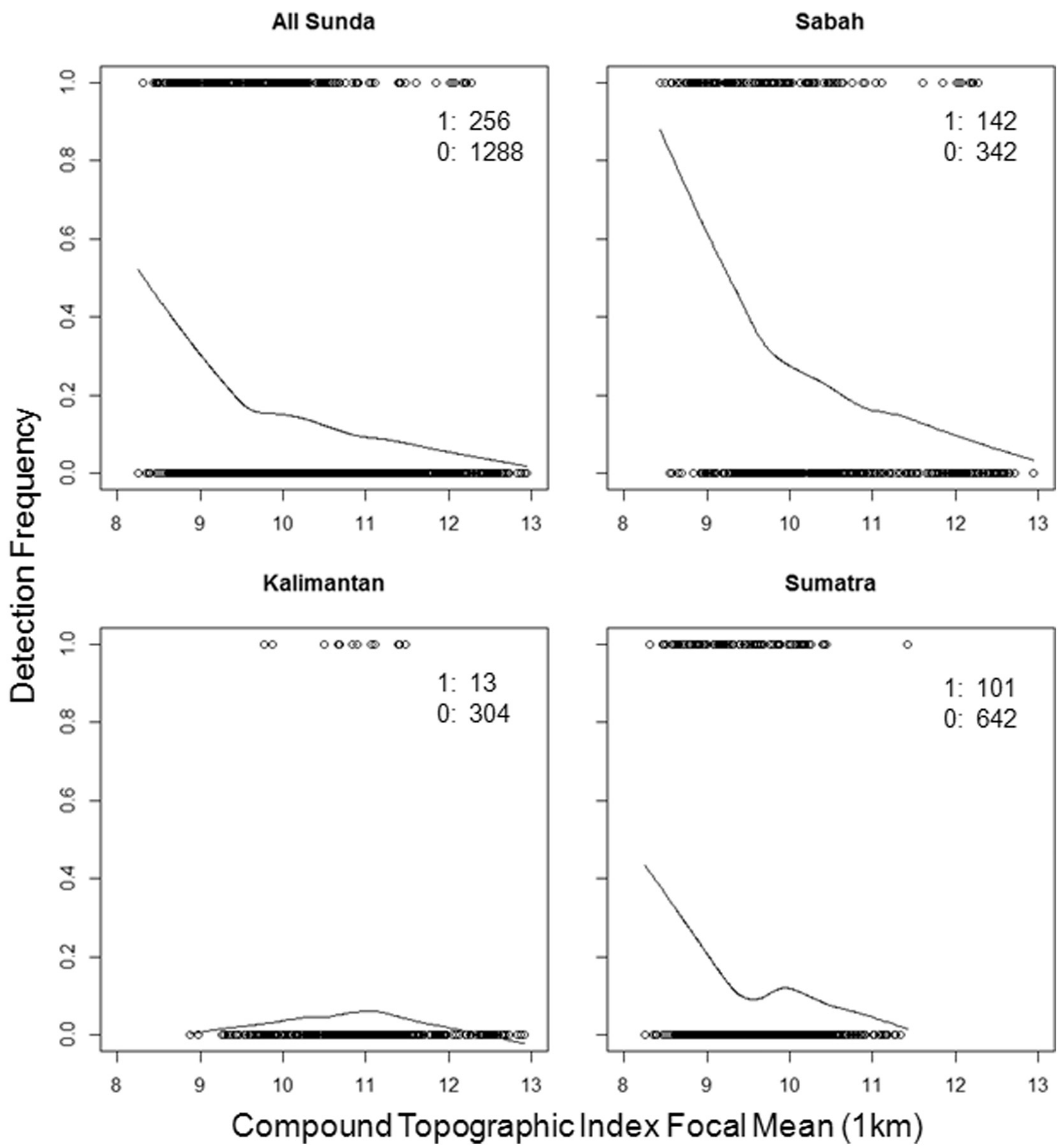

Fig. 3. Clouded leopard detection frequency was negatively associated with increasing compound topographic index. For the whole Sunda region, we detected clouded leopards at > 50% of camera stations when the mean CTI within a 1 km-radius focal window was < 8.5. We observed a sharp decline in detection frequency associated with CTI values > 9.5, suggesting a potential threshold response in preference for higher elevation ridgelines and avoidance of lower elevation drainages. 1 = number of camera stations that detected clouded leopard; 0 = number of camera stations where no clouded leopards were detected.

