Informing tropical mammal conservation in human-modified landscapes using remote technologies and hierarchical modelling

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Thesis submitted for the degree of Doctor of Philosophy in Biodiversity Management
December 2018
Word count: 56,397

This thesis is dedicated to the loving memory of my grandmother

Margaret Sarson

29th March 1937 – 14th February 2018

"All that is gold does not glitter;
all that is long does not last;
all that is old does not whither;
not all that is over is past."

J.R.R. Tolkien, 1954

Acknowledgements

First and foremost, I would like to thank my supervisory dream team for this incredible opportunity. I am indebted to Matt Struebig for providing overwhelming support, facilitating fruitful collaborations and developing my academic network. I am particularly grateful for his tireless efforts reining in my laissez-faire attitude to air travel. Special thanks to Zoe Davies for her guidance, attention to detail and capacity to find the right words in moments of crisis. I am also thankful to my statistical supervisor, Gurutzeta Guillera-Arroita for making complex statistical principles accessible. I wholeheartedly appreciate the role each has played in my personal and professional development over the last four years.

This PhD would not have been possible without external support from a number of individuals. I would like to express my appreciation to NERC and EnvEast for funding this research and providing invaluable training opportunities. I am eternally grateful to my “academic Yoda”, Andy Marshall, for the many doors he has opened for me during my academic journey. Many thanks to Glen Reynolds for his assistance in navigating Southeast Asian research politics. Gratitude to Andreas Wilting for guidance with field methods and his infectious enthusiasm for all things mammal. Many thanks to team LiDAR, particularly Tom Swinfield and David Milodowski, for going above and beyond the call of duty in the development and processing of remote-sensing data. Special mention to Ollie Wearn for being a pillar of support during the intimidating initial phases of the PhD process.

In Malaysia, fieldwork was greatly assisted by a highly dedicated team. Thanks to Jamiluddin “Unding” Jami and Ryan Gray for coordinating field logistics with military precision. I would like to express gratitude to the field assistants that accompanied me on my Bornean adventures: Arnold “Noy” James, Mohd. “Kiky” Shah Nizam Bin Mustamin, Ampat “Anis” Siliwong and Najmuddin “Mudin” Jamal. I reserve special thanks for Sabidee “Didy” Mohd. Rizan, the self-proclaimed “Monkey King”, whose companionship and optimism were, and continue to be, an inspiration. Finally, my gratitude to Lonnie Baking for training me in the dark arts of camera-trapping and leading data collection in my absence. This thesis is testament to all of their dedication and hard work.

I would like to thank friends and colleagues at DICE for helping a reluctant northerner feel at home behind enemy lines. I feel honored to have shared my PhD journey with Simon Mitchell, whose sharp mind has motivated me to achieve more than I thought possible. Special mention to Gwili Gibbon for his insightful perspectives and always offering a much-needed social outlet. Beyond the unofficial DICE triumvirate, I thank all the incredible people I have met throughout the course of this PhD, particular mentions go to Dave Seaman, Jess Haysom, Jake Bicknell, Gui Braga Ferreira, (Isa)Bela Menezes-Barata, Adriana Lowe, Valeria Boron, Tristan Pett and Lydia Tiller. I would also like to acknowledge Unicorn stalwarts Bob Smith and James Kloda for providing a consistent, and much needed, social outlet. Four years is too short a time to have spent in such great company.

Last but by no means least I would like to thank my family. My parents have encouraged my love of the natural world since I was a child and provided me with the freedom to pursue my ambitions and learn from my own mistakes. Gratitude also to my brother for his unwavering support. Finally, eternal thanks to my beloved Grandma. This accomplishment reflects the immeasurable influence she had on my life.

Author's declaration

All chapters contained within this thesis were written by Nicolas J. Deere, incorporating comments and editorial feedback from supervisors Matthew J. Struebig and Zoe G. Davies. Statistical guidance for all data chapters (2-4) was provided by Gurutzeta Guillera-Arroita. Data associated with this study are to be made available via the NERC Environmental Data Centre. Chapters 2-4 represent collaborations with external institutions and international non-governmental organisations.

Chapter 1: written by Nicolas J. Deere and reviewed by Matthew J. Struebig and Zoe G. Davies.

Chapter 2: Nicolas J. Deere conceived the idea and designed the camera-trap network. Field data were collected by Nicolas J. Deere, Esther Baking and Jessica K. Haysom. Remote sensing data products were provided by David Coomes and processed by Tom Swinfield and David Milodowski. Data analysis was conducted by Nicolas J. Deere. All authors contributed to the revision of the manuscript. Figures were produced by Nicolas J. Deere.

Chapter 3: Nicolas J. Deere conceived the idea and designed the camera-trap network, with guidance from Matthew J. Struebig. Field data were collected by Nicolas J. Deere and Esther Baking. Processing of remote-sensing data was conducted with partners at The Forest Trust and Greenpeace. Data analysis was conducted by Nicolas J. Deere. Gurutzeta Guillera-Arroita, Oliver R. Wearn, Marion Pfeifer, Glen Reynolds and Henry Bernard contributed to the revision of the manuscript, with additional feedback from Grant Rosoman and Sharon Smith. Figures were produced by Nicolas J. Deere. This chapter was published in the *Journal of Applied Ecology*.

Chapter 4: Nicolas J. Deere conceived the idea and designed the camera-trap network. Field data were collected by Nicolas J. Deere, Esther Baking, Jessica K. Haysom and David J.I. Seaman. Remote-sensing data was collected by the Carnegie Airborne Observatory and provided by Glen Reynolds and the Sabah Forestry Department. Data analysis was conducted by Nicolas J. Deere. All authors contributed to the revision of the manuscript. Figures were produced by Nicolas J. Deere.

Chapter 5: written by Nicolas J. Deere and reviewed by Matthew J. Struebig and Zoe G. Davies. Figures were produced by Nicolas J. Deere.

On behalf of all co-authors, I hereby declare that there were no competing interests.

Abstract

The aggressive expansion of anthropogenic activities is placing increasing pressure on biodiversity, particularly in tropical regions. Here, conservation efforts are hindered by poor understanding of species ecology and the failure of policy instruments to account for multiple stressors of land-use change. While protected areas are central to conservation strategies, there is a general consensus that the future of tropical biodiversity will be determined by how well modified landscapes are managed. In this thesis I advance our understanding of biodiversity persistence in modified tropical landscapes to inform emerging incentive-based policy mechanisms and supply-chain initiatives. Capitalising on recent advances in remote-sensing and hierarchical occupancy modelling, I provide a spatial appraisal of biodiversity in a modified landscape in Sabah, Malaysian Borneo. Fieldwork was conducted at the Stability of Altered Forest Ecosystems (SAFE) project, a large-scale landscape modification experiment, comprising a degradation gradient of old growth forest, selectively logged forest, remnant forest patches and oil palm plantations. The assessment focused on camera-trapping of tropical mammals, as they are sensitive to anthropogenic stressors, occupy key trophic positions, and prioritised in conservation. In Chapter 2 I link mammal occupancy data to airborne multispectral remote-sensing information to show how the conservation value of modified landscapes is dictated by the intensity of the underlying land-use. Logged forests retained appreciable levels of mammal diversity, and oil palm areas were largely devoid of forest specialists and threatened taxa. Moreover, many mammal species disproportionately occupied forested areas that retained old growth structural characteristics. The most influential structural measures accounted for vertical and horizontal components in environmental space, which cannot currently be derived from conventional satellite data. Using a novel application of ecological threshold analysis, I demonstrate how multispectral data and multi-scale occupancy models can help identify conservation and restoration areas in degraded forests. In Chapter 3 I assess the potential for carbon-orientated policy mechanisms (High Carbon Stock, HCS, Approach and REDD+) to prioritise high carbon areas with corresponding biodiversity value in highly modified landscapes. The areas of highest carbon value prioritised via HCS supported comparable species diversity to old growth forest. However, the strength, nature and extent of the biodiversity co-benefit was dependent on how carbon was characterised, the spatial resolution of carbon data, and the species considered. In Chapter 4 I further scrutinised HCS protocols to evaluate how well they delineated high priority forest patches that safeguard species most vulnerable to land-use change (i.e. IUCN threatened species). The minimum core area required to define a high priority patch (100 ha) supported only 35% of the mammal community. In fact the core area criterion would need to increase to 3,199 ha in order to sustain intact mammal assemblages, and an order of magnitude higher if hunting pressure was considered. These findings underline the importance of integrating secondary disturbance impacts into spatial conservation planning. Provided landscape interventions are directed to where they will have the greatest impact, they can be financially sustaining and garner local support for conservation. To this end I provide recommendations to guide policy implementation in modified tropical landscapes to support holistic conservation strategies.

Keywords: Camera-trapping, hierarchical modelling, human-modified landscapes, land-use change, mammals, oil palm, selective logging, Southeast Asia.

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Chapter 1. Introduction

Tropical forest ecosystems: value, status and an uncertain future

Tropical forests are distributed across four biogeographic realms (Neo-: South/Central America; Afro-: continental Africa, Madagascar; Asian-: continental/insular Asia; Australasian-tropics: Australia, Papua New Guinea, insular Pacific; Achard et al., 2002) and account for less than 12% of the world's terrestrial surface area (Bonan, 2008), yet, are amongst the most significant ecosystems on the planet. Globally, tropical forests are reservoirs of biological diversity (Barlow et al., 2018), regulate biogeochemical and hydrological cycles (Lewis et al., 2015, MEA, 2005), and store ~30% (200-300 Pg C) of the carbon held in the terrestrial biosphere (Mitchard, 2018, Pan et al., 2011). Locally, they provide economic goods, ecosystem services and climatic stability to 1.5 billion people living in extreme poverty (World Bank, 2004, Vira et al., 2015). Given the scale of influence that tropical forests exert on ecological processes and rural livelihoods, it is widely recognised that biodiversity conservation, climate change and human well-being are all tethered to the fate of these ecosystems (Díaz et al., 2006, Gardner et al., 2010).

Since the 1980s, the tropical forest extent has declined from 1.7 to 1.1 billion ha, equating to a range contraction of 35% (Wright, 2010). In recent decades, tropical deforestation has continued at a consistent rate of 5 million ha year^{-1}, though the geographic focus of forest loss has shifted during this period from Brazil to other countries of South America and insular Southeast Asia (Curtis et al., 2018). The remaining forest estate has been substantially altered, with recent estimates suggesting up to 82% of the area has already been degraded by some form of human use (Watson et al., 2018). Current levels of deforestation and unsustainable exploitation release 2.9 Pg C year^{-1} into the atmosphere, contributing to 30% of anthropogenic greenhouse gas emissions (Pan et al., 2011). Moreover, the continued loss of tropical forests greatly diminishes the environmental and societal benefits they provide. Despite this, global efforts to temper land-use change have proved largely ineffective (Butchart et al., 2010).

Tropical deforestation and environmental degradation are driven by a complex interplay of local and global stressors embedded within changing socio-economic contexts (Barlow et al., 2018), which renders mitigation efforts challenging. Forest loss is mediated by human population growth, increasing per capita consumption and globalisation, which dictate demand for forest resources to address the needs of a burgeoning population (d'Annunzio et al., 2015, Geist and Lambin, 2002). These global stressors orchestrate the extent to which proximate mechanisms, such as agricultural conversion, resource extraction, infrastructure development and urbanisation, contribute to land-use change (Curtis et al., 2018, Potapov et al., 2017). Global socio-economic changes indicate an uncertain future for tropical forests. By 2050, projected population growth (United Nations, 2013) and substantial increases in the gross domestic product of rapidly industrialising nations (Lewis et al., 2015) is expected to lead to a further 710 million ha of agricultural land being needed (Tilman et al., 2017), and escalate international and domestic demand for forest resources to unprecedented levels. These demands are likely to be met in the tropics, where the majority of population growth is expected to occur (United Nations, 2013), and favourable climatic conditions, coupled with competitive land prices, provide environmental and economic incentives for forest conversion (Laurance et al., 2014).

To ensure that future resource acquisition does not follow the current template of unsustainable exploitation, more effective environmental governance is required.

The global biodiversity crisis

The global proliferation of human activities at the expense of natural habitat has resulted in precipitous biodiversity declines (Dirzo et al., 2014). Current extinction rates are several orders of magnitude higher than the background rate (Ceballos et al., 2015) and comparable to the five previous mass extinction events (Barnosky et al., 2011). This equates to 338 documented vertebrate losses since 1500 (Young et al., 2016), with a further 11,981 species threatened with extinction (Hoffmann et al., 2010). Human impacts have accelerated in recent decades, resulting in a 52% decline in remaining vertebrate populations (McLellan et al., 2014). Biodiversity losses are most pronounced in tropical forests (Hoffmann et al., 2010), which sustain half of the world's described taxa (Dirzo and Raven, 2003, Scheffers et al., 2012), including exceptional concentrations of endemic species (Myers et al., 2000), but are subjected to some of the highest rates of habitat loss globally (Hansen et al., 2013). Biodiversity underpins ecosystem functioning, stability and resilience (Cardinale et al., 2006, Seddon et al., 2016), thus impoverished faunal communities can compromise the myriad ecosystem services provided by tropical forests and jeopardise their capacity to resist state-shifts following environmental perturbations (Hooper et al., 2005, Thompson et al., 2009). This implies that biodiversity loss in tropical forests will result in negative feedback loops for human well-being and climate change (Díaz et al., 2006). Given the high proportion of data deficient species in the tropics and the likelihood of extinction debts owing to a legacy of forest exploitation, the true extent of the biodiversity crisis in tropical ecosystems is likely underestimated.

In recognition of the role of tropical deforestation in the global biodiversity crisis, ambitious multi-lateral government agreements have emerged to curtail current rates of land-use change. The New York Declaration on Forests (United Nations, 2014) and the UN Sustainable Development Goals (United Nations, 2015) both seek to fully halt deforestation by 2020 and 2030 respectively. Moreover, the New York Declaration on Forests further aims to restore up to 350 million hectares of degraded forest before 2030. To maximise the impact of these progressive agreements, and ensure ambitious proposals translate into effective conservation action, governmental commitments must be underwritten by policy instruments developed from a robust scientific evidence-base (Sutherland et al., 2004).

Human-modified tropical landscapes

The expanding sphere of anthropogenic influence across the tropics raises the question, how will biodiversity persist in an increasingly human-dominated world? Biologically rich primary, or old growth, forests are considered fundamental to biodiversity preservation (Gibson et al., 2011), yet they account for only a small fraction of the remaining tropical forest estate (Potapov et al., 2017, Watson et al., 2018). Therefore, policies focussing solely on primary forest retention will be of limited value. There is therefore increasing recognition amongst conservation practitioners that human-modified landscapes can play a significant role in safeguarding biodiversity in tropical regions (Chazdon et al., 2009, Gardner et al., 2009, Kremen and Merenlender, 2018, Melo et al., 2013). Human-modified landscapes typically comprise remnant primary- and secondary vegetation embedded within human-dominated land-uses such as farmland and logged forests (Malhi et al., 2014). These systems cover large areas of the tropical biome and could potentially form integral links between isolated primary forests and protected areas (Gardner et al., 2009, Struebig et al., 2015). Moreover, in regions devoid of intact primary forest cover, human-modified landscapes provide critical refugia for biodiversity (Chazdon et al., 2009). The conservation value of these landscapes is principally determined by the nature and intensity of the underlying land-use (Burivalova et al., 2014, Edwards et al., 2011, Edwards et al., 2014) and the spatial characteristics of the remaining vegetation (Ewers and Didham, 2006). Therefore, the capacity for human-modified landscapes to support biodiversity is contingent on active management practices that reconcile production goals and conservation objectives (Gardner et al., 2010, Koh and Gardner, 2010). If human-modified landscapes are to be integrated within a new holistic conservation paradigm, baseline information on biodiversity persistence is essential to inform land-use regulations in modified systems.

Biodiversity responses to landscape-modification

To gauge the potential for human-modified systems to contribute to the conservation agenda, it is necessary to understand biodiversity responses to land-use change and secondary disturbance impacts. Given that prominent drivers of land-use change also represent dominant land-use designations in human-modified landscapes, this information provides a valuable insight into prospects for biodiversity in anthropogenically-altered systems. It is important to note that these threats operate over different temporal and spatial scales, can impact forest ecosystems independently, concurrently or interactively, and are exacerbated by natural driving forces such as climate change (Gardner et al., 2009). It is well-recognised that biodiversity declines along a gradient of structural and floristic complexity (Gibson et al., 2011), though the severity of impacts are moderated by traits that confer sensitivity to land-use change (Newbold et al., 2014).

Oil palm agricultural expansion

In recent decades, the expansion of commodity agriculture has emerged as the most pervasive threat to tropical forests and biodiversity (Kehoe et al., 2017, Tilman et al., 2017). Since 1980, 83% of the agricultural land established came at the expense of tropical forests (Gibbs et al., 2010). Of these commodities, oil palm (*Elaeis guineensis*) is at the forefront of agriculturally-orientated conservation concerns. Driven by biofuel markets and demand for palm oil derivatives, oil palm currently occupies 18.7 million ha of land (Meijaard et al., 2018), predominantly replacing lowland tropical forest (Gaveau et al., 2017, Gibbs et al., 2010). Much of the biologically suitable land to meet future demand for oil palm corresponds with highly biodiverse tropical forest ecosystems (Pirker et al., 2016). An understanding of oil palm impacts on biodiversity is, therefore, paramount to determine the ecological consequences of future expansion.