Similarly, the percent of lower montane forest was significantly greater at our sites in Sabah (Fig. S10; $p < 0.0001$; $\bar{x} = 12.02 \pm 1.50$) and Sumatra ($\bar{x} = 23.76 \pm 1.19$) compared to our sites in Kalimantan ($\bar{x} = 0.00 \pm 1.83$). Exhibiting the opposite pattern, average travel distance within plantations and regrowth (correlation length) was highest in Kalimantan (Fig. S13; $\bar{x} = 358.30 \pm 14.20$), lowest in Sabah ($\bar{x} = 104.50 \pm 11.50$), and intermediate in Sumatra ($\bar{x} = 296.72 \pm 9.23$).

Percent of the landscape designated as protected areas was strikingly different among our sites across regions, with limited extent of protected areas in our Kalimantan sites (Fig. 4; $p < 0.0001$; $\bar{x} = 11.83 \pm 1.40$) compared to Sabah ($\bar{x} = 67.87 \pm 1.13$) and Sumatra ($\bar{x} = 73.18 \pm 0.91$). With limited protected areas at our Kalimantan sites, percent forest loss was more than double in this region (Fig. S11; $\bar{x} = 10.34 \pm 0.26$) compared to Sabah ($\bar{x} = 5.43 \pm 0.21$) and Sumatra ($\bar{x} = 4.76 \pm 0.17$). Lastly, we found significant differences in poachers detected among all regions, with much higher detection rates in Sumatra than the other two regions (Fig. S14; Kalimantan ($\bar{x} = 0.04 \pm 0.43$), Sabah ($\bar{x} = 0.12 \pm 0.32$), Sumatra ($\bar{x} = 2.30 \pm 0.25$)). The frequency of *N. diardi* detection decreased rapidly when even a few poachers were detected for our sites in Sabah and Sumatra (Fig. S6).

To better understand regional differences beyond our study sites and to simplify conservation planning efforts, we reclassified the final model into low, medium, and high quality habitat, according to quantiles predicted by the final model-averaged coefficients (Fig. 5). Comparing islands, we found that Borneo (Kalimantan: 10.35%; Sabah, Sarawak, & Brunei: 8.72%) and Sumatra (8.98%) host approximately the same percentage of high quality habitat (Table 3). Importantly, our final model predicts a more positive outlook for the broader Kalimantan landscape, in contrast to our Kalimantan sampling locations, which are primarily located in lower elevations associated with the margins of *N. diardi's* distribution. The more northern and central highlands of Kalimantan, which represent the core of *N. diardi's* distribution on Borneo, have nearly three times greater extent (correlation length = 15.27 km) available within high quality habitat patches compared to neighboring Malaysian Borneo (5.32 km), yet just a third of the average travel distance available to *N. diardi* in Sumatra (43.67 km). Sumatra also boasts

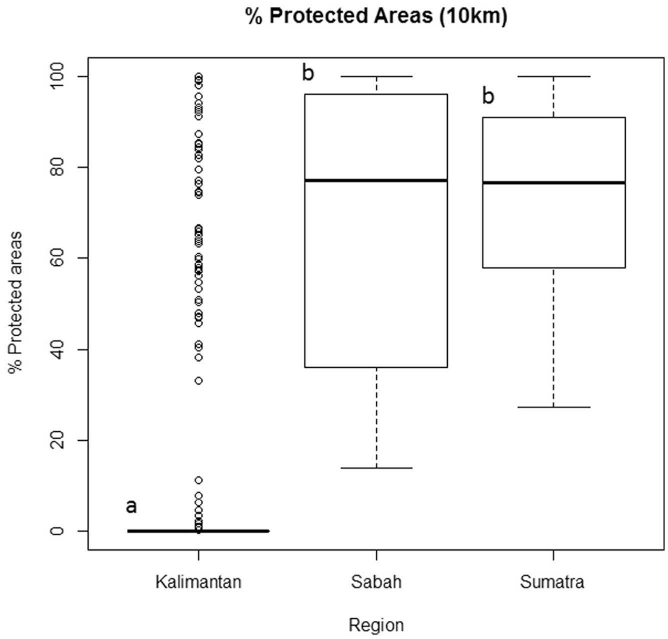

Fig. 4. Percent of the landscape designated as protected was significantly less at our study sites in Kalimantan ($\bar{x}$ = 11.83, SE = 1.40) compared to Sabah ($\bar{x}$ = 67.87, SE = 1.13) and Sumatra ($\bar{x}$ = 73.18, SE = 0.91). Different letters indicate significant differences (Steel-Dwass All Pairs test (p < 0.0001), following Kruskal-Wallis test).

a substantially greater LPI (i.e., percentage of the landscape occupied by the largest habitat patch) compared to the other two regions (Table 3). Considering total area of high quality habitat, Kalimantan harbors 1.36× (55,175 km^2) that available on Sumatra (40,547 km^2) and 3.13× that available within Malaysian Borneo (17,622 km^2). Collectively, Borneo harbors 1.8× (72,797 km^2) the area of high quality habitat compared to Sumatra.

We further ranked the top most important patches within each island, based on patch area of Mid to High quality habitat. We identified

Table 3
Comparative analysis of landscape metrics based on the multi-scale model reclassified into Low, Mid, and High quality habitat, including percent suitable habitat, number of patches, correlation length, and largest patch index.

Region	Habitat quality	% Suitable habitat	Number of patches	Correlation length (km)	Largest patch index
Sumatra	Low	48.52	5252	382.92	40.84
	Mid	28.3	8703	123.85	11.21
	High	8.98	8269	43.67	2.19
Borneo					
Kalimantan	Low	47.32	8898	196.88	38.53
	Mid	29.35	7287	155.39	23.9
	High	10.35	18,530	15.27	0.76
Sabah,	Low	55.34	4821	189.72	50.15
Sarawak	Mid	30.33	6851	58.02	11.02
& Brunei	High	8.72	12,064	5.32	0.28

28 patches on Sumatra and 30 on Borneo > 100 km^2; low quality habitat (gray areas) may provide critical linkages between core areas (Fig. 6). Patch statistics (patch area, correlation length) associated with Patch IDs (1 – 30) are presented in Table S4. The three largest Sumatran patches (1–3) represent 92.8% of habitat area occupied by the top 28 patches and form a nearly contiguous habitat network extending throughout the western highlands from the northern to the southern tip of the island. While extensive protected areas coincide with these three key habitat patches, the gaps between them lack protection (A and B in Fig. 6). In contrast, habitat patches in the central and eastern Sumatran lowlands are highly fragmented, typically restricted to smaller protected areas, and disconnected from the western highland core habitat. Although these patches represent only 7.2% of top patch area, the central and eastern lowlands are ecologically distinct from the core highland habitat, and therefore may be of unique conservation interest. On Borneo, the single largest patch, located in the central highlands, represents 83.3% of habitat area occupied by the top 30 patches across the island. In contrast, the next largest patch occupies only 5% of this area. While peripheral patches are similarly smaller and fragmented, they are generally better connected by low quality habitat to the central

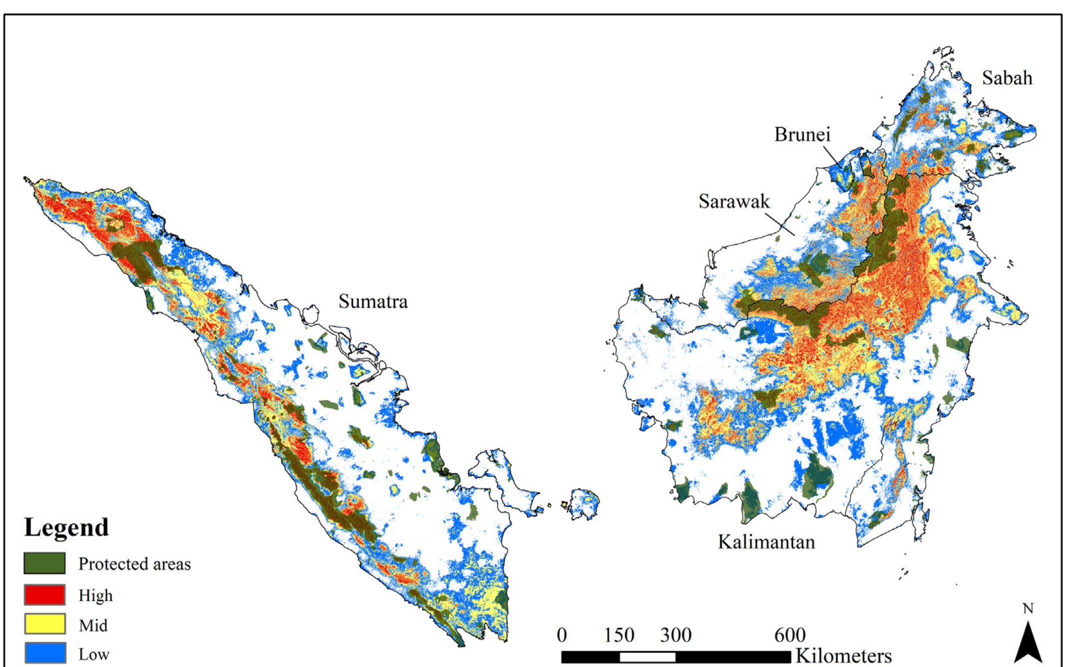

Fig. 5. Multi-scale model of predicted clouded leopard detection, reclassified into Low, Mid, and High quality habitat. Transparent green polygons represent protected areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