Recent estimates suggest that agricultural activities have a negative effect on half of the world’s threatened species (Tanentzap et al., 2015). Global increases in agricultural land mass have resulted in dramatic species declines, the magnitude of which is modulated by patterns of bilateral trade and per capita consumption (Chaudhary and Kastner, 2016, Lenzen et al., 2012). Oil palm expansion has a profound influence on biodiversity, negatively impacting up to 85% of species (Danielsen et al., 2009, Fitzherbert et al., 2008). The displacement of tropical forests by oil palm monocultures causes taxonomically consistent reductions in species richness, disproportionately affecting forest specialists and species of conservation concern (mammals: Wearn et al., 2016, Yue et al., 2015, birds: Edwards et al., 2010b, Edwards et al., 2014, invertebrates: Ewers et al., 2015, Fayle et al., 2010, plants: Danielsen et al., 2009, Drescher et al., 2016). These changes are the result of biotic homogenisation and altered microclimate conditions (Foster et al., 2011). Given the ecological footprint of commodity production, mitigation measures that reconcile biodiversity conservation and oil palm development are essential in vulnerable tropical regions. However, oil palm is a highly efficient, profitable crop, providing substantial social and economic benefits which complicates environmental decision making (Meijaard et al., 2018). Thus, effective policies in production landscapes must consider the socio-economic trade-offs associated with interventions.

Selective logging

Selective logging refers to the discriminatory harvest of timber. Selective logging is a significant driver of forest degradation due to economic globalization and the demand for high-value timber (Lambin and Meyfroidt, 2011, Laurance, 2007). Between 2000 and 2005, over 400 million ha of tropical forest was allocated to the permanent timber estate and subject to some degree of logging (Asner et al., 2009, Blaser et al., 2011). During this period, tropical timber exports generated an annual revenue of US$2.1 billion (Malhi et al., 2014), highlighting the economic motives underpinning wood extraction. It is important to note that, when practiced sustainably, logging does not result in forest degradation (Bryan et al., 2013). However, short-term profits incentivize unsustainable harvest intensities that compromise forest integrity (Putz et al., 2012). Unsustainable logging is characterised by the disproportionate removal of large trees and substantial collateral damage to residual vegetation (Pinard and Putz, 1996). This results in structural simplification of the remaining forest, characterised by a lower, less variable canopy height profile, fewer vegetation strata (Kumar and Shahabuddin, 2005, Okuda et al., 2003) and a spatially dispersed canopy (Hardwick et al., 2015). The immediate environmental consequences of logging are accompanied by insidious secondary impacts. Logging provides the economic impetus for road construction (364,489 km built in Malaysian Borneo alone; Bryan et al., 2013), which subjects the remaining stand to a suite of environmental pressures, including illegal colonisation, increased incidence of wild fire, and hunting (Bicknell et al., 2015, Laurance and Arrea, 2017).

Logged forests are central to global conservation planning due to their well-documented biological value. Selectively logged forests have been found to retain between 70 and 90% of the species found in primary forest (Berry et al., 2010, Edwards et al., 2011, Edwards et al., 2014, Struebig et al., 2013, Wearn et al., 2017). Though reported compositional shifts in faunal communities suggest that forest specialist species may be sensitive to the structural alterations associated with timber extraction (Edwards et al., 2014). Nuanced assessments of the biodiversity value of logged forest have provided a more conservative appraisal of their capacity to retain species. Biodiversity has shown to be sensitive to harvest intensity (Burivalova et al., 2014), extraction method (Bicknell et al., 2014) and frequency of temporal rotation (Edwards et al., 2011). Taken as a whole, these findings suggests that logged forests can make a significant contribution to biodiversity conservation provided they are managed responsibly and sustainably. Moving forward, it is imperative to safeguard logged forests from conversion to agricultural land of lower biodiversity value (Barlow et al., 2007, Edwards et al., 2010a), which has become a common land-use trajectory in tropical regions. Given limited conservation funding (McCarthy et al., 2012) and the vast extent of the timber estate, a deeper understanding of the specific structural features of logged forest that promote biodiversity retention to inform conservation prioritisation would be desirable.

Habitat fragmentation

Fragmentation refers to the process by which habitat loss fractures continuous tracts of habitat into a spatial subset of ecological islands that are nested within a human-modified matrix (Ewers and Didham, 2006). Globally, proximate mechanisms of land-use change have greatly accelerated the extent and magnitude of habitat fragmentation (Wilson et al., 2016). The remaining forest estate comprises 130 million fragments across the world, averaging 29 ha in size (Brinck et al., 2017, Taubert et al., 2018). Consequently, a growing proportion of biodiversity resides within fragmented landscapes across the tropics (Gibson et al., 2011), which requires an understanding of fragmentation impacts on biodiversity persistence.

Habitat fragmentation processes operate at both patch- and landscape scales to influence the distribution of biodiversity (Fahrig, 2003). At the patch scale, Island

Biogeography Theory (MacArthur and Wilson, 2001) predicts that smaller, isolated patches support impoverished faunal communities due to extinction-colonisation dynamics. Habitat size places constraints on the number of species a patch can sustain. Smaller fragments support fewer species, occurring at lower densities, which are more vulnerable to local extinction due to stochastic events (Ewers and Didham, 2006). Patch isolation determines the rate of colonisation, isolated patches receive fewer immigrants to buffer resident populations against local extinction (Brown and Kodric-Brown, 1977). However, the degree to which a fragment is isolated is dictated by fragment shape, the structural connectivity of the landscape and the dispersal capacity of the species (Cote et al., 2017). A global synthesis of fragmentation impacts on biodiversity confirmed these theoretical underpinnings, documenting consistent population declines and reduced local species richness for a number of species in smaller, more isolated fragments (Haddad et al., 2015).

At the patch-scale, edge effects are key determinants of biodiversity. Edge effects refer to the proportion of habitat influenced by environmental externalities, and become more pronounced with decreasing fragment size (Laurance, 2008). Edge habitat is characterised by distinct abiotic conditions and altered biotic interactions that obligate forest species cannot tolerate (Laurance et al., 2011). Population declines for 652 species have been documented in edge-effected habitat (Pfeifer et al., 2017). Moreover, edge effects were found to permeate up to 400 m into the forest, though other estimates suggest these effects can extend up to 4 km from the forest edge (Brodie et al., 2015a). Edge effects alter microclimatic conditions and biotic interactions, resulting in elevated tree mortality, proliferation of invasive species and dominance of ecotone-tolerant generalists (Laurance, 2008). Collectively, these modifications disrupt ecological processes and place pressure on sensitive obligate forest species (Ewers and Didham, 2006, Pfeifer et al., 2017). It is estimated that 70% of the world's forests are situated within 1 km of a forest edge (Haddad et al., 2015), indicating the scale of edge influences on biodiversity.

Patch-scale dynamics are mediated by the landscape context, specifically the proportion of habitat remaining in the landscape and matrix attributes (Fahrig, 2017). The habitat amount hypothesis suggests that patch-scale influences on biodiversity are redundant until the total available habitat within a landscape drops below a threshold of 30% (Banks-Leite et al., 2014). This hypothesis was corroborated in an oil palm-dominated landscape, though at a higher forest habitat threshold of 25-55% (Pardo et al., 2018). This suggests that the threshold value may be contingent on matrix attributes. Commonly neglected in theoretical frameworks of fragmentation, matrix qualities have been shown to supersede patch-level influences on species occupancy and community composition (Garmendia et al., 2013). It has been suggested that species can persist in sub-optimal habitat patches and overcome dispersal limitations provided they can exploit supplementary resources in the matrix (Antongiovanni and Metzger, 2005, Ricketts, 2001, Sodhi et al., 2005). Taken as a whole, the distribution and persistence of biodiversity in fragmented landscapes is determined by processes operating across multiple spatial-scales, which must be uncoupled to ascertain and mitigate the distinct drivers of species loss.

The retention of forest fragments within human-modified landscapes has long been recognised as a valuable management tool to secure biodiversity retention. Understanding the dynamics of biodiversity persistence in fragmented landscapes is, therefore, central to developing effective management strategies and policies

(Meijaard and Sheil, 2007). However, quantifying the optimal characteristics of remnant vegetation that promote biodiversity retention has proved challenging (Fahrig, 2003). This information is fundamental to guide policies that seek to establish ecologically functional forest networks in human-modified environments.

Hunting

The ‘empty forest syndrome’ is a pervasive phenomenon describing the widespread defaunation of forests as a result of hunting (Redford, 1992, Harrison, 2011). Across the tropics, intact vertebrate assemblages are estimated to occur in only 1-35% of the remaining forest extent (Morrison et al., 2007). Wildlife are generally hunted for food, medicine, ornamentation or illegal trade (Corlett, 2007). Subsistence hunting is considered sustainable at a population density of 1 person per km^2 (Robinson and Bennett, 2004), however current population densities in human-modified areas across the tropics range between 46 and 522 people per km^2 (Bennett, 2002). Bushmeat harvest rates reflect this discrepancy, with between 150 and 4,900 tonnes harvested across tropical regions annually (Fa et al., 2002). Though these figures likely underestimate current levels of offtake. Moreover, infrastructure development and growing affluence stimulate remote demand for wildlife derivatives (Harrison et al., 2016). Yet, despite substantial impacts, hunting continues to represent a source of uncertainty in studies investigating biodiversity persistence in human-modified landscapes.

Hunting can have profound impacts on the abundance, diversity and composition of wildlife communities (Peres, 2001). In a pantropical meta-analysis, Benítez-López et al. (2017) documented an 83% reduction in mammal populations due to hunting with accessibility being the most influential determinant of biotic declines. Hunting pressure is therefore exacerbated by proximate mechanisms of land-use change that develop infrastructure to facilitate access to remote forest frontiers. Humans are typically central place foragers, thus hunting intensity is a function of distance from human settlements and generally decays beyond a threshold of 20 km (Peres, 2000). Technological advances in weaponry and the accessibility of international markets for the exportation of animal products have intensified offtake in affected regions (Harrison et al., 2016). Hunting pressure is a delicate balance between hunter preference and species sensitivity. Human hunting practices can be examined in relation to optimal foraging theory, whereby maximum returns are sought per unit effort (Cowlishaw and Dunbar, 2000). Accordingly, large game offer the best return on effort, while abundant species, or those displaying behavioural traits that facilitate identification and location (i.e. group living, vocal, predictable behaviour patterns), are desirable harvest options due to ease of capture (Stafford et al., 2017, Wright, 2003). Vulnerability to hunting is also dependent on the biological characteristics of the target organism, with long-lived species, persisting at low densities with long generation times being sensitive to exploitation (Ripple et al., 2016). Furthermore, the selective removal of preferential species alters biotic interactions across multiple trophic levels, with cascading effects on biodiversity and ecosystem services (Brodie, 2018, Rosin, 2014, Wright, 2003). For example, the persecution of large frugivorous mammals and birds disrupts the process of seed dispersal, influencing the spatial and genetic signatures of plants and trees, and thus the services provided by the forest (Harrison, 2011). Thus, hunting has far-reaching consequences beyond numerical and distributional restrictions on forest-dwelling taxa.

Hunting is a cryptic phenomenon that is notoriously difficult to quantify, restricting our capacity to manage unsustainable exploitation in human-modified landscapes (Benitez-Lopez et al., 2017, Peres, 2001). Current understanding of hunting impacts is predominantly derived from coarse comparisons of hunted versus non-hunted sites (Cullen Jr et al., 2000, Galetti et al., 2009) or direct/indirect encounters with human hunters (Brodie et al., 2015b, Sampaio et al., 2010). Both approaches are problematic to execute. Statistics would suggest that no area of the tropics is truly free of hunting pressure, while it is simplistic to infer absence of evidence based on evidence of absence given potential for imperfect detection. Qualitative methods, particularly specialised interview techniques (Nuno and St. John, 2015), offer promising tools to investigate hunting, while mitigating non-response (Groves, 2006) and social desirability bias (Fisher, 1993) commonly associated with investigations regarding illegal behaviour. However, these techniques require large sample sizes, impose limitations on survey design and introduce a methodological complexity that may prove challenging for people with a limited educational background (Nuno and St. John, 2015). Alternatively, proxies for anthropogenic pressure based on proximity to infrastructure are commonly employed (Benitez-Lopez et al., 2017, Michalski and Peres, 2007). While hunting has been consistently linked to distance to access points (Symes et al., 2016), basic Euclidean distance measures fail to capture the complexity of accessibility. Collectively, this implies a need for a spatially explicit hunting index that captures the nuance of contemporary hunting practices.

Policy options for biodiversity conservation in human-modified landscapes

Halting the modification and conversion of forests is perhaps the most effective strategy to ensure species persistence in tropical landscapes. Protected areas are known to be an effective tool to safeguard biodiversity in the tropics (Beaudrot et al., 2016a, Laurance et al., 2012) and attenuate forest loss (Gaveau et al., 2007, Geldmann et al., 2013, Linkie et al., 2008). However, they are spatially underrepresented and under-resourced (Butchart et al., 2015). It is widely acknowledged that key biodiversity areas are not captured by the current protected area configuration (Watson et al., 2014), which accounts for only 9.8% of the tropical biome (Schmitt et al., 2009). Moreover, there is lingering uncertainty as to how static protected areas will capture dynamic shifts in species distributions due to climate change (Guisan et al., 2013). It is estimated that less than 10% of the current protected area network is expected to represent present climatic condtions in the next century (Loarie et al., 2009). Although international commitments to expand the global extent of the protected area network will afford some security to tropical forests and biodiversity (Aichi Target 11; Convention on Biological Diversity, 2010), previous expansions have been predominantly opportunistic, resulting in unrepresentative, biased spatial coverage (Butchart et al., 2012, Joppa and Pfaff, 2009). Only 6% of protected areas reported sufficient resources for effective management (Convention on Biological Diversity, 2003), with cascading influences on boundary delineation, enforcement, resource management and the provision of infrastructure (Bruner et al., 2001). The economic sustainability of protected areas has also been questioned. Less than 10% of maintenance costs are met by tropical nations, suggesting an over-reliance on external support to meet management costs (Balmford et al., 2003). Collectively, these limitations encourage poor governance and reduce protected area effectiveness, which, in turn, compromises biodiversity conservation objectives. While protected areas remain a fundamental element of global conservation strategies, their capacity to safeguard biodiversity is contingent on informed expansion and financial reinforcement (Pouzols et al., 2014).

There is increasing recognition that the efficacy of protectionist approaches to conservation is inextricably linked to the socio-economic factors that underpin land-use change (Symes et al., 2016). Thus the potential for the reserve network to contribute to biodiversity objectives is determined by the extent to which anthropogenic pressures are managed in adjacent human-modified landscapes (Chazdon et al., 2009). Two dominant paradigms have emerged to reconcile the socio-economic dimensions of land-use change and biodiversity persistence in modified systems: conservation payment mechanisms and supply-chain initiatives. These instruments are voluntary, market-based and predominantly incentive-driven, but vary in their degree of state involvement (Lambin et al., 2018, Lambin et al., 2014). Common to both is explicit consideration of the landscape-level impacts of human actors (Perfecto and Vandermeer, 2008) and an understanding of the coupled socio-ecological dynamics inherent in human-modified landscapes (Liu et al., 2007).

Market-based payment mechanisms

Market-based payment mechanisms describe a range of policy instruments that assign economic value to natural capital to provide financial encouragement for conservation (Miles and Kapos, 2008, Wunder, 2007). They are founded on the tenet that benefits derived from nature must be perceived before conservation can be justified (Barlow et al., 2018). Commoditising ecosystem services derived from tropical forests provides the economic impetus for their protection, which improves prospects for biodiversity in vulnerable landscapes while garnering local support for conservation (Tilman et al., 2017). Payment mechanisms are inherently performance-based and characterised by conditional voluntary agreements (Wunder et al., 2008). Financial incentives can be structured to compensate avoided action or reward pro-active environmental management (Wunder, 2005). Adjacent policies are underwritten by the dual concepts of dependency and willingness to pay (Redford and Adams, 2009). Willingness to pay by consumers must exceed the inclination of the provider to accept payment, thus, to guarantee successful implementation, perceived benefits must offset incurred opportunity costs (Lambin et al., 2014). Moreover, payment mechanisms are dependent on institutional frameworks to facilitate financial transactions and secure compliance from service providers (Muradian et al., 2010, Van Noordwijk et al., 2012).

A suite of problems relate to the commoditization of natural capital provided by forests. Some ecosystem services are not amenable to economic valuation (Abson and Termansen, 2011), and, while effective markets exist for provisioning services, they are lacking for cultural, supporting and regulating services, necessitating charitable support (Adams, 2014). Even when effective markets exist, the value of the ecosystem service is dictated by market forces, supply and demand, all of which may fluctuate to remove economic value from the ecosystem and thus financial motivations for conservation (Vira and Adams, 2009). If the quantity or value of the final ecosystem service is of overarching importance, there are concerns that delivery can be met in impoverished environments, or, novel, synthetic ecosystems that maximise ecosystem service delivery yet retain little native biodiversity (Redford et al., 2014). Finally, the social success of ecosystem service orientated policy is contingent on the equitable distribution of benefits; a failure to incorporate local communities into benefit-sharing can lead to conflict, leakage and institutional failure (Birch et al., 2014).

The United Nations Reducing Emissions from Deforestation and forest Degradation (REDD+) policy is perhaps the most prominent conservation payment mechanism. REDD+ provides a financial alternative to the proximate mechanisms of land-use change. Within the REDD+ framework developing nations are compensated for actions that maintain, enhance or restore the carbon stored in tropical forests (Miles and Kapos, 2008). Qualifying actions comprise a range of management strategies, including avoided deforestation, sustainable forest management and afforestation (Venter and Koh, 2012). From a biodiversity conservation perspective, REDD+ is an attractive prospect due to its potential to deliver biodiversity co-benefits (Gardner et al., 2012). These “win-win” outcomes allude to regions where carbon value is intrinsically linked to high biodiversity, thus management actions that maintain carbon simultaneously protect biodiversity at no additional cost. To date there is little consensus on the capacity for REDD+ to deliver co-benefits (Anderson et al., 2009, Ferreira et al., 2018, Naidoo et al., 2008, Turner et al., 2007), indicating they are likely scale-dependent and context-specific. Understanding the conditions necessary for co-benefits is essential to target REDD+ applications to where they will be most effective.