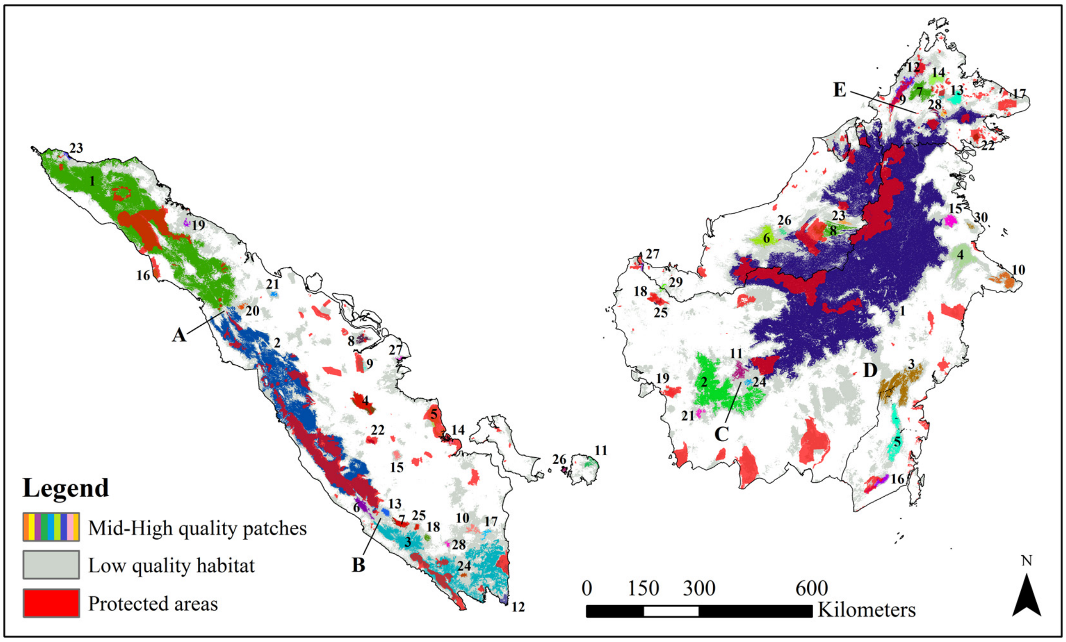

Fig. 6. Top 28 and 30 habitat patches on Sumatra and Borneo, respectively, based on patch area (> 100 km^2). Patch statistics associated with Patch IDs (1–30) can be found in Table S4. Upper case letters (A-E) indicate areas of low quality habitat (gray areas) which may provide critical gaps between major habitat patches. Protected areas are represented by transparent red; Mid-High quality patches are colour-coded in cooler tones. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

highlands than are peripheral patches on Sumatra. Our analysis identified three critical gaps that may contribute to isolating, or conversely provide opportunities for facilitating *N. diardi* movement. **C** in Fig. 6 identifies a critical gap between the top two largest patches in southwestern Kalimantan. Gap **D** is an important corridor between three key patches (3, 5, and 16) in southeastern Kalimantan. Typical of range edge populations (Hampe and Petit, 2005), habitat in Sabah is represented by a fragmented network of smaller habitat patches, constituting just 3% of the area occupied by the top 30 patches. **E** denotes opportunities for bridging the gap between Sabah patches and the central highland core, as well as corridors to better connect habitat patches within the state.

4. Discussion

Megafauna throughout Southeast Asia are threatened by rapid deforestation and land conversion. The strong association between clouded leopards and extensive regions of high forest cover makes them potent ambassadors for conserving broader forest biodiversity (Macdonald et al., 2017). Yet clouded leopards are enigmatic, their habitat use poorly known, and therefore the opportunities to plan their conservation and utilize their potential as umbrella and ambassador species have been limited. Here, in one of the largest camera-trapping studies ever undertaken for any felid species, we developed a multi-scale habitat model to identify key variables influencing *N. diardi* detection spanning its full range, including an assessment of contrasting differences among regions and islands within Sundaland. Deforestation and subsequent conversion to plantations emerged as the primary drivers associated with declining *N. diardi* detection, which adds to the growing body of knowledge on the detrimental impact of this type of land conservation on Southeast Asia's large mammal fauna (Wibisono et al., 2011; Linkie et al., 2013). Conversely, we found strong, positive associations between clouded leopard detection and large, contiguous forested regions and areas encompassing higher elevation ridgelines.

Identifying the optimal scale of habitat use is critical for characterizing the requirements of protected areas (McGarigal et al., 2016). We found that key variables related to forest cover were most strongly associated with *N. diardi* at the broadest spatial scales included in our study, namely a strong, positive association with large tracts of lowland forest, and a strong, negative association with broad-scale deforestation. In agreement with our findings, Hearn et al. (in review) also found that Sunda clouded leopards selected higher elevation forest landscapes at fine scales, and exhibited negative relationships with human-dominated, highly disturbed habitat types at broad scales. Combined with previous knowledge of the clouded leopard's relatively large home ranges (Hearn et al., 2013; Hearn et al., 2018a), our findings clearly demonstrate that large, contiguous tracts of forest are critical to this species' survival.

4.1. Regional variation

Comparing sampling locations among regions revealed striking differences. We observed substantially higher rates of *N. diardi* detection in Sabah compared to Sumatra, and much lower detections in the Kalimantan sampling locations than in either Sabah or Sumatra. Some of this observed difference may be attributable to differences in the extent of protected areas in the three study regions. While protected status was not significant in our final model, we did observe a positive relationship between increasing detection frequency and increasing proportion of the landscape characterized by extensive, contiguous protected areas at our sampling locations in Sabah and Sumatra (Figs. 4 & 7). In contrast, clouded leopards were rarely detected in southern and eastern Kalimantan, where our sampling locations were not associated with protected areas recognized by the IUCN and UNEP World Database of Protected Areas (2017). We suspect the lack of a significant relationship stems from low model power associated with two factors. First, the majority of sampling sites were located in protected areas, hence the model had little data available from non-protected areas to differentiate the influence of the two habitat classes. Second, detection data in the few non-protected sites in Kalimantan was very low, with only 13 total detections. This supports Cheyne et al.'s (2016) previous finding of low detection rates in Central and East Kalimantan. In this study, we treated protected areas as categorical, however it is critical to note that all protected areas are not equal. While four of the five