Supply chain initiatives

Supply chain initiatives describe a broad suite of environmental commitments proposed by private actors to demonstrate sustainability within their operations (Lambin et al., 2018). They reflect a corporate response to growing consumer unease concerning the links between commodity production and environmental degradation. Supply chain initiatives have been aligned with the New York Declaration on Forests, under which, corporate actors pledged to eliminate deforestation associated with commodities before 2020 (United Nations, 2014). These developments indicate increasing traction for environmentally-conscious production.

Supply chain initiatives encompass two complimentary paradigms: sectoral standards and corporate pledges. Sectoral standards refer to principles and criteria adopted by coalitions of companies that define sustainable standards of practice (Lambin et al., 2018). These standards are conventionally formalised within the context of eco-certification schemes which require compliance from affiliated companies, often at significant opportunity costs (Auld et al., 2008). In recompense, companies receive price premiums on certified products and preferential access to lucrative, environmentally-vigilant Western markets (Lambin et al., 2014). In recent decades, nearly 400 certification standards have incorporated environmental safeguards on a range of goods and services, including the tropical soy, beef, forestry and oil palm sectors (Carlson et al., 2018). Timber and oil palm certification are governed by the Forest Stewardship Council (FSC) and Roundtable on Sustainable Palm Oil (RSPO), respectively. Critics have argued that certification schemes are compromised by weak standards (Laurance et al., 2010), ambiguous guidelines (Dennis et al., 2008), limited enforcement (Ruysschaert and Salles, 2014) and a failure to reprimand non-compliance (Meijer, 2015). Moreover, limited uptake constrains the environmental scope of certification. For example, certified oil palm accounts for only 20% of the global trade (Garrett et al., 2016). The shortcomings of certification schemes to safeguard biodiversity is evidenced by a 500,000 ha loss of Sumatran orang-utan (*Pongo abelii*) habitat during the operational tenure of the RSPO (Ruysschaert and Salles, 2014). Conversely, since 2000, certified Indonesian oil palm concessions were associated with a 33% reduction in deforestation compared to non-certified plantations (Carlson et al., 2018), indicating that continual revisions of sustainability criteria may be overcoming some of the these limitations.

Corporate pledges are publicly stated, non-governmental commitments to source and produce commodities independently of deleterious social and environmental impacts. Recent “zero-deforestation” pledges to eliminate forest loss from commodity supply-chains demonstrate corporate commitment to sustainability. Sustainability pledges arose from the perceived inadequacy of sectoral standards (Khor, 2011). While corporate pledges do not yield financial benefits equivalent to certification, they reduce the reputational risk associated with commodity production and create a favourable brand image (Lambin et al., 2018), which can be used to leverage an increased market share and maximise profits (Alves, 2009, Elder et al., 2014). However, tracking compliance with zero-deforestation commitments has proved challenging due to land tenure disputes (Gaveau et al., 2016a). Moreover, in the context of corporate pledges, deforestation can refer to net- or gross-deforestation, which have contrasting implications that can translate to perverse practical outcomes for conservation (Brown and Zarin, 2013). There are also concerns that zero-deforestation could limit socio-economic growth in nations with a high proportion of primary forest cover (Senior et al., 2015). If corporate commitments are to safeguard tropical forests and their biodiversity, there needs to be greater standardisation in the formulation, adoption and implementation of sustainability pledges.

Effective methodologies to identify and prioritise forest habitat in human-modified landscapes are essential to translate corporate commitments into environmentally sustainable operations. Presently, High Conservation Value (HCV) criteria guide the implementation of many supply-chain initiatives in the forestry, agriculture and mining sectors. The HCV concept seeks to identify areas with exceptional ecological, social or cultural importance, and ensure that they are managed in a manner that maintains or enhances their inherent value (Brown et al., 2013). A key criticism of the HCV tool is that the criteria are too spatially restrictive to provide sufficient security to the vast expanses of forest vulnerable to conversion (Edwards et al., 2012). HCV criterion 3 focuses on endangered, rare or endemic species and ecosystems, which are intrinsically range restricted, thus limiting the geographical scope of the concept (Edwards et al., 2012). Moreover, HCV criteria afford no explicit security to degraded forests that comprise the majority of the remaining forest estate and retain considerable ecological value (Barlow et al., 2007, Berry et al., 2010, Struebig et al., 2013). Though, it is worth noting that social or cultural HCV criteria (4-6) may afford species protection where explicit recognition is absent. However, HCV implementation is further hindered by a weak logistical framework (Yaap et al.,

2010) and implementation guidelines that are open to interpretation and malpractice (Koh et al., 2009). The success of supply-chain initiatives is dependent on consumer and corporate belief in the integrity of the product, which could be jeopardised by the misapplication of tools that strive to deliver environmental sustainability. Evidently, there is a need to develop and evaluate alternative instruments that can objectively and transparently identify areas of conservation value within production landscapes.

Status of the world's mammals

The taxonomic class Mammalia, colloquially termed mammals, is a diverse grouping of 5,487 species distributed across 1,229 genera, 153 families and 28 orders (Bininda-Emonds et al., 2007, Schipper et al., 2008). Mammals are an exceptionally adaptive group inhabiting most of the world's terrestrial and marine biomes. Mammals occupy key ecological roles in tropical forest ecosystems, including trophic regulation (predation: Estes et al., 2011, Terborgh et al., 2001, herbivory: Jia et al., 2018, Smith et al., 2016), seed dispersal (Corlett, 2017, Granados et al., 2018), seed predation (Asquith et al., 1997) and biogeochemical cycling (Berzaghi et al., 2018, Sobral et al., 2017). It is estimated that 90% of tropical tree species depend on interactions with wildlife to complete their life cycles (Malhi et al., 2014). Consequently, mammal extirpation can have cascading effects on ecosystem functioning and stability (Kurten, 2013). For example, Brodie (2018) linked the loss of tropical mammals to large-scale compositional shifts in tropical tree communities and concomitant declines in carbon sequestered by tropical forests. Moreover, no other taxonomic group has captivated humanity more than mammals. They are frequently cited as high profile species with demonstrated public appeal (Macdonald et al., 2015). Mammals are thus highly effective conservation ambassadors to raise public awareness of critical ecological issues and garner financial support for interventions through international marketing campaigns (Macdonald et al., 2017).

Despite their inherent value, conservation efforts to safeguard mammals have often proved ineffective. Twenty-five percent of mammals, equating to 1139 species, are considered threatened with extinction, most of which are concentrated in the tropics (Hoffmann et al., 2010, Schipper et al., 2008). Land-use change is a principal driver of threat status (Crees et al., 2016, Tilman et al., 2017), with estimates suggesting affected species have lost an average of 50% of their historical range (Ceballos and Ehrlich, 2002). Dwindling habitat availability coupled with wide-ranging habits suggests that conservation strategies focussing solely on the preservation of primary forest will be of little value. New approaches to compliment protectionist strategies are therefore essential to safeguard vulnerable mammal populations.

Effective conservation requires accurate information on the distribution, occurrence and abundance of threatened species. In the tropics, mammal conservation is hindered by an alarming paucity of information on the ecology of threatened species (Sodhi, 2008). This is reflected in the fact that 15% of described species are considered data-deficient on the IUCN Red List (Schipper et al., 2008). Acquiring the necessary information to inform mammal conservation is complicated by their ecology. Mammals are inherently cryptic, persist at low densities and range over wide areas which makes them logistically challenging to study (Brodie et al., 2015b). Developing evidence-based solutions to the threats facing mammals requires methodologies that can overcome these limitations.

Technological and statistical mitigation measures

Modern advances in remote technologies and statistical methods present opportunities to overcome the obstacles associated with sampling tropical mammals. Remotely operated digital cameras, or camera-traps, have emerged as an effective tool to gather ecological information on cryptic, data-deficient species. Camera-traps are continuous time detectors that employ motion- and passive infra-red sensors, triggered by a combination of movement and anomalous heat signatures. The use of camera-traps as a Eulerian approach to biodiversity monitoring has increased markedly in recent decades as units have become more affordable and efficient (Rowcliffe and Carbone, 2008). Camera-traps are now widely-recognised as the principal sampling strategy for a range of applications, including abundance estimations, taxonomic inventories, conservation assessments and behavioural evaluations (Burton et al., 2015). The main advantages of camera-traps are that they provide a non-invasive, labour-efficient means to collect robust information on wildlife populations largely free of observer bias (Kays et al., 2009). When compared to alternative sampling methods such as line transects and track counts, camera-traps were found to be the optimal sampling method for medium-large mammals (Silveira et al., 2003).

Despite these benefits, biodiversity monitoring using camera-trap methods is confounded by imperfect detection, where a species is present but not detected within a sampling unit (Guillera-Arroita, 2017, MacKenzie et al., 2017). Failure to account for imperfect detection results in an underestimation of the biological response of the target species, introducing inferential bias that can propagate into management recommendations (Benoit et al., 2018). Moreover, rare species, that are often most vulnerable to land-use change, often yield insufficient data for reliable inference, regardless of survey effort (Sollmann et al., 2013, Zipkin et al., 2010). Recent innovations in hierarchical modelling have provided a framework to mitigate the consequences of imperfect detection and rare species occurrence (Dorazio and Royle, 2005). Hierarchical models comprise conditionally-dependent, sub-components describing the ecological and sampling processes underpinning the data (Gelman and Hill, 2006). Thus the state process of interest can be corrected through explicit recognition of detectability (Zipkin et al., 2009). In the case of rare species, multi-species modelling approaches introduce an additional hierarchical component that draws species-specific inferences from collective community data. This has been shown to improve parameter precision for species infrequently detected during sampling (Broms et al., 2016, Pacifici et al., 2014). From a conservation management perspective, multi-species models provide an efficient procedure to optimise camera-trap by-catch and determine the impact of interventions across a range of species, rather than merely those targeted by conservation/research initiatives (Benoit et al., 2018, Zipkin et al., 2010).

Conservation assessments typically require species locality data be coupled with covariates describing the biotic and abiotic conditions of a site. These species-habitat associations underpin our understanding of how a species will respond to environmental perturbations. Given the vast area requirements of larger mammals, it is logistically unfeasible to collect environmental covariates at ecologically meaningful scales *in situ*. Moreover, species-habitat associations are multi-factorial processes, operating across a range of spatial and temporal scales (Chalfoun and Martin, 2007). To capture this complexity, biotic and abiotic conditions need to be quantified over a range of spatial extents that are rarely known *a priori* (Mayor et al., 2009).

Advances in remote-sensing have provided ecologists with a toolkit to couple *in situ* biodiversity data with global environmental datasets to develop informed mitigation actions for land-use change (Turner, 2014). Remote-sensing products provide extensive spatio-temporal coverage of the tropical biome, facilitating the characterisation of biodiversity patterns across remote, under-sampled regions (Anderson, 2018, Pettorelli et al., 2014, Turner et al., 2015). However, tropical forest applications are hindered by technological constraints and environmental challenges. Optical remote-sensing techniques cannot reliably detect forest disturbance (Bryan et al., 2013). For example, satellite-imagery has been shown to underestimate forest degradation by up to 50% (Asner et al., 2005). Moreover, cloud cover, atmospheric disturbances and topographic shadow effects restrict the quality and availability of valid observations (Miettinen et al., 2014). Yet, even when data of sufficient quality are accessible, the temporal window to quantify forest disturbance is limited due to rapid regrowth of secondary vegetation (Peres et al., 2006). The scope of remote-sensing is also restricted to appraisals of upper canopy elements due to the inability of sensing apparatus to sufficiently penetrate the uppermost layer of vegetation (Gibbs et al., 2007, Morel et al., 2011). High-resolution airborne Light Detection and Ranging (LiDAR) has emerged as a possible panacea to these challenges and has become a popular tool to characterise fine-scale habitat influences on biodiversity (Lefsky et al., 2002). However, to date, LiDAR applications to support the conservation of terrestrial mammals in tropical regions are largely lacking (Davies and Asner, 2014).

Southeast Asia: a region in crisis

Southeast Asia's forests are considered the most intensively used across the tropical biome (Laurance, 2007). Southeast Asia is defined by member states of the Association of Southeast Asian Nations: Cambodia, Lao PDR, Myanmar, Thailand, Viet Nam (continental); Brunei, Indonesia, Malaysia, Papua New Guinea, Timor Leste (insular); Miettinen et al. (2014). The region has lost 32 million ha of forest cover since 1990 and has been subjected to some of the highest deforestation rates in the world (Sodhi et al., 2010, Stibig et al., 2013). The dominant drivers of deforestation include the proliferation of commodity agriculture and industrial-scale selective logging, which represent 77- and 13% of forest loss respectively (Curtis et al., 2018). Southeast Asia exports in excess of 62 million tonnes of oil palm annually, which equates to 85% of the global supply (Meijaard et al., 2018). It is estimated that 55% of the region's current oil palm extent came at the expense of primary forest (Koh and Wilcove, 2008). Moreover, the region contributes 67% of the total volume of harvested tropical timber (Sodhi, 2008). The commercial value of Southeast Asia's dominant dipterocarp trees has resulted in the highest timber extraction rates across the tropics, exceeding 100 m^3 ha^{-1}, which is an order of magnitude greater than those experienced in South America or Africa (Fisher et al., 2011a, Sodhi et al., 2004). The remaining forest across the region is highly fragmented and susceptible to secondary disturbance impacts (Brinck et al., 2017). The initial intrusion caused by anthropogenic habitat modification increases accessibility to remote forest frontiers and extends the reach of human hunters (Harrison et al., 2016). It is estimated that only 1% of the remaining forest cover is free of some level of hunting pressure (Morrison et al., 2007). With the Southeast Asian population scheduled to increase to

2.6 billion before 2050 (Laurance, 2007), these pressures are likely to intensify over time.

Pervasive forest modification threatens Southeast Asia’s exceptional biological diversity. The region overlaps with four global biodiversity hotspots, characterised by rarity and endemism (Myers et al., 2000). For example, the Sundaland hotspot accommodates 3% of the planet’s endemic vertebrates (Myers et al., 2000). However, if patterns of land-use change continue upon their present trajectory, it is estimated that 79% of the region’s vertebrates will be consigned to extinction by 2100, 48% of which are mammals (Brook et al., 2008). Mammals have lost 70% of their original habitat across the region (Myers et al., 2000), though the development of effective conservation measures has proved challenging due to a weak ancilliary evidence-base. Basic ecological knowledge is lacking for most Southeast Asian vertebrate species, 32% of which are considered data-deficient (Li et al., 2016). The case study of Singapore provides a stark reminder as to the ecological consequences of unabated land-use change, with a 95% reduction in forest cover precipitating the loss of 87% of the faunal community (Brook et al., 2003). Given the scale of regional forest modification, evidence-based conservation interventions that recognise the role of human-modified landscapes are essential to safeguard Southeast Asia’s imperilled, but poorly understood, mammal diversity.

Thesis structure

This thesis aims to ascertain the biological value of human-modified landscapes for tropical mammals that are acutely threatened by land-use change but poorly known to science. To this end, I aim to fill critical knowledge gaps in tropical mammal ecology, while assessing how well they are represented within policy options that seek to enhance the conservation potential of human-modified landscapes and address the distal drivers of land-use change. Capitalising on contemporary advances in remote technologies and statistical modelling, I aim to understand the value of coupled applications to overcome impediments associated with sampling rare, cryptic and wide-ranging species. Throughout, I focus on Southeast Asia, a region characterised by unsustainable levels of land-use change and wildlife exploitation. Evaluating policy options in this geographic context provides a much needed evidence-base for a vulnerable tropical region while strengthening the conservation toolkit to prevent environmentally analogous outcomes elsewhere in the tropics. To achieve these principal aims, this thesis comprises three data chapters, each of which constitutes a stand-alone research paper. Due to the collaborative nature of these chapters I adopt a shift in passive voice, replacing singular- with plural pronouns.

Chapter 2 provides a nuanced appraisal of the biodiversity value of logged forests. Using high-resolution remote-sensing data and novel processing techniques, we describe forest architectural properties across a gradient of disturbance at unprecedented levels of detail. We characterise mammal-habitat associations using bespoke multi-species, multi-scale occupancy models to capture the hierarchical nature of habitat selection relative to the structural environment. Using a high conservation value species as a case study, we demonstrate how model outputs can be practically applied to inform the prioritisation of conservation and restoration areas to support ambitious policy targets for degraded land rehabilitation.

Chapter 3 explores the potential for carbon-orientated policy mechanisms to safeguard forest remnants of biodiversity value in production landscapes. Specifically, we investigate spatial concordance between carbon and biodiversity to understand the potential for aligned climate change mitigation and conservation outcomes in human-modified landscapes. We develop robust estimates of mammal occupancy and species richness to provide the first scientific appraisal of the biodiversity credentials of phase one High Carbon Stock protocols, which we critically compare to a REDD+ application. Our assessment builds on the shortcomings of previous research by using primary biodiversity data and adopting spatial scales appropriate to decision makers.

Chapter 4 builds on the work of **Chapter 3** by assessing the value of phase two HCS protocols to design ecologically functional forest mosaics in human-modified landscapes, which we use to ascertain the value of tools aligned to zero-deforestation commitments. Specifically, we characterise mammal abundance in forest fragments to understand the patch- and landscape-level properties that promote biodiversity persistence. Moreover, we incorporate a bespoke spatially-explicit hunting pressure variable to quantify secondary disturbance impacts on mammal populations. We use these outputs to understand whether current HCS recommendations safeguard vulnerable mammals in fragmented landscapes.

Chapter 2. Prioritising high conservation value forests for tropical mammals using coupled technological and statistical approaches

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Manuscript in preparation

Abstract

Logged forests are considered integral to global conservation planning, yet our understanding of the specific structural properties that facilitate species persistence in degraded habitats is lacking. Moreover, forests are inherently three-dimensional environments yet this is rarely incorporated into assessments of species-habitat associations to inform conservation action. Focussing in Sabah, Malaysian Borneo, a region characterised by high levels of forest degradation, we couple airborne multispectral remote-sensing methods (LiDAR) and camera-trapping to capture the three-dimensional properties of forest architecture and quantify the terrestrial mammal community across a gradient of disturbance. Here we reveal how habitat structural properties mediate biodiversity declines relative to logging-induced structural degradation. Mammals were most responsive to covariates that explicitly captured vertical structure and heterogeneity and actively selected habitats retaining old growth structural characteristics, including tall canopies, increased plant area density throughout the vertical column and the availability of a greater diversity of environmental niches. We find mammals to be more responsive at the scale of third-order habitat selection, indicating that resources are tracked at successively lower hierarchical levels to overcome limitations in impoverished environments. Our results demonstrate the sensitivity of mammals to logging-induced changes in forest structure, providing empirical support for sustainable forestry practices that maintain architectural diversity. To support policies aimed at prioritising degraded land for conservation, we introduce a framework to integrate biodiversity considerations into environmental decision-making. Focussing on a high conservation priority species, we demonstrate how ecological thresholds, delineating abrupt changes in the occurrence state relative to aspects of the structural environment, can be practically applied to prioritise conservation and restoration areas in degraded systems.

Keywords: Camera-trapping, ecological thresholds, forest structure, LiDAR, occupancy, prioritisation, selective logging, Southeast Asia, Sunda clouded leoprard.

Introduction

Habitat degradation is globally pervasive in forest ecosystems, affecting ~4 billion hectares (82%) of the remaining forest extent (Watson et al., 2018). Forest degradation can have profound impacts on habitat suitability for terrestrial vertebrates, particularly in tropical regions where biodiversity is most concentrated (Barlow et al., 2018). This has led to degradation concerns being integrated into policy, most notably by the Bonn Challenge which seeks to restore 350 million hectares of degraded land before 2030 (http://www.bonnchallenge.org/). However, frameworks to integrate biodiversity considerations into the prioritisation of vulnerable degraded forests for conservation are currently lacking, though remain essential in tropical regions with limited institutional or regulatory capacity.

Logging in the tropics, albeit selective, can be destructive (Asner et al., 2005), resulting in structural simplification of forests due to the disproportionate removal of high biomass trees and collateral damage to residual vegetation (Pinard and Putz, 1996). Degraded forests now rival intact primary forests as the dominant form of forest cover within the tropical biome and have become central to global conservation planning. While the value of logged forest for biodiversity conservation is well established for a range of taxonomic groups (Edwards et al., 2014, Putz et al., 2012, Wearn et al., 2016), this perspective is primarily derived from coarse comparisons of logged and primary forest. By coercing habitat into uniform classifications, studies overlook spatial heterogeneity within and between logging concessions, which can be substantial (Berry et al., 2008). When defined along a continuum, the conservation value of logged forest is known to decline with increasing logging intensity (Burivalova et al., 2014), extraction technique (Bicknell et al., 2014) and temporal frequency of rotation (Edwards et al., 2011). While these findings allude to the ecological consequences of biomass extraction, we still have a limited understanding of the specific structural attributes associated with biodiversity retention in degraded forest ecosystems. This information is fundamental to capitalise on conservation opportunities within the vast tropical timber estate and direct interventions to where they will have the greatest impact.

Forest structure is synonymous with habitat quality which has long established consequences for wildlife. Structurally complex environments provide a greater breadth of environmental niches (MacArthur, 1984) and accommodate higher species diversity by facilitating co-existence through mechanisms such as resource partitioning and niche diversification (Hearn et al., 2018b). In forests, structure can be partitioned into horizontal and vertical components, which determine the distribution (Palminteri et al., 2012), diversity (Gouveia et al., 2014), abundance (Martins et al., 2017) and behaviour (Loarie et al., 2013, Lone et al., 2014) of animals. Despite the multidimensionality of tropical forest ecosystems (Oliveira and Scheffers, 2018), considerations of the three-dimensional environment are rarely incorporated into conservation planning. Given that up to 75% of forest-dwelling vertebrates access canopy resources (Kays and Allison, 2001), a broader perspective is desirable.

For forest management to align with biodiversity conservation objectives, an understanding of the structural features of the forest environment that species actively utilise (Moreira-Arce et al., 2016) and how these are associated with ecological processes (Lone et al., 2014) is required. Positive associations with species diversity have been identified in 77% of studies exploring the influence of forest structure (Simonson et al., 2014), indicating active selection for structurally complex environments. Active habitat selection is an adaptive process seeking to balance reward (resource acquisition, mating opportunities) relative to risk (energy expenditure and predation) (Mayor et al., 2009). Therefore, it is generally assumed that preferential habitat use corresponds to areas that convey ecological benefits (Mosser et al., 2009). Given the limited funding available for conservation (McCarthy et al., 2012), knowledge of preferential habitat for vulnerable species is paramount to inform conservation investment. This is particularly pertinent in degraded forests which retain appreciable levels of biodiversity but are susceptible to conversion to agricultural lands of limited biological value (Edwards et al., 2014).

Efforts to characterise habitat selection and inform conservation are hindered by simplifying assumptions that overlook the inherent complexity underpinning species-habitat associations. Habitat selection is a nested hierarchical process describing home range establishment and episodic use of home range elements to meet ecological demands; termed second- and third-order habitat selection respectively (Johnson, 1980). Despite the sensitivity of ecological analyses to scale, habitat selection models predominantly adopt a single-scale focus (McGarigal et al., 2016), which obscure scale-dependent associations and hierarchically-specific environmental interactions (Mayor et al., 2009). Forest architecture is expected to influence patterns of biodiversity at a range of spatial scales (Tews et al., 2004), yet there are few quantitative assessments of habitat structure and biodiversity across multiple scales concurrently (but see Mateo-Sánchez et al., 2016).

The advent of multi-scale occupancy models (Mordecai et al., 2011, Nichols et al., 2008) provides an analytical platform to account for the hierarchically structured, scale-dependent nature of habitat selection while correcting for sampling bias. However, to date, applications have been largely limited to single-species approaches (Aing et al., 2011, Crosby and Porter, 2018, Lipsey et al., 2017, Mordecai et al., 2011). Tropical forest mammals are inherently rare and cryptic, complicating quantitative assessment (Brodie et al., 2015b). Multi-species occupancy models circumvent this issue to provide robust parameter estimates for species infrequently encountered during biodiversity surveys (Dorazio and Royle, 2005). Thus, the formal integration of multi-species methods within a multi-scale framework would provide a powerful statistical tool to capture the complexity of habitat selection for vulnerable species to support conservation interventions in degraded forest ecosystems.

Here, we assess degradation impacts on habitat structure and biodiversity across a gradient of disturbance to provide a nuanced perspective on the conservation value of logged tropical forests. Our detailed appraisal focuses on the Malaysian state of Sabah, in a region characterised by high levels of forest degradation (Gaveau et al., 2016b, Hansen et al., 2013). Of the remaining forest area, 46% is considered degraded, a figure which could likely rise to 88% if current land-use designations are honoured (Gaveau et al., 2014). Combining high resolution airborne LiDAR with sophisticated processing protocols (MacArthur and Horn, 1969, Stark et al., 2012)**,** we develop forest structural metrics based explicitly on three-dimensional plant area distributions and chart their deterioration across a degradation gradient. Drawing on an extensive camera-trap dataset, we identify the specific structural attributes of degraded forest ecosystems that facilitate habitat use. Adopting a novel extension to multi-scale occupancy models we explicitly account for the scale-dependent, hierarchical nature of habitat selection within a multi-species framework. Given the current policy focus of identifying degraded lands for conservation, we demonstrate how species-structure habitat associations can be practically applied to delineate priority restoration and conservation areas in logged forests and guide reactive environmental management plans.

Methods

Study site and sampling design

Fieldwork was undertaken at the Stability of Altered Forest Ecosystems Project (SAFE; www.SAFEproject.net) and neighbouring oil palm estates in Sabah, Malaysian Borneo (Ewers et al., 2011). The SAFE Project experimental area is nested within the Kalabakan Forest Reserve (KFR; 4°33'N, 117°16'E), comprising lowland and hill dipterocarp forest. A legacy of selective logging has resulted in a heterogeneous landscape encompassing a degradation gradient (Fig. 2.1). Between 1978 and 2008, KFR was subjected to multiple logging rotations extracting a total of 179 m^3 ha^{-1}, leaving the remaining stand in a heavily-degraded state (Struebig et al., 2013). Similarly, the adjacent Ulu Segama Forest Reserve underwent two rounds of timber extraction at a reduced cumulative rate of 150 m^3 ha^{-1}, and with more stringent size quotas. In contrast, the adjoining Brantian-Tantulit Virgin Jungle Reserve (VJR) retains near-pristine, old growth forest, though the signature of illegal encroachment is apparent on the western and southern borders. The disturbance gradient is broadly representative of the transitional degradation states typical of landscapes in Borneo and elsewhere in much of tropical Southeast Asia.

We established 74 sampling locations to characterise forest structural properties and the mammal community across the study landscape (Fig. 2.1).

Locations were selected to capture the degradation gradient relative to logging intensity using the Putz and Redford (2010) classification scheme: Old Growth Forest (VJR; *N*=10), Managed Forest (Ulu Segama Forest Reserve; *N*=15) and Heavily-degraded forest (KFR; *N*=28). We also sampled remnant forest embedded within an oil palm matrix (*N*=21), differentiated from degraded forest due to isolation and increased exposure to anthropogenic stressors.

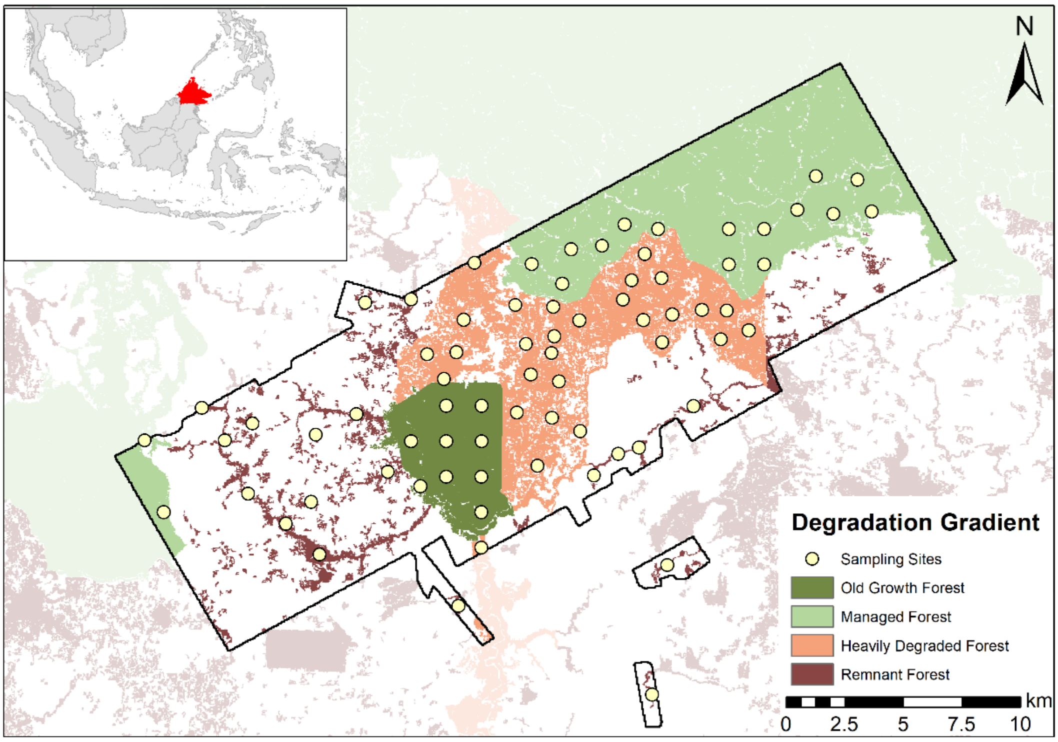


Figure 2.1: Map of the study site and sampling design. Map details the broader geographic context of the study site in Malaysia (inset), the classification of forest across the disturbance gradient within the Stability of Altered Forest Ecosystems (SAFE) project area, LiDAR flight path (black outline) and camera-trap locations (*N*=74).

LiDAR methods and structural variable development

To characterise the structural properties of the landscape, discrete-return airborne Light Detection and Ranging (LiDAR) surveys were conducted in November 2014 by NERC's Airborne Research Facility (Fig. 1b). LiDAR is an active remote sensor that emits a laser pulse of light from a light aircraft towards a target object and quantifies distance based on the time elapsed between emission and reflection (Lefsky et al., 2002). Surveys employed a Leica ALS50-II sensor attached to a Dornier 228-201 light aircraft, flown at an elevation of 1400-2400 m.a.s.l. and a velocity of 120-240 knots. The sensor emitted pulses at a frequency of 120 kHz, encompassing a scan angle of 12° and a footprint of 40 cm, resulting in a point-cloud density of 25-50 points m^{-2}. Concurrent ground surveys using a Leica base station facilitated accurate georeferencing of the point-cloud.

To quantify structural metrics, point-cloud data were subjected to two processing procedures. Initially, ground and non-ground returns were partitioned from the point-cloud, using the former to generate a 1 m resolution digital elevation model (DEM). We constructed a canopy height model (CHM) of similar resolution by normalising non-ground returns and subtracting ground observations derived from the DEM. To complement this approach, and develop a nuanced insight into canopy structure, plant area density (PAD) distributions were generated from point-cloud data using a variant of the MacArthur-Horn (1969) method, modified for use with discrete-return LiDAR (Stark et al., 2012). The MacArthur-Horn method corrects PAD for shadow effects caused by canopy elements closer to the sensor, and thus higher in the vertical column. This approach has distinct advantages over other methodologies. For example, PAD distributions are based strictly on vegetation properties, rather than the underlying point-cloud, thus providing a three-dimensional perspective of the vertical column that cannot be achieved by CHMs. Moreover, independent verification has found strong correspondence between PAD distributions and vegetation samples harvested directly from the vertical column (Stark et al., 2012)**.**

From the CHM and PAD distributions we extracted metrics to capture three distinct axes of the structural environment (Table 2.1; Davies and Asner, 2014): horizontal structure, the arrangement of vegetation in the *x* and *y* dimensions; vertical structure, the arrangement of vegetation in the *z* dimension, and; vertical structural heterogeneity, the variability of canopy properties. We complimented these metrics with structural landscape context variables derived from the CHM to broadly capture the availability and quality of forest habitat (Table 2.1).

As a preliminary assessment of the structural signature of forest degradation, we employed Bayesian linear models to determine differences in forest canopy properties across a degradation gradient. Structural covariates were extracted as mean values across buffer radii corresponding to optimal scales of third-order habitat selection (detailed in Table S2.1). Linear models were implemented in the statistical software JAGS (Just Another Gibbs Sampler) version 4.3.0 (Plummer, 2017), called through R using the package “jagsUI” (Kellner, 2016).

Table 2.1: Structural covariates quantified from LiDAR-derived point cloud data. Covariates capture three distinct axes of forest structure (horizontal structure, vertical structure, vertical heterogeneity) and were derived from either canopy height models (CHM) or plant area density (PAD) distributions developed using the MacArthur-Horn Method and adjusted for use with discrete-return LiDAR.

Structural Axis	Metric	Processing Method	Description
Horizontal Structure	Gap fraction	CHM	Proportion of focal patch containing vegetation below 5 m in height, indicative of forest gaps.
	Number of layers	PAD	Number of contiguous canopy layers within the vertical column, indicative of connectivity
Vertical Structure	Canopy height	CHM	Average canopy height as derived from the CHM surface
	Plant Area Density	PAD	Plant area density, inclusive of vegetation, stems and branches.
Vertical Heterogeneity	Shannon Index	PAD	The diversity of environmental niches within the canopy profile
	Shape	PAD	Morphological measurement of the relative distribution of vegetation within the canopy. Ratio of the height in the canopy with the highest vegetation density and the height of the 99th percentile of the distribution

Landscape Context	Forest Cover	CHM	Proportion of forest cover. Forest defined as trees >10 m in height. Indicative of habitat availability.
	Canopy height variability	CHM	Standard deviation of canopy height. Indicative of forest quality.

Mammal surveys

To characterise the mammal community, we collected detection/non-detection data using camera-traps between June 2015 and August 2017. Remotely-operated digital cameras (Reconyx HC500, Wisconsin, USA) were deployed across the 75 sampling locations, randomly stratified across the degradation gradient (Fig. 1b) and separated by a mean distance of 1.6 km. Within each location, we established two camera-trap stations positioned up to 250 m apart depending on the terrain and availability of forest cover (mean=185 m), resulting in a total of 148 stations. Accounting for theft, vandalism, malfunction and animal damage, data were obtained from 125 units distributed across 74 sampling locations.