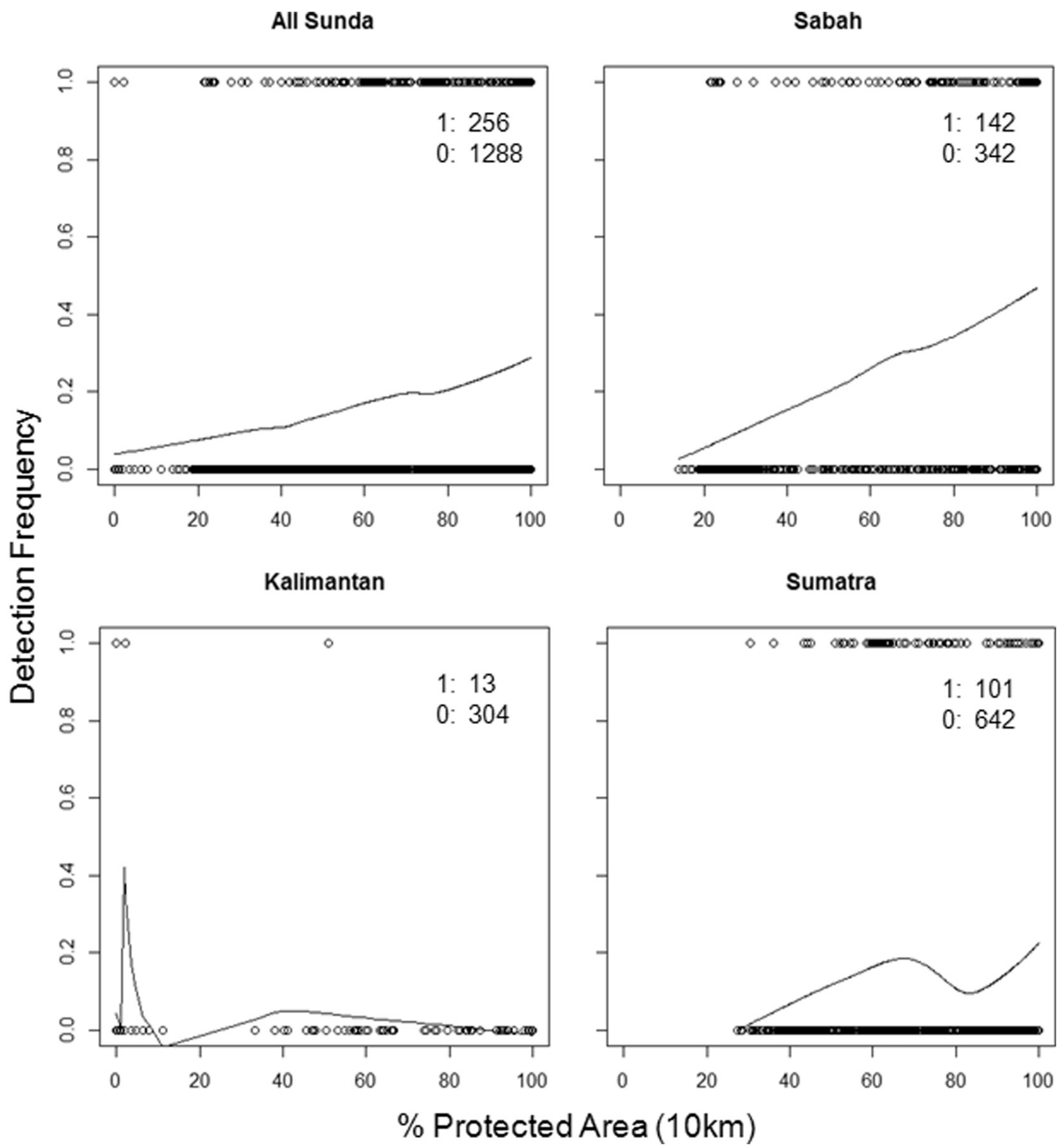

Fig. 7. Clouded leopard detection frequency increased with increasing percentage of the landscape designated under protected status. For the whole Sunda region, we detected clouded leopards at ~30% of camera stations when 100% of the landscape within a 10 km-radius focal window was protected. When only 40% of the landscape was designated as protected, detection frequency decreased to 0.1. 1 = number of camera stations that detected clouded leopard; 0 = number of camera stations where no clouded leopards were detected.

Kalimantan sites technically had legal protection status under local law, enforcement on the ground was limited. Level of enforcement within protected areas varies with local resources and policy circumstances. Future work should expand investigations beyond protected areas and further quantify how gradients in protection and enforcement impact clouded leopards.

Topography also varied substantially among regions. On average, available habitat in the areas we surveyed in Kalimantan was characterized by much higher CTI compared to our sites in Sabah or Sumatra (Fig. S7). Our sites in Sabah are intermediate in topography, with Sumatran sites characterized by even lower mean CTI. Our lower elevation study sites in Kalimantan had minimal access to higher elevation regions with extensive networks of ridgelines. Such ridgelines likely facilitate the large-scale movements of clouded leopard males through the landscape. Hearn et al. (in review) found that male Sunda clouded leopard detection in Sabah was strongly and positively associated with ridgelines (and somewhat less so with roads), possibly because they provide low resistance travel conduits during territorial movements. In contrast, the occurrence of females was unrelated to either roads or ridgelines; females appear to have more restricted range sizes and may choose to avoid encounters with males (Hearn et al. in review). Camera traps placed along ridgelines may also be more successful due to factors unrelated to habitat use, for example, less dense understory vegetation and/or the physical restriction of movement channeled by narrow topography may contribute to higher probability of detection associated with ridges.

The lower overall detections in Sumatra, even with lower CTI, suggests the influence of other variables. Guild composition is a likely candidate, as both tigers and golden cats are sympatric with clouded leopards in Sumatra but not in Borneo (Haidir et al., in press). Poaching is another obvious candidate that merits further investigation. Brodie et al. (2015) found that local abundance of clouded leopards was negatively related to poacher presence, and Hearn et al. (2017) demonstrated that their population density in Sabah was lower in more heavily poached areas. While our GLMM analysis did not find poaching to be a significant influence on *N. diardi* detections, we did find that total number of poacher detections varied significantly among regions (Fig. S14), and *N. diardi* detection probabilities decreased sharply when even a few poachers were detected in Sumatra and Sabah (Fig. S6). Although Sumatra and Sabah showed negative associations with poaching, our Kalimantan sites appear to be confounding the general pattern. Historical hunting pressure may have contributed to significantly reduced numbers of clouded leopards in the Kalimantan lowlands, therefore limiting the power of our model to detect a significant relationship with current levels of poaching in this region. Relatively high densities of clouded leopards have been documented in low elevation protected areas (Cheyne et al., 2013), suggesting that low numbers observed in our study may be less likely due to lowlands being unsuitable habitat and more likely a result of past and current hunting pressure. Furthermore, there is a clear interaction between logging and poaching, insofar as logging roads facilitate poachers penetrating deeply into the forest (Linkie et al., 2015). The reduced accessibility of mountainous regions may provide clouded leopards with a release from anthropogenic influences. Indeed, lowland and peat-swamp forests are experiencing 6× and 11× the deforestation rate of lower montane forests (Miettinen et al., 2011). Additionally, there are limitations to using camera trap data for understanding the influence of poaching on clouded leopards. Continuing investigations are needed to more directly explore differences among regions in direct harvest and indirect influences of poaching prey on clouded leopards. Given the nearly 20-fold higher number of poachers detected in Sumatra ($\bar{x}$ = 2.30 ± 0.25) compared to Sabah ($\bar{x}$ = 0.12 ± 0.32), even with lower average camera effort (81.87 versus 106.85 mean trap nights), increased poacher presence is a likely contributor to the lower numbers of clouded leopards predicted in Sumatra compared to Borneo. Curbing the synergistic threats of poaching and deforestation are major priorities for conservation efforts of Southeast Asian biodiversity.