Camera-traps were deployed for a minimum of 42 consecutive nights per camera station, yielding a total survey effort of 5,472 camera-trap nights. Cameras were positioned at a standardised height of 30cm and positioned on flat surfaces targeting low resistance travel routes and randomised locations simultaneously to maximise detections and capture intra- and inter-specific difference is species’ use of habitat features (Cusack et al., 2015, Wearn et al., 2013).

Modelling framework

We developed a multi-species extension to multi-scale occupancy models to explore second- and third-order habitat selection by medium-large terrestrial mammals relative to LiDAR-derived structural variables. Within a traditional single-season, single-species framework, occupancy is estimated at defined locations using spatially or temporally replicated samples to account for imperfect detection and thus differentiate between true absence and non-detection (MacKenzie et al., 2017). We extend this framework to incorporate spatial and temporal replication and multi-species inference.

Our model formulation employed single-species models as analytical building blocks (Guillera-Arroita, 2017) and comprised three conditionally-dependent sub-components describing the partially observed processes of occupancy (*z*), habitat use (*a*) (state process model) and detection (observation model). These sub-models corresponded to the hierarchical nature of our sampling design, equivalent to site, camera station (spatial replicate) and survey (temporal replicate) respectively. We modelled occurrence, *z*, of species *i* at site *j* as the realisation of Bernoulli trial:

$$z_{i,j} \sim Bernoulli(\psi_{i,j})$$

where $z_{i,j}$ is a binary variable indicating species presence/absence and $\psi_{i,j}$ expresses the probability of species occurrence at a given site. Habitat use, α, of species *i* within site *j* at camera station *l*, is defined as the outcome of a second Bernoulli process conditional on species presence, $z_{i,j}$:

$$a_{i,j,l} | z_{i,j} \sim Bernoulli(z_{i,j} \cdot \vartheta_{i,j,l})$$

where $a_{i,j,l}$ is a binary variable indicating presence/absence at the camera station and ϑ expresses the probability of habitat use. To account for imperfect detection in habitat use, we specified a third Bernoulli process:

$$y_{i,j,l,k} | a_{i,j,l} \sim Bernoulli(a_{i,j,l,k} \cdot p_{i,j,l,k})$$

where $y_{i,j,l,k}$ represents a 4-dimensional array containing the observed detection/non-detection data, k is the temporal replicate and $p_{i,j,l,k}$ is the detection probability conditional on species presence. Under this formulation we interpret model parameters as: (1) the probability that a site is occupied relative to coarse covariates influencing home range establishment (second-order habitat selection); (2) episodic occupation within the home range given that the site is occupied to meet ecological demands relative to fine-scale covariates (third-order habitat selection), and, (3) the probability of detecting a mammal species during a survey replicate given that the site was being utilised.

Single-species models were linked by an additional hierarchical component that modelled species-specific parameters as realisations from a community-level distribution. This approach assumes species respond similarly, but not identically, to environmental conditions. Species-specific parameter estimates thus reflect a compromise between individual response and the average response of the community, modulated by detection history. This process induces shrinkage (the borrowing of statistical strength by individual species across the community), which has been shown to improve estimation precision for data-poor species infrequently detected during sampling (Pacifici et al., 2014).

Detection/non-detection data for each camera station were binned into independent sampling occasions of six-days in length (2-7 replicates per site). We excluded three species with fewer than five detections throughout sampling (banded linsang, *Prionodon linsang*; banteng, *Bos javanicus*; smooth-coated otter, *Lutrogale perspicillata*), as models are unable to discern changes in occupancy from those in detection when observations are very sparse (Brodie et al., 2015b). Moreover, we acknowledge that strictly arboreal species (i.e. gibbons, *Hylobates* sp., langurs, *Presbytis* sp., small-toothed palm civets, *Arctogalidia trivirgata*) cannot be reliably monitored using our sampling design and restrict inference to terrestrial species.

Multi-scale occupancy models assume independence between spatial replicates (Mordecai et al., 2011), however, spatially clustered designs may result in Markovian dependence as a result of animal ranging behaviour (Hines et al., 2010). To test this assumption, we employed a Jaccard Index (*J*), to determine the degree of similarity in detection histories between camera stations nested within sites for all study species (Dorazio et al., 2011). We found little evidence of similarity, with the exception of the bearded pig (J=0.51; P=0.008), Bornean yellow muntjac (J=0.33; 0.015), red muntjac (J=0.27; P=0.048) and pig-tailed macaque (J=0.31; 0.008), for which correspondence was attributed to high levels of abundance.

To assess mammalian responses to habitat configuration and forest architectural properties, we developed occupancy, habitat use and detection models of the form:

$$\text{logit}(\psi_{i,j}) = \alpha_{0i} + \alpha_{1i}\text{Forest Cover}_{j} + \alpha_{2i}\text{Forest Quality}_{j} + \varepsilon(\text{Year}_{j})_{i}$$

$$\text{logit}(\vartheta_{i,j,l}) = \beta_{0i} + \beta_{1i}\text{Structure}_{j,l} + \beta_{2i}\text{Structure}^{2}_{j,l} + \varepsilon(\text{Year}_{j,l})_{i}$$

$$\text{logit}(p_{i,j,l,k}) = \delta_{0i} + \delta_{1i}\text{Trap\_Effort}_{j,l} + \delta_{2i}\text{PAD\_Herb}_{j,l} + \delta_{3i}\text{Nlay}_{j,l}$$

Occupancy, habitat use and detection probabilities were modelled on the logit scale with random slopes and intercepts relative to species. We modelled second-order habitat selection ($\psi_{i,j}$) as a function of habitat availability (Forest Cover) and quality (Canopy Height Variability), at coarse spatial-scales relevant to home range establishment. We assessed third-order habitat selection ($\vartheta_{i,j,l}$) relative to variables associated with our three structural axes, and incorporated second-order polynomial terms to account for non-linear responses. Due to analytically prohibitive levels of multicollinearity ($|r| > 0.7$; GVIF >5) independent models were constructed for each structural predictor (N=6). Scale optimisation methods were applied to second-order- (circular buffers of radii: 1, 1.5, 2 km) and third-order habitat selection (radii: 10, 25, 50, 100, 150, 250, 500 m) sub-models to characterise optimal scales of selection for environmental predictors and determine sensitivity to spatial extent. We implemented temporal random effects (ε) for both the occurrence and habitat use models to address unmeasured inter-annual variation due to multi-year sampling. We modelled detection as a function of structural and sampling covariates presumed to influence the observation process, including: sampling intensity (“Trap_Effort”), obstructing vegetation features in the camera-trap detection zone (“PAD_HERB”) and alternative pathways in the vertical column (“Nlay”). Detection covariates were extracted across a fixed buffer of 25 m, corresponding to the detection zone of our camera-trap models. Prior to analysis, all continuous covariates were centred and standardised to place them on a comparable scale and improve model convergence.

Hierarchical multi-species occupancy models were implemented using a Bayesian framework (for details of model code see supplement S2.1), specified with uninformative priors for intercept and slope parameters. We modelled variance parameters associated with temporal random effects hierarchically using a half-Cauchy distribution to mitigate potential overestimation due to few factor levels (Gelman, 2006). We specified three Markov chains per parameter, each comprising 150,000 iterations with a thin rate of 100 and a burn-in period of 50,000. Convergence was assessed visually, to determine adequate mixing of chains, and statistically, using the Gelman-Rubin statistic, with values <1.1 indicating convergence (Gelman et al., 1996). Model fit was assessed using a predictive posterior check, which compares the observed data against a simulated, idealised dataset (Gelman et al., 1996). We extracted Bayesian P values as a numerical summary of the posterior predictive distribution, with values of 0.5 indicating adequate model fit. We assessed model fit using a Pearson χ^2 discrepancy measure for binomial data and a “lack of fit” statistic (Kéry and Schaub, 2011).

To compare competing models between structural covariates (N=6) and scales (N=7), we ranked models using Watanabe Akaike-Information-Criterion (Watanabe, 2010), a within-sample model selection criteria analogous to AIC and robust to latent parameters (Broms et al., 2016). Unless stated otherwise, we present results as the posterior distribution means with 95% Bayesian Credible Intervals (BCI: 2.5th and 97.5th percentiles of the posterior distribution). Parameters are considered influential if their BCI does not overlap zero. We report findings for occurrence and detection parameters corresponding to the overall best fitting model, we present findings for habitat use parameters according to the highest ranked spatial-scale associated with that structural covariate.

Delineating restoration and conservation priority areas

Focussing on a high conservation priority species, the Sunda clouded leopard (*Neofelis diardi*), we implemented change point analysis to link abrupt shifts in the occurrence state to specific forest architectural properties. We restrict change point analysis to structural properties, relative to which, the species demonstrated a significant response. We define an ecological threshold as a zone of transition between two stable states, characterised by a rapid rate of change (Huggett, 2005). Using the "bcp" package in R (Erdman and Emerson, 2007), we employed a Bayesian algorithm (10,000 iterations, 2,000 burn-in) to identify points in the predicted sigmoidal occupancy response of the clouded leopard that exhibited the highest rate of change. Threshold values were used to partition the predicted response into three occupancy states: (1) zone of stress – low occupancy, low rate of change; (2) zone of transition – high rate of change, and (3) zone of tolerance – high occupancy, low rate of change. From a prioritisation perspective, zones of tolerance were considered to represent conservation priority areas, as they were characterised by high, stable occurrence. Moreover, zones of transition were viewed as optimal restoration areas as they would provide the highest rate of change in occupancy.

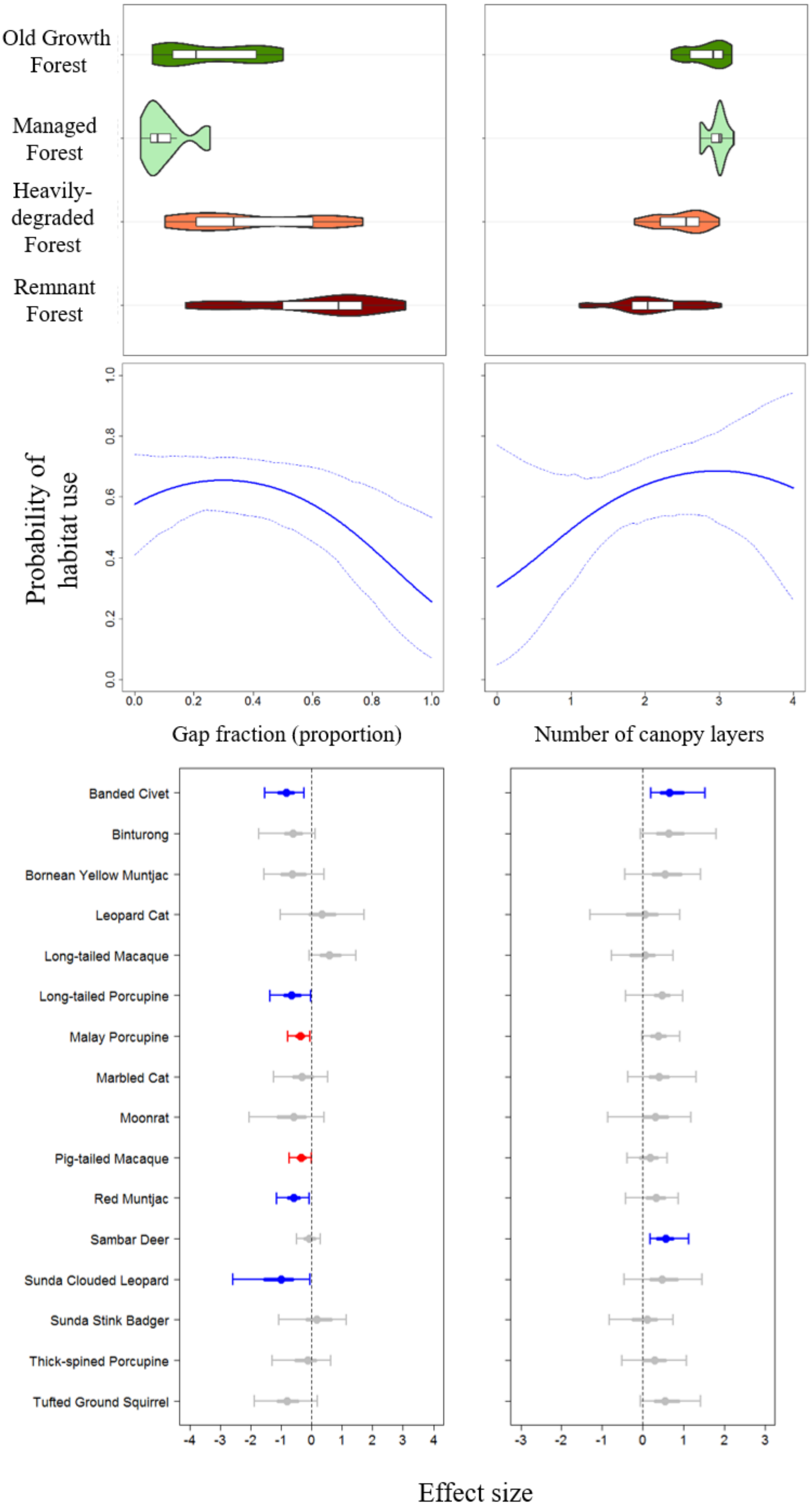
To develop a spatially explicit surface of conservation and restoration priority areas, we quantified corresponding structural values from thresholds to define covariate-specific environmental bounds related to our occupancy states. These environmental values were subsequently employed to reclassify gridded raster surfaces of structural covariates. Based on our four significant predictors, we developed a consensus map of conservation designations to visualise the extent of these areas and the level of agreement between covariates.

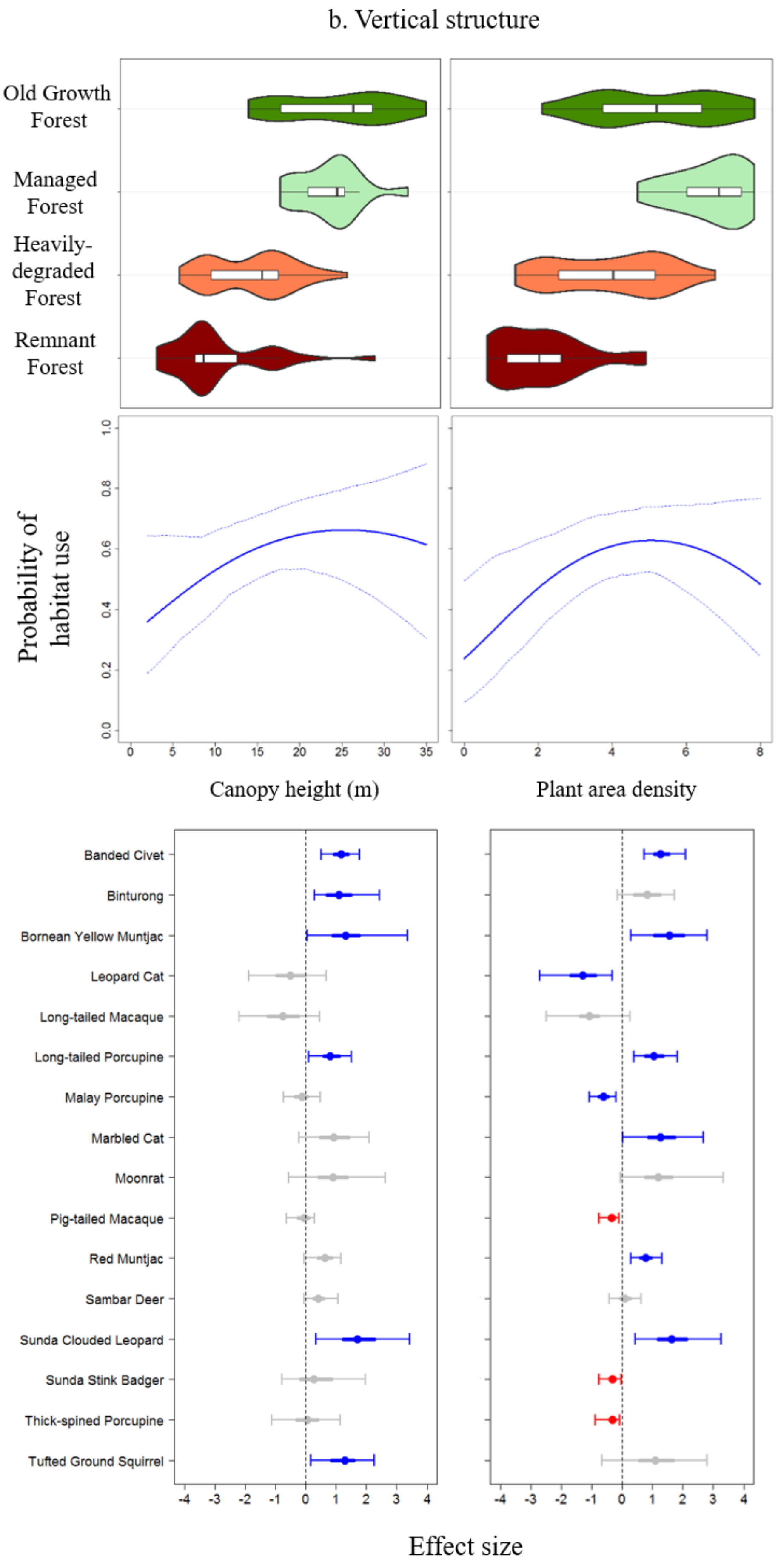
Results

The structural signature of forest degradation

We compared structural forest properties across a degradation gradient and identified consistent patterns of structural simplification relative to logging intensity (Fig. 2.2). Typically, logging-induced degradation resulted in: a higher proportion of canopy gaps (Old Growth: mean: 0.24, BCI: 0.15-0.34; Managed: 0.09, 0.0-0.18; Heavily-degraded: 0.39, 0.33-0.44; Remnant: 0.61, 0.54-0.67); lower connectivity throughout the canopy (Old Growth: 2.83, 2.66-2.99; Managed Forest: 2.96, 2.79-3.12; Heavily-degraded: 2.47, 2.38-2.56; Remnant: 2.07, 1.95-2.19); lower height profiles (Old Growth: 24.22 m, 21.82-26.79; Managed Forest: 23.37 m, 20.92-25.85; Heavily-degraded: 13.95 m, 12.56-15.31; Remnant: 9.93 m, 8.14-11.75), reduced vegetation density throughout the vertical column (Old Growth: 5.24, 4.61-5.89; Managed Forest: 6.71, 6.07-7.36; Heavily-degraded: 3.96, 3.58-4.33; Remnant: 2.08, 3.58-4.33) and fewer environmental niches, as determined by Shannon Index values of the plant area distribution (Old Growth: 2.76, 2.57-2.94; Managed Forest: 2.69, 2.50-2.86; Heavily-degraded: 1.63, 1.53-1.73; Remnant: 1.35, 1.22-1.48).

a. Horizontal structure





b. Vertical structure

c. Vertical heterogeneity

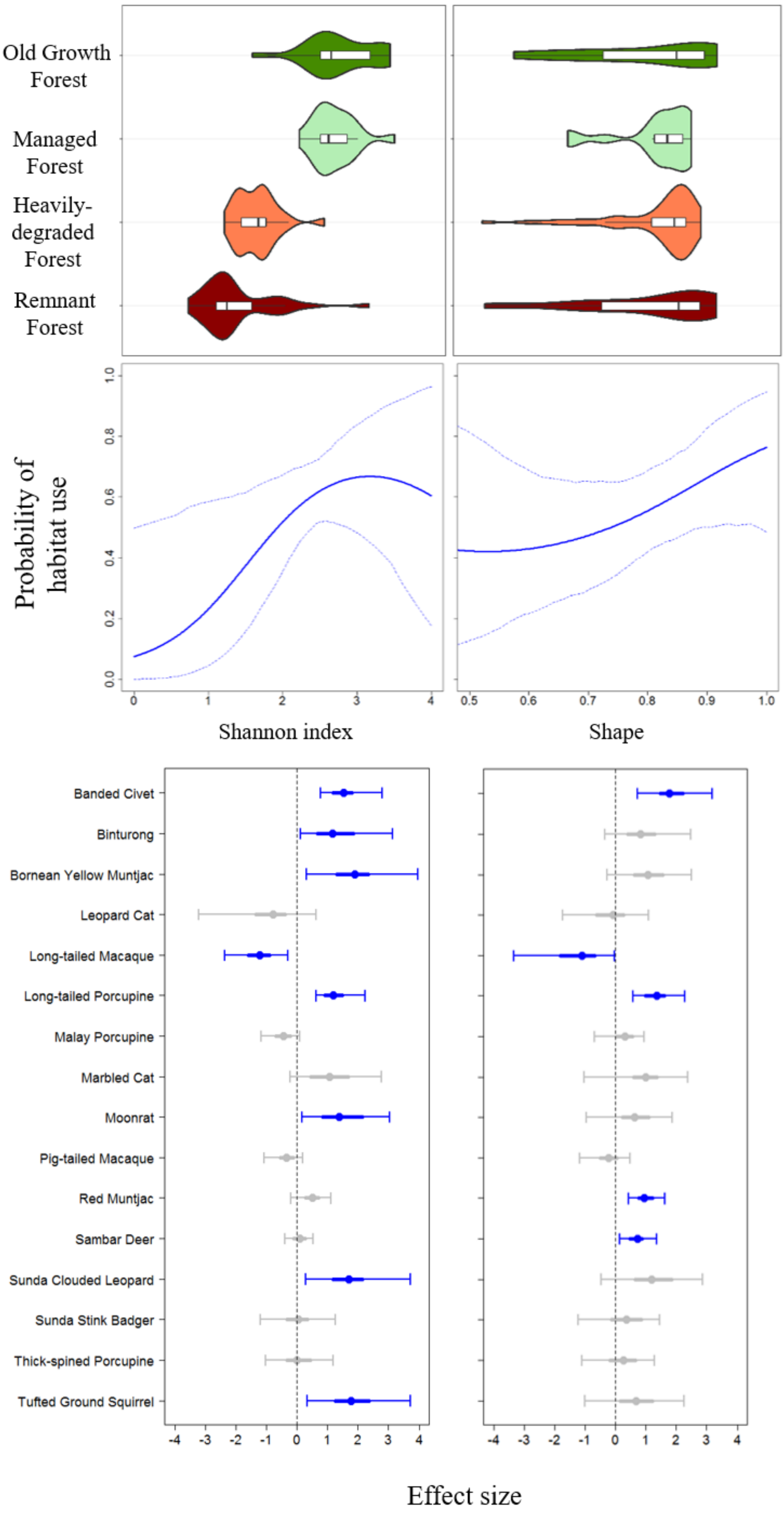


Figure 2.2: Probability of habitat use (third-order habitat selection) by tropical forest mammals in response to structural degradation of forest architecture. Structural changes in horizontal structure (panel a), vertical structure (panel b) and vertical heterogeneity (panel c). Top rows represent structural modification across a tropical disturbance gradient. Violin plots depict the kernel density distribution of the data (coloured shapes), wider sections indicate greater probability that structural characteristics within a disturbance class will take a given value. Boxplots contained therein describe the median (central vertical line), interquartile range (outer vertical lines of the box) and 95% Bayesian Credible Interval (thin horizontal lines). Middle rows demonstrate the occupancy response of the mammal community to structural alterations. Community trends are presented as predicted responses derived from posterior means and 95% Bayesian Credible Intervals (BCI). Bottom rows denote effect sizes for species-specific responses to structural modification. We present effect sizes for species parameters (c) as posterior means (points) and BCI (horizontal lines). Grey points and horizontal lines represent non-responsive species, blue suggests influential unimodal effects and red indicates influential non-linear associations described by second-order polynomial terms. Effects for species-specific associations are considered substantial if the BCI does not overlap zero (vertical dashed black line).

Pairwise comparisons between disturbance classes found consistently significant declines in structural attributes between Managed and Heavily-degraded Forest and Heavily-degraded and Remnant Forest (see Table S2.1). Contrary to these trends Old Growth and Managed Forest were structurally similar. However, our results indicated a greater proportion of gaps and lower vegetation density throughout the canopy in Old Growth Forest.

Mammalian responses to forest structural properties

At both scales of habitat selection, models containing covariates extracted across larger spatial extents were consistently identified as providing the best fit to the data. We found occurrence relative to second-order habitat selection was best modelled with covariates extracted across buffers with a radius of 2 km (1979.98≤WAIC≤2167.38), while structural covariates associated with third-order habitat selection demonstrated the greatest response relative to 250 m (Gap Fraction, Number of Layers, Canopy Height) and 500 m (Plant Area Density, Shannon Index, Shape) buffer radii (see supplementary Table S2.2 for details).

Factors affecting second-order habitat selection

At the community-level, we found no consistent response relative to Forest Cover (mean effect size: -0.11, BCI: -0.56-0.40) or Canopy Height Variability, likely driven by marked differences between species. At the scale of second-order habitat selection, multi-scale, multi-species occupancy models revealed Forest Cover and Canopy Height Variability to be influential predictors for several species (Fig. 2.3). For example, the Bornean yellow muntjac (*Muntiacus atherodes*; 1.14, 0.36-2.26) and banded civet (*Hemigalus* derbyanus; 0.83, 0.01-2.02) demonstrated positive associations with Forest Cover. Conversely, the leopard cat (*Prionailurus bengalensis*: -1.27, -2.49 to -0.38), greater mouse-deer (*Tragulus napu*: -0.99, -1.78 to -0.28) and long-tailed macaque (*Macaca fascicularis*: -0.82, -1.65 to -0.03) responded negatively to the availability of forest habitat, and consequently were more prevalent in heavily degraded forests with open canopy. Forest quality was identified as an important determinant of second-order habitat selection for the Bornean yellow muntjac (1.53, 0.62-2.56), lesser mouse-deer (*Tragulus* kanchil: 0.89, 0.16-1.79), marbled cat (*Pardofelis* marmorata: 0.93, 0.06-2.09), red muntjac (*Muntiacus* muntjak: 1.38, 0.17-2.54) and thick-spined porcupine (*Hystrix* crassispinis: 0.82, 0.01-1.73). Conversely, the leopard cat (-2.00, -3.58 to -0.45) demonstrated a preference for lower quality habitat characterised by a less variable canopy.

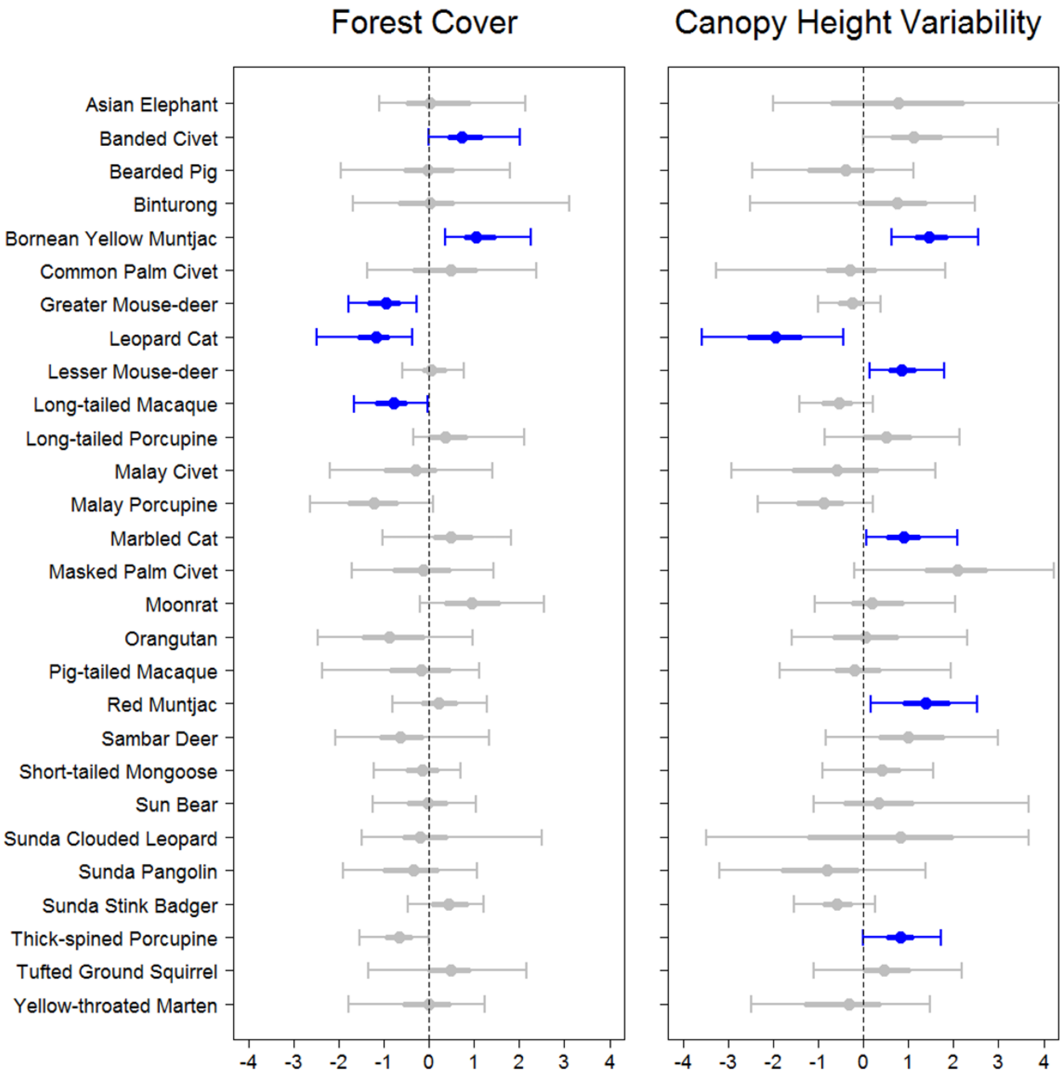


Figure 2.3: Landscape context factors influencing Bornean mammal occupancy (second-order habitat selection). Covariates delineate the extent (forest cover) and quality (canopy height variability) of forest habitat. Effect sizes for species parameters are presented as posterior means (points) and 95% BCI (horizontal lines). Grey points and horizontal lines represent non-responsive species, while blue suggests influential relationships. Effects are considered substantial if the 95% BCI does not overlap zero (vertical dashed black line).

Factors affecting third-order habitat selection

At finer spatial scales, the hierarchical models identified active habitat selection for structurally complex environments to be evident at both the community- and species-levels (Fig. 2.2). Mammal assemblages demonstrated non-linear, second-order polynomial responses to Gap Fraction and Plant Area Density, suggesting a complexity that could not be captured by linear methods. We found evidence of weak positive relationships (identified using 90% BCI) with the Number of Canopy Layers (0.28, 0.04-0.54), Shannon Index (0.38, 0.06-0.77), Canopy Height (0.35, 0.07-0.69) and Shape (0.44, 0.11-0.85), implying the importance of mature, connected forest habitat, containing a breadth of environmental niches for community persistence. Using WAIC scores to rank models, structural variables associated with vertical heterogeneity (Plant Area Density: WAIC=1979.98; Canopy Height: WAIC=2039.60) and vertical complexity (Shannon Index: WAIC=2016.74; Shape: WAIC=2030.87) were found to be stronger predictors of mammalian habitat use than horizontal heterogeneity (Gap Fraction: WAIC=2059.08; Number of Layers = 2072.13), emphasizing the importance of the vertical axes of forest structure in influencing habitat use.

Forest structure was identified as a key determinant of third-order habitat selection for 16 of the 28 Bornean mammals sampled (Fig. 2.2). Species of conservation concern demonstrated strong positive associations with measures of vertical heterogeneity and complexity, including the Sunda clouded leopard (Canopy Height = 1.76, 0.33-3.42; Plant Area Density: 1.66, 0.43-3.25; Shannon Index: 1.75, 0.29-3.73), binturong (*Arctictic binturong*: Canopy Height = 1.17, 0.28-2.42; Shannon Index: 1.32, 0.12-3.15), tufted ground squirrel (*Rheithrosciurus macrotis*: Canopy

Height = 1.25, 0.17-2.26; Shannon Index: 1.84, 0.34-3.73) and marbled cat (Plant Area Density: 1.33, 0.03-2.67). Vertical heterogeneity and complexity were similarly important in governing habitat selection by the Bornean yellow muntjac, long-tailed porcupine (*Trichys fasciculata*) and banded civet (all detailed in Fig. 2.2). The horizontal arrangement of vegetation was also found to be an influential predictor; aversion to canopy gaps was found for the Sunda clouded leopard (-1.11, -2.59 to -0.05), banded civet (-0.84, -1.52 to 2.46), long-tailed porcupine (-0.65, -1.37 to -0.02) and red muntjac (-0.59, -1.14 to -0.07), while the sambar deer (*Rusa unicolor*: 0.57, 0.18-1.12) and banded civet (0.73, 0.20-1.53) demonstrated positive associations with the number of contiguous layers within the canopy.

Not all species selected structurally complex environments. The leopard cat (-1.35, -2.69 to -0.32) and Malay porcupine (*Hystrix brachyura*:-0.61, -1.08 to -0.20) demonstrated negative associations with Plant Area Density, while the long-tailed macaque was found to have a negative response to measures of vertical complexity (Shannon Index: -1.25, -2.37 to -0.30; Shape: -1.04, -2.16 to -0.06). Furthermore, polynomial trends were identified for a number of species relative to Plant Area Density (pig-tailed macaque. *Macaca nemestrina*: -0.35, -0.75 to –0.09; Sunda stink badger, *Mydaus javanensis*: -0.33, -0.77 to -0.03; thick-spined porcupine: -0.35, -0.87 to -0.08) and Gap Fraction (Malay porcupine: -0.38, -0.77 to -0.06; pig-tailed macaque: -0.34, -0.74 to -0.01) indicating tolerance to moderate levels of structural degradation. Species-specific outputs for all top-ranking models are available in supplementary figures S2.1-S2.12.

Delineating restoration and conservation priority areas

Bayesian change point analysis identified zones of transition, characterised by high rates of change in Sunda clouded leopard occupancy, for Canopy Height (lower bound = 10.68; upper bound = 21.11 m; Fig. 2.4b), Gap Fraction (0.32 – 0.68; Fig. 2.4c), Plant Area Density (2.11 – 5.05; Fig. 2.4d) and Shannon Index (1.68 – 2.74; Fig. 2.4e). Areas within these zones were considered priority restoration areas, while areas exceeding the upper bound were viewed as priority conservation areas. Based explicitly on clouded leopard habitat use, 12,290 ha (40.7%) of the total forest area would be identified as priority conservation zones, and 12,640 ha (41.9%) of the landscape for potential restoration (Fig. 2.4a). Relative to extent, the largest concentrations of conservation priority areas were identified in Old Growth (1,555 ha, 12.7%) and Managed Forest (8,200 ha, 66.7%). Furthermore, these forest classes demonstrated the highest levels of consensus between all four structural metrics (65.0 and 67.8% of total designated area respectively). Restoration opportunities were predominantly identified in Managed (3.340 ha/26.4) and Heavily-degraded Forests (6,705 ha/53.1%) but agreement between metrics was less convincing. Low priority conservation areas were typically situated in Heavily-degraded (3,120 ha/60.0%) and Remnant Forest (1,845 ha/35.2%) and were consistently demonstrated for three to four of the structural metrics (38.9 and 75.3% of total designated area).