4.2. Methodological considerations

This research represents one of the largest camera-trapping studies ever undertaken, with enormous effort invested in sampling diverse forest types and habitats to better understand *N. diardi's* environmental niche throughout Borneo and Sumatra. Yet the vast area, time and expense, and sheer diversity of habitats encompassed within these islands preclude exhaustive sampling. To maximize likelihood of detecting this rare species, sampling was largely biased towards habitats where we expected to encounter *N. diardi*. While our model clearly identifies forested landscapes and ridgelines as key components of *N. diardi's* niche, and forest loss and conversion to large-scale plantations as threats, our findings are limited with respect to habitat types outside the range of those encountered at our sampling locations. For example, peat-swamp forests were removed from our analysis due to occurrence at < 10% of all camera stations, although previous work found that Sabangau Forest, one of the largest contiguous peat-swamp forests remaining in Kalimantan, supports densities of clouded leopards ranging from 0.72 to 4.41 individuals per 100 km^2 (Cheyne et al., 2013). Similarly, lowland open and lowland mosaic land cover classes were not well represented at our sampling locations, therefore limiting predictive power associated with these habitat types. Riau and South Sumatra provinces in Sumatra are among the most degraded regions on the island, primarily consisting of open farmland, oil and acacia plantations, and rubber estates falling into the aforementioned lowland open and lowland mosaic land cover classes. Because the top two negatively associated covariates in our model (forest loss and plantations & regrowth) were very low in this region (Figs. S28 & S30), our model predicted moderate levels of detections here. Had we been able to conduct more extensive sampling in association with open farmland and oil and acacia plantations, we predict we would have detected a similarly negative association with *N. diardi* detections as we found with palm plantations.

The current study provides the most geographically comprehensive habitat selection model for the Sunda clouded leopard to date, yet it also highlights critical differences among both islands and regions within islands. Additional research is needed to further characterize clouded leopard habitat use with respect to marginal habitat types and limiting factors that vary throughout its range to more precisely define the edges of its distribution and further assess the influence of regional differences. Future studies with increased sampling effort spanning the full range of environmental variation throughout Borneo and Sumatra would reduce potential bias resulting from habitat types not included in the current model, and provide the additional power necessary for the development of regional models, following the same multi-scale approach utilized here. The ideal study design to robustly predict the multi-scale habitat niche of widely ranging species such as the clouded leopard would involve placing sampling stations in a spatially representative, diffuse grid across the range without gaps, and sufficiently far apart to achieve high statistical independence across all spatial scales of analysis. Future camera trap studies focused on multi-scale habitat selection should take this into consideration in their design.

4.3. Conservation management implications

The predicted habitat suitability maps presented here have important implications for clouded leopard conservation (Figs. 5, 6, S15–S16). The Bornean map is largely consistent with our earlier presence-only modeling work, which is the current basis for the IUCN evaluation (Hearn et al., 2016). While both models show strong agreement with respect to *N. diardi's* core distribution, our current model is more conservative with respect to range margins. Differences appear to be primarily driven by the additional percent forest loss variable included here and our finer resolution treatment of palm plantations. While the previous model included plantations as a categorical variable, here we investigated plantations as a continuous, multi-scale variable; our current, finer-scale investigation suggests that plantations are having an even stronger negative impact than previously predicted. The more intensive surveys included in this study provide a more robust evaluation to strengthen conservation planning. Furthermore, although mindful that our span of sampling locations in Sumatra was less widely dispersed than those in Borneo, the resultant maps indicate that the habitat available to *N. diardi* in Sumatra is roughly half the area available to clouded leopards in Borneo. Our analysis also draws attention to gaps in knowledge about other threats, such as the degree of contact with local communities and the extent of conflict and retaliatory killing. However, it does show that for Sumatra the identified priority areas are closely associated with the UNESCO Tropical Rainforest Heritage of Sumatra sites comprising the national parks of Kerinci Seblat, Gunung Leuser and Bukit Barisan Selatan.