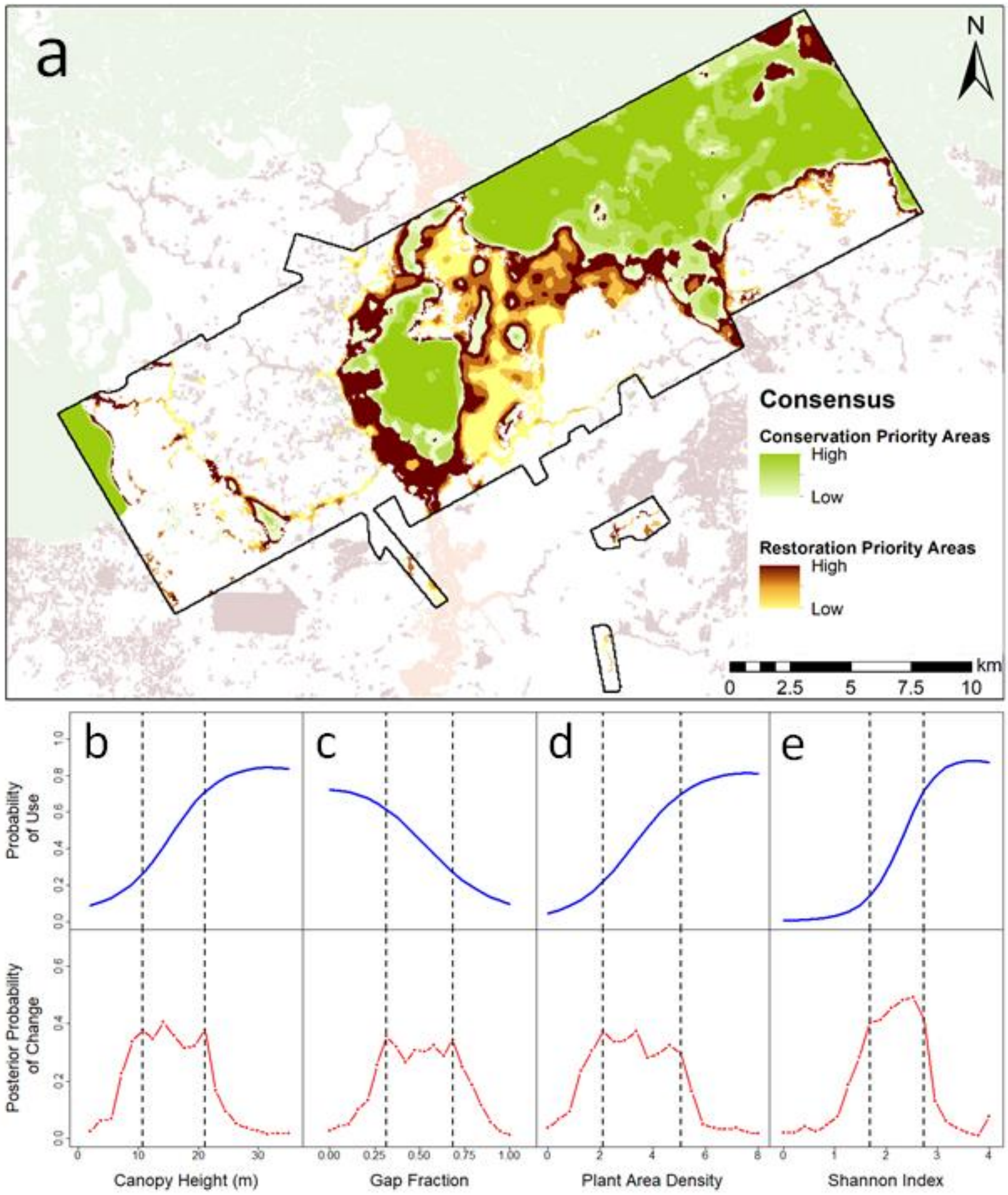


Figure 2.4: A spatial delineation of conservation and restoration priority areas for the Sunda clouded leopard (*Neofelis diardi*). Priority conservation and restoration areas (Panel a) as predicted by Bayesian change point analysis on predicted occupancy trends (blue lines) relative to informative structural

characteristics (b-e). Vertical dashed black lines (b-e) represent the lower and upper bounds of the zone of transition, characterised in red line graphs by the highest posterior probability of change.

Discussion

Logged forests are integral to global conservation planning, yet our understanding of the specific structural properties that facilitate species persistence in degraded habitats is lacking. Among the many studies exploring the conservation value of logged tropical forest for biodiversity (Burivalova et al., 2014, Edwards et al., 2011, Edwards et al., 2014, Putz et al., 2012) ours is the first to consider multidimensionality to identify the architectural elements that underpin the ecological significance of degraded ecosystems. We demonstrate concomitant biodiversity declines relative to structural degradation across a gradient of logging intensity. Moreover, we illustrate how species-habitat associations can be aligned with conservation planning to integrate biodiversity considerations into the designation of priority conservation areas.

When evaluating forest structural properties across a degradation gradient, we found consistent evidence of structural simplification relative to logging intensity between the Managed, Heavily-degraded and Remnant Forest classes. The observed simplification was characterised by a lower height profile with reduced vegetation density, resulting in fewer environmental niches, less connected canopy pathways and a spatially dispersed canopy. Unsustainable selective logging, distinguished by high biomass removal and a short rotational length, has been implicated as the primary driver of forest degradation across Southeast Asia (Miettinen et al., 2014). Unsustainable practices facilitate structural simplification by causing soil compaction and reductions in the seed bank (Pinard et al., 2000), which restrict the successional capacity of forest habitats (Bischoff et al., 2005). Furthermore, fragmented forests, analogous to our remnant forest class, are susceptible to wind damage and altered microclimatic conditions which precipitate additional mortality of large trees (Laurance et al., 2000). Our findings echo previous structural assessments of degraded forests (Hardwick et al., 2015, Kent et al., 2015, Kumar and Shahabuddin, 2005, Okuda et al., 2003), while empirically demonstrating progressive architectural deterioration associated with repeated logging and fragmentation.

Structural properties were found to be comparable between the Old Growth and Managed Forest classes. This anomaly could reflect the rapid recovery of our Managed Forest which has been unencumbered from logging pressure for the last decade (Reynolds et al., 2011). Elsewhere in Southeast Asia, restoration of structural canopy elements has been shown to take up to 55 years post-logging (Brearley et al., 2004), though only negligible differences in canopy height have been documented following 23 years of recovery (Okuda et al., 2003). While the prescribed interval between logging rotations is 15-30 years, the realised relaxation period across Southeast Asia averages 16 years (Fisher et al., 2011a). These figures indicate that current practices are insufficient to facilitate natural recovery following logging-induced structural degradation.

The ecological neighbourhood concept describes the spatial extent at which a species becomes receptive to environmental variation (Addicott et al., 1987, McGarigal et al., 2016). Defining these neighbourhoods is fundamental to understanding the complexity of habitat selection in degraded ecosystems. Our analyses consistently identified the mammal community as most responsive to covariates aggregated across the largest spatial extents. Ecologically, this implies that larger areas are required to accrue ecological benefits from available habitat features in impoverished environments. From a conservation perspective, this reinforces the widely-recognised notion that large areas of suitable habitat are essential to facilitate ecological processes and safeguard tropical mammals.

Previous studies of tropical mammals have found optimal spatial extents to range between 50 m (Niedballa et al., 2015) and 7.7 km (Hearn et al., 2018b), though these extents are likely to be species- and habitat-specific. Identifying optimal spatial scales is fundamental to ensure that ecological associations can be identified and practically applied to inform policy. While there is a general consensus that spatial extent should be tailored to the ranging behaviour of the study system (Mayor et al., 2009), detailed information on the spatial ecology of cryptic tropical species is rarely available. To this end, our study demonstrates the value of iterative scale optimisation methods to identify optimal ecological neighbourhoods when movement data are unavailable.

Our multi-scale appraisal reveals novel insights into habitat selection by tropical mammals. This information is paramount in degraded systems where species persistence is dependent upon identifying the specific factors that underpin habitat suitability. We found that forest availability and quality, as indicated by forest cover and canopy height variability respectively, were important drivers of second-order habitat selection. Forest cover describes the geographic bounds of suitable habitat, while canopy height variability illustrates the coarse complexity of the forest (Bergen et al., 2009) and defines the continuum across which resources are distributed throughout the suitable space. Habitat availability has been shown to be an important factor defining species occurrence (Hearn et al., 2018b, Michalski and Peres, 2005). However, our results indicate contrasting responses, predominantly driven by species that have adapted to take advantage of resources in degraded or non-forest habitats (greater mouse-deer: Heydon and Bulloh, 1997, leopard cat: Mohamed et al., 2013).

We found greater support for the positive influences of forest quality on second-order habitat selection (i.e. home range establishment). This finding likely reflects increased resources in structurally complex habitats, such as fruit and browse availability for ungulates (Brodie and Giordano, 2013), and the abundance of small canopy mammals for arboreal predators such as the marbled cat (Moreira-Arce et al., 2016). The contrasting influences of forest availability and quality may be indicative of the level of degradation across our study landscape. Home range establishment was not based on forest cover because degraded forest is not preferential to the same degree as old growth forest, which accounts for only 8.3% of our landscape. In response, species appear to be actively selecting home range areas that retain adequate structural quality to meet their ecological requirements. Our findings support those of Barlow et al. (2016) in emphasizing the importance of maintaining forest quality as well as extent.

At the scale of habitat use, we elucidate the structural properties that constitute quality habitat and how they facilitate ecological processes. Plant area density throughout the vertical column was the strongest predictor of third-order habitat selection, emphasizing the importance of variables that capture the multidimensionality of forest ecosystems. For arboreal ambush predators, such as the Sunda clouded leopard and marbled cat, vegetation density provides cover that increases hunting efficiency through visual or locomotive obstruction, as has been demonstrated for lions (Davies et al., 2016). Conversely, vegetation density and distribution may provide refugia for prey species such as ungulates, particularly when engaged in vulnerable behaviours such as resting or rumination (Brodie and Brockelman, 2009).

Mammals actively selected for forest areas with taller canopies and a greater breadth of environmental niches, which are characteristic properties of late-successional stands (Peña-Claros, 2003). Mature, diverse forests demonstrate higher primary productivity (Apps et al., 2004) and afford greater resources to primary consumers such as the Bornean yellow muntjac. Moreover, tall trees are fruiting oases for frugivorous species such as binturong (Felton et al., 2003) and have shown to be preferential habitat features for species with similar dietary preferences (Davies et al., 2017), suggesting supplementary ecological benefits of mature stands. Forests with late-successional characteristics accumulate leaf litter at a faster rate (Scherer-Lorenzen et al., 2007), attracting a diverse, abundant invertebrate community that could benefit insectivorous species like the banded civet.

Generally, our results indicate that mammals actively selected structurally complex environments at fine-scales suggesting sensitivity to disturbance that simplifies canopy elements. This emphasises the importance of maintaining and restoring structurally intact forests for biodiversity conservation. Taken as a whole, our results confirm the hypothesis that species will track resources at successively lower hierarchical levels of habitat selection to overcome limitations at the preceding level (Mayor et al., 2009). Our mammal community was more responsive at the scale of habitat use, presumably because resources were not sufficiently available at coarser designations of habitat selection. Moreover, these findings allude to the potential for negative feedback loops in degraded systems. Mammals occupy key ecological roles in forest ecosystems, including trophic regulation (Estes et al., 2011), seed dispersal (Brodie and Brockelman, 2009) and seedling recruitment (Granados et al., 2018). Active avoidance of heavily-degraded areas could potentially affect the resilience of these systems, preventing natural post-disturbance recovery and leaving ecosystems in a state of arrested succession (Ghazoul et al., 2015), and ultimately, defaunation (Dirzo et al., 2014).

The capacity to identify and prioritise degraded forests for conservation is imperative to inform biodiversity management in tropical countries with limited regulatory and institutional frameworks. This is particularly important since logged forests play a pivotal role in safeguarding biodiversity against the impacts of environmental change (Struebig et al., 2015). Capitalising on occupancy response curves to prioritise land revealed 12,290 ha of potential conservation areas based on records of active habitat selection by a high conservation priority species, the Sunda clouded leopard. These areas were predominantly distributed within Old Growth and Managed Forests and rarely Heavily-degraded Forests. Collectively, these findings provide further evidence of declining conservation value with increasing logging intensity (Burivalova et al., 2014). We delineate a further 12,640 ha of forest qualifying for restoration. Based on figures provided in Budiharta *et al.* (2014a) combined restoration and opportunity costs for the study site would be financially prohibitive (>US$5 million), and potentially ineffective given the lack of consensus among structural variables. An optimal strategy may be to concentrate restoration within Old Growth and Managed Forest sites, to promote connectivity in forests retaining a higher proportion of conservation priority areas. Natural regeneration may be a more viable strategy for low priority areas in Heavily-degraded Forest. Implementation is encouraged by evidence that degraded forests can recover significant biodiversity within 10-years following the cessation of harvesting (Brodie et al., 2015b).

The analytical framework presented in this chapter could have practical applications for Southeast Asian conservation policy. Recent proposals by the Sabah government to increase protected area coverage by 5%, coupled with the state-wide availability of LiDAR data (Asner et al., 2018), provides an unparalleled opportunity to mobilise a collaborative network of camera-trap data and fully integrate biodiversity considerations into conservation planning. Capitalising on these developments could greatly augment policy instruments that seek to mobilise the conservation potential of degraded logged forests.

Synthesis and application

Ambitious policy targets proposed by the Bonn Challenge provide the roadmap to attenuate forest degradation (Chazdon et al., 2016). Logged forests will no doubt be central to restoration efforts and conservation planning in tropical countries. Our findings provide a nuanced perspective on the conservation value of degraded logged forests. The ecological significance of these modified habitats is primarily governed by fine-scale structural characteristics, which are an artefact of the legacy of logging across the landscape. To date there has been little consensus on the impacts of logging on tropical mammals, suggesting that uniform classifications of logged forest do not sufficiently capture the inherent heterogeneity of degraded systems. Tropical forests are multidimensional environments, which must be recognised by evidence-based frameworks to guide policy implementation in degraded habitats. Here, we identify consistent active selection by biodiversity for structurally complex environments, and advocate reduced-impact logging as a preventative measure to maintain forest architectural integrity and reconcile production and conservation (Bicknell et al., 2014).

For the substantial areas of forest already subjected to unsustainable practices, we provide further evidence of the value of LiDAR to demarcate degraded forests. However, the associated cost of surveys may prove financially prohibitive over spatial extents adequate enough to facilitate up-scaling for developing nations. To ensure biodiversity considerations are integrated into degradation assessment, we provide an analytical framework to map conservation priority areas in degraded systems. Moreover, we caution against an over-reliance on traditional degradation measures, such as biomass, and advocate the use of metrics that capture ecologically meaningful components of the structural environment from the perspective of biodiversity.

Acknowledgements

This study was funded by the UK Natural Environment Research Council (NERC) (NE/K016407/1; http://lombok.hmtf.info/ and http://bali.htmf.info; NE/KO16377/1) and a NERC EnvEast PhD studentship to NJD. GGA is the recipient of a Discovery Early Career Research Award from the Australian Research Council (DE160100904). We thank the Sabah Biodiversity Council, Sabah Forest Department, Yayasan Sabah, Sime Darby and Benta Wawasan for permitting access. We are indebted to Jamiluddin Jami, Arnold James, Mohd. Mustamin, Ampat Siliwong, Sabidee Mohd. Rizan and Najmuddin Jamal for field assistance. Our gratitude to Jessica K. Haysom for assistance in coordinating data collection. Special thanks to Andreas Wilting for advice regarding camera-trap field methods.

Supplementary information

Table S2.1: Response of forest architectural properties to structural degradation. Using outputs from a mean parameterisation of a Bayesian linear model, we detail average structural covariate value across each degradation class (Old Growth, Managed Forest, Heavily-degraded Forest, Remnant Forest) and structural differences between classes. Parameter estimates are presented as the mean, standard deviation, 2.5th and 97.5th percentile values of posterior distributions. Differences in structural covariates between degradation classes were considered significant if Bayesian credible intervals (2.5th percentile and 97.5th percentile) did not overlap zero (highlighted in bold).

Structural Variable	Parameter	Mean	SD	2.5th Percentile	97.5th Percentile
Canopy height	Old Growth	24.22	1.27	21.82	26.79
	Managed Forest	23.37	1.24	20.92	25.85
	Heavily-degraded Forest	13.95	0.71	12.56	15.31
	Remnant Forest	9.93	0.90	8.14	11.75
	Old Growth vs. Managed	-0.84	1.75	-4.24	2.61
	Old Growth vs. Heavily-degraded	**-10.27**	**1.44**	**-13.15**	**-7.54**
	Old Growth vs. Remnant	**-14.29**	**1.55**	**-17.32**	**-11.28**
	Managed vs. Heavily-degraded	**-9.43**	**1.44**	**-12.21**	**-6.56**
	Managed vs. Remnant	**-13.44**	**1.52**	**-16.46**	**-10.46**
	Heavily-degraded vs. Remnant	**-4.01**	**1.15**	**-6.26**	**-1.73**
Gap fraction	Old Growth	0.24	0.05	0.15	0.34
	Managed Forest	0.09	0.05	0.00	0.18
	Heavily-degraded Forest	0.39	0.03	0.33	0.44
	Remnant Forest	0.61	0.03	0.54	0.67
	Old Growth vs. Managed	**-0.15**	**0.07**	**-0.28**	**-0.03**
	Old Growth vs. Heavily-degraded	**0.14**	**0.05**	**0.04**	**0.25**
	Old Growth vs. Remnant	**0.36**	**0.06**	**0.25**	**0.47**
	Managed vs. Heavily-degraded	**0.29**	**0.05**	**0.19**	**0.40**

	Managed vs. Remnant	**0.51**	**0.06**	**0.40**	**0.63**
	Heavily-degraded vs. Remnant	**0.22**	**0.04**	**0.13**	**0.31**
Number of layers	Old Growth	2.83	0.08	2.66	2.99
	Managed Forest	2.96	0.08	2.79	3.12
	Heavily-degraded Forest	2.47	0.05	2.38	2.56
	Remnant Forest	2.07	0.06	1.95	2.19
	Old Growth vs. Managed	0.13	0.12	-0.10	0.36
	Old Growth vs. Heavily-degraded	-0.36	0.10	-0.55	-0.16
	Old Growth vs. Remnant	-0.75	0.11	-0.96	-0.55
	Managed vs. Heavily-degraded	-0.49	0.10	-0.67	-0.30
	Managed vs. Remnant	-0.88	0.10	-1.08	-0.68
	Heavily-degraded vs. Remnant	-0.39	0.08	-0.55	-0.24
Plant area density	Old Growth	5.24	0.33	4.61	5.89
	Managed Forest	6.71	0.33	6.07	7.36
	Heavily-degraded Forest	3.96	0.19	3.58	4.33
	Remnant Forest	2.08	0.24	1.60	2.56
	Old Growth vs. Managed	**1.47**	**0.46**	**0.54**	**2.35**
	Old Growth vs. Heavily-degraded	**-1.28**	**0.38**	**-2.04**	**-0.54**
	Old Growth vs. Remnant	**-3.16**	**0.41**	**-3.98**	**-2.38**
	Managed vs. Heavily-degraded	**-2.75**	**0.38**	**-3.50**	**-1.99**
	Managed vs. Remnant	**-4.63**	**0.41**	**-5.43**	**-3.82**
	Heavily-degraded vs. Remnant	**-1.89**	**0.31**	**-2.48**	**-1.27**
Shannon Index	Old Growth	2.76	0.09	2.57	2.94
	Managed Forest	2.69	0.09	2.50	2.86
	Heavily-degraded Forest	1.63	0.05	1.53	1.73

	Remnant Forest	1.35	0.07	1.22	1.48
	Old Growth vs. Managed	-0.07	0.13	-0.32	0.18
	Old Growth vs. Heavily-degraded	**-1.12**	**0.11**	**-1.34**	**-0.91**
	Old Growth vs. Remnant	**-1.40**	**0.11**	**-1.63**	**-1.18**
	Managed vs. Heavily-degraded	**-1.06**	**0.11**	**-1.26**	**-0.85**
	Managed vs. Remnant	**-1.33**	**0.11**	**-1.55**	**-1.11**
	Heavily-degraded vs. Remnant	**-0.28**	**0.08**	**-0.44**	**-0.11**
Shape	Old Growth	0.21	0.03	0.16	0.27
	Managed Forest	0.20	0.03	0.15	0.25
	Heavily-degraded Forest	0.20	0.02	0.17	0.23
	Remnant Forest	0.22	0.02	0.18	0.25
	Old Growth vs. Managed	-0.01	0.04	-0.09	0.06
	Old Growth vs. Heavily-degraded	-0.01	0.03	-0.08	0.05
	Old Growth vs. Remnant	0.00	0.03	-0.06	0.07
	Managed vs. Heavily-degraded	0.00	0.03	-0.06	0.06
	Managed vs. Remnant	0.01	0.03	-0.05	0.08
	Heavily-degraded vs. Remnant	0.02	0.03	-0.03	0.07

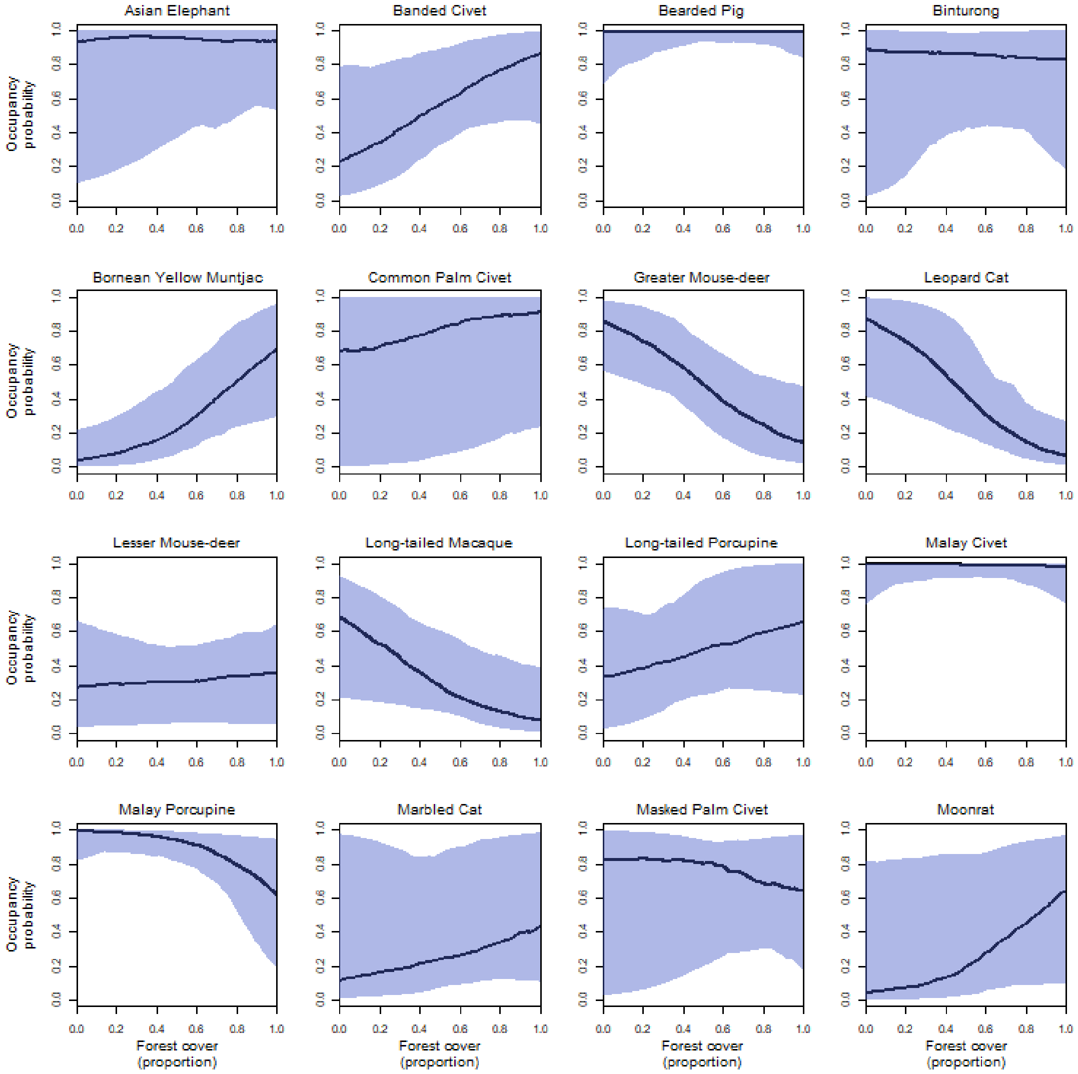
Table S2.2: Model selection, scale optimisation and model fit summary statistics. Model selection and scale optimisation were based on comparison of Watanabe AIC values, with the lowest scoring WAIC values indicating the overall best model (presented in bold and italics) and the most responsive scales for each structural covariate (presented in bold). Model fit was judged using Bayesian *P* values (BPV) and the “lack-of-fit” statistic (Chat). BPV values between 0.05 and 0.95 and Chat scores ~1 indicate adequate model fit.

Model	**Coarse-scale (m)**	**Fine-scale (m)**	**BPV**	**Chat**	**WAIC**
Forest cover + Forest quality + Canopy height	1000	10	0.45	1.01	2150.68
	1000	25	0.43	1.02	2112.06
	1000	50	0.39	1.02	2177.02
	1000	100	0.49	1.02	2152.13
	1000	150	0.45	1.01	2115.11
	1000	250	0.52	1.00	2144.21
	1000	500	0.57	1.00	2112.66
Forest cover + Forest quality + Gap fraction	1000	10	0.41	1.03	2140.72
	1000	25	0.41	1.02	2143.88
	1000	50	0.44	1.02	2085.62
	1000	100	0.43	1.02	2118.44
	1000	150	0.38	1.02	2108.36
	1000	250	0.50	1.01	2151.82
	1000	500	0.50	1.01	2059.08
Forest cover + Forest quality + Number of layers	1000	10	0.44	1.01	2161.04
	1000	25	0.41	1.02	2220.23
	1000	50	0.39	1.03	2144.92
	1000	100	0.41	1.02	2152.17
	1000	150	0.37	1.03	2178.11
	1000	250	0.46	1.01	2197.16
	1000	500	0.51	1.01	2098.42
Forest cover + Forest quality + Plant area density	1000	10	0.35	1.03	2110.17
	1000	25	0.49	1.01	2094.70
	1000	50	0.39	1.02	2113.79
	1000	100	0.37	1.03	2122.11
	1000	150	0.51	1.01	2133.49
	1000	250	0.45	1.01	2117.06
	1000	500	0.45	1.01	2101.87
Forest cover + Forest quality + Shannon Index	1000	10	0.44	1.01	2132.22
	1000	25	0.49	1.01	2077.82
	1000	50	0.49	1.01	2083.64
	1000	100	0.45	1.02	2129.03
	1000	150	0.41	1.03	2112.02
	1000	250	0.39	1.03	2117.09
	1000	500	0.40	1.03	2159.95

Forest cover + Forest quality + Shape	1000	10	0.46	1.01	2202.90
	1000	25	0.43	1.02	2096.46
	1000	50	0.44	1.03	2079.89
	1000	100	0.41	1.02	2136.63
	1000	150	0.41	1.02	2128.74
	1000	250	0.41	1.02	2091.47
	1000	500	0.43	1.02	2085.71
Forest cover + Forest quality + Canopy height	1500	10	0.43	1.02	2113.98
	1500	25	0.46	1.01	2169.51
	1500	50	0.43	1.02	2217.24
	1500	100	0.43	1.01	2100.56
	1500	150	0.51	1.01	2166.22
	1500	250	0.43	1.02	2095.71
	1500	500	0.46	1.02	2089.22
Forest cover + Forest quality + Gap fraction	1500	10	0.44	1.02	2067.09
	1500	25	0.38	1.03	2179.06
	1500	50	0.49	1.01	2108.49
	1500	100	0.34	1.03	2136.28
	1500	150	0.49	1.01	2071.86
	1500	250	0.41	1.03	2138.21
	1500	500	0.44	1.02	2071.38
Forest cover + Forest quality + Number of layers	1500	10	0.40	1.03	2203.62
	1500	25	0.43	1.02	2134.85
	1500	50	0.40	1.03	2115.06
	1500	100	0.40	1.03	2143.96
	1500	150	0.43	1.03	2111.04
	1500	250	0.41	1.03	2088.62
	1500	500	0.40	1.03	2111.11
Forest cover + Forest quality + Plant area density	1500	10	0.46	1.01	2085.83
	1500	25	0.45	1.02	2107.45
	1500	50	0.56	1.01	2128.49
	1500	100	0.41	1.02	2027.27
	1500	150	0.45	1.02	2147.01
	1500	250	0.48	1.01	2125.74
	1500	500	0.44	1.01	2156.04
Forest cover + Forest quality + Shannon Index	1500	10	0.37	1.02	2044.55
	1500	25	0.37	1.04	2119.33
	1500	50	0.52	1.01	2090.21
	1500	100	0.45	1.02	2143.25
	1500	150	0.41	1.01	2135.54
	1500	250	0.41	1.02	2123.93
	1500	500	0.40	1.02	2071.30
Forest cover + Forest quality + Shape	1500	10	0.43	1.02	2084.54
	1500	25	0.37	1.03	2054.64
	1500	50	0.37	1.02	2108.23
	1500	100	0.31	1.03	2096.33
	1500	150	0.41	1.02	2079.46
	1500	250	0.49	1.02	2174.09

	1500	500	0.43	1.03	2075.23
Forest cover + Forest quality + Canopy height	2000	10	0.43	1.03	2043.00
	2000	25	0.36	1.03	2082.02
	2000	50	0.35	1.03	2073.89
	2000	100	0.40	1.02	2109.40
	2000	150	0.43	1.02	2074.70
	2000	**250**	**0.41**	**1.03**	**2039.60**
	2000	500	0.49	1.02	2041.85
Forest cover + Forest quality + Gap fraction	2000	10	0.47	1.02	2075.88
	2000	25	0.47	1.01	2133.52
	2000	50	0.45	1.02	2111.67
	2000	100	0.38	1.02	2142.91
	2000	150	0.35	1.04	2061.01
	2000	**250**	**0.47**	**1.02**	**2057.30**
	2000	500	0.33	1.03	2060.42
Forest cover + Forest quality + Number of layers	2000	10	0.47	1.02	2126.80
	2000	25	0.38	1.03	2162.80
	2000	50	0.49	1.01	2167.38
	2000	100	0.44	1.01	2121.95
	2000	150	0.43	1.03	2112.24
	2000	**250**	**0.41**	**1.02**	**2072.13**
	2000	500	0.38	1.02	2096.35
Forest cover + Forest quality + Plant area density	2000	10	0.50	1.01	2076.72
	2000	25	0.45	1.02	1996.37
	2000	50	0.38	1.02	2049.63
	2000	100	0.37	1.04	2089.81
	2000	150	0.43	1.02	2079.39
	2000	250	0.39	1.02	2061.02
	2000	***500***	***0.46***	***1.01***	***1979.98***
Forest cover + Forest quality + Shannon Index	2000	10	0.39	1.03	2074.32
	2000	25	0.49	1.01	2027.01
	2000	50	0.41	1.02	2032.58
	2000	100	0.46	1.02	2123.47
	2000	150	0.45	1.01	2054.50
	2000	250	0.48	1.02	2070.89
	2000	**500**	**0.45**	**1.02**	**2016.74**
Forest cover + Forest quality + Shape	2000	10	0.43	1.02	2062.02
	2000	25	0.45	1.02	2084.87
	2000	50	0.42	1.02	2046.02
	2000	100	0.45	1.02	2047.44
	2000	150	0.43	1.02	2066.08
	2000	250	0.44	1.02	2044.24
	2000	**500**	**0.40**	**1.03**	**2020.87**

Figure S2.1: Occupancy (second-order habitat selection) relative to forest cover (m). Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.



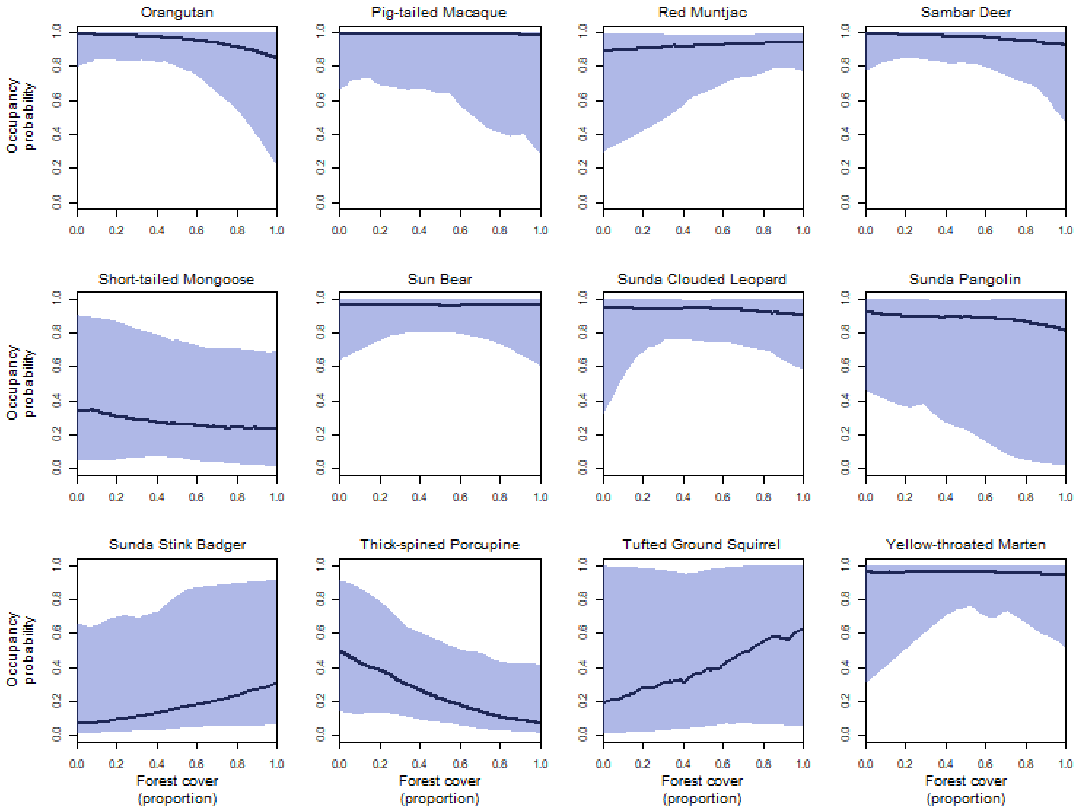