Our findings reveal important insights about the factors that affect clouded leopard habitat suitability and differences in the amount and pattern of habitat across insular Southeast Asia. We conducted a patch analysis to identify core conservation areas, based on patch size, as well as key connectivity corridors and/or gaps among major habitat patches. While size does not necessarily equate to importance, larger habitat patches are likely to support larger populations of interbreeding individuals, and greater habitat connectivity has been shown to support greater genetic diversity (Bothwell et al., 2017; Macdonald et al., in review). Therefore, conservation efforts should focus on protecting these remaining core areas, particularly the largest ones, and those representing the full range of ecological conditions (e.g., lowland and highland). In addition, networks of corridors connecting major habitat patches are essential for maintaining dispersal, gene flow, and evolutionary potential of the species. On Sumatra, we identified three major patches representing 92.8% of habitat area occupied by the top 28 patches. While much of this habitat coincides with large protected areas as noted above, our results reveal unprotected gaps among the three primary patches (**A** and **B** in Fig. 6). Conservation efforts aimed at protecting these gaps are important for promoting dispersal and mating, and reducing the risk of inbreeding and associated population bottlenecks. Furthermore, our model illustrates the highly fragmented nature of the central and eastern Sumatran landscape (Figs. 5, 6, & S16). In combination, our findings indicate greater challenges facing clouded leopards on Sumatra, including higher poaching pressure, increased fragmentation, and roughly half the total habitat availability compared to Borneo. The central highlands of Kalimantan - representing the core of *N. diardi's* distribution on Borneo - harbor 3.13 × more high quality habitat compared to neighboring Sabah, Brunei, and Sarawak. The steep terrain of Borneo's remote central highlands has rendered it largely untouched by poachers and researchers alike, yet our model suggests this relatively understudied interior is likely of high importance to *N. diardi*. On Borneo, we identified three critical corridors in need of protection to connect southwestern Kalimantan (**C**), southeastern Kalimantan (**D**), and Sabah patches (**E**) with the core central highlands. While the central highlands boast several large protected areas coincident with high quality habitat, our model illustrates almost no overlap between Mid to High quality habitat and protected areas in Central Kalimantan, and only moderate overlap in East Kalimantan and Sabah. For Central Kalimantan in particular, the majority of National Parks are located in association with coastal lowlands. These parks are likely vital for a wealth of other species, yet they represent low quality, highly fragmented habitat for clouded leopards. As human population growth increases, enhancing the protection status of patches 2–5 in Kalimantan, 6 and 8 in Sarawak, and 7, 13, 14, and 28 in Sabah will be critical to avoid further *N. diardi* decline in these regions. Overall, while many key patches do not coincide with protected areas recognized by the IUCN and UNEP World Database of Protected Areas (2017), numerous patches do coincide with less stringent land management units (e.g., forest reserves, production forests; Table S4). Working with local land managers to increase legal protection status and enforcement capacity will be valuable to conservation management efforts moving forward.

The clearest and most important conservation message arising from our findings is that clouded leopards are strongly associated with large extents of forest and are strongly, negatively impacted by forest loss and plantations and regrowth. In short, deforestation and subsequent conversion to oil palm and other plantations are major threats. This reemphasizes Macdonald et al.'s expert opinion (in press) and Hearn et al.'s (2018a) empirical finding that Sunda clouded leopard movements are closely associated with forest habitats and resisted by oil palm plantations. A top priority for conservation, therefore, is that land-use planning should consider the strong negative effects of forest loss and oil palm plantations on presence (and dispersal) of clouded leopards. Conservation efforts should prioritize the protection of large remaining core areas with high forest cover and direct particular focus towards preserving connectivity corridors among major patches. In particular, new developments that disrupt connectivity among large tracts of closed canopy forests should be strongly opposed. Furthermore, increased law enforcement efforts to curb poaching are imperative. These efforts are important not only for conservation of clouded leopards themselves, but also because of their capacity to act as umbrellas (Dickman et al., 2015), ambassadors (Macdonald et al., 2017), and charismatic icons (Macdonald et al., 2015) for the broader conservation of their diverse associated communities also challenged by rapid global change.

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Author contributions

[Confidential for double blind review.]

Appendix A. Supplementary data

All data are archived in duplicate on two servers located at [confidential] and at the [confidential]. GIS layers of covariates and a high resolution, interactive map of the final model projection can be obtained by contacting [confidential]. Supplementary data to this article can be found online at doi:https://doi.org/10.1016/j.biocon.2018.08.027.

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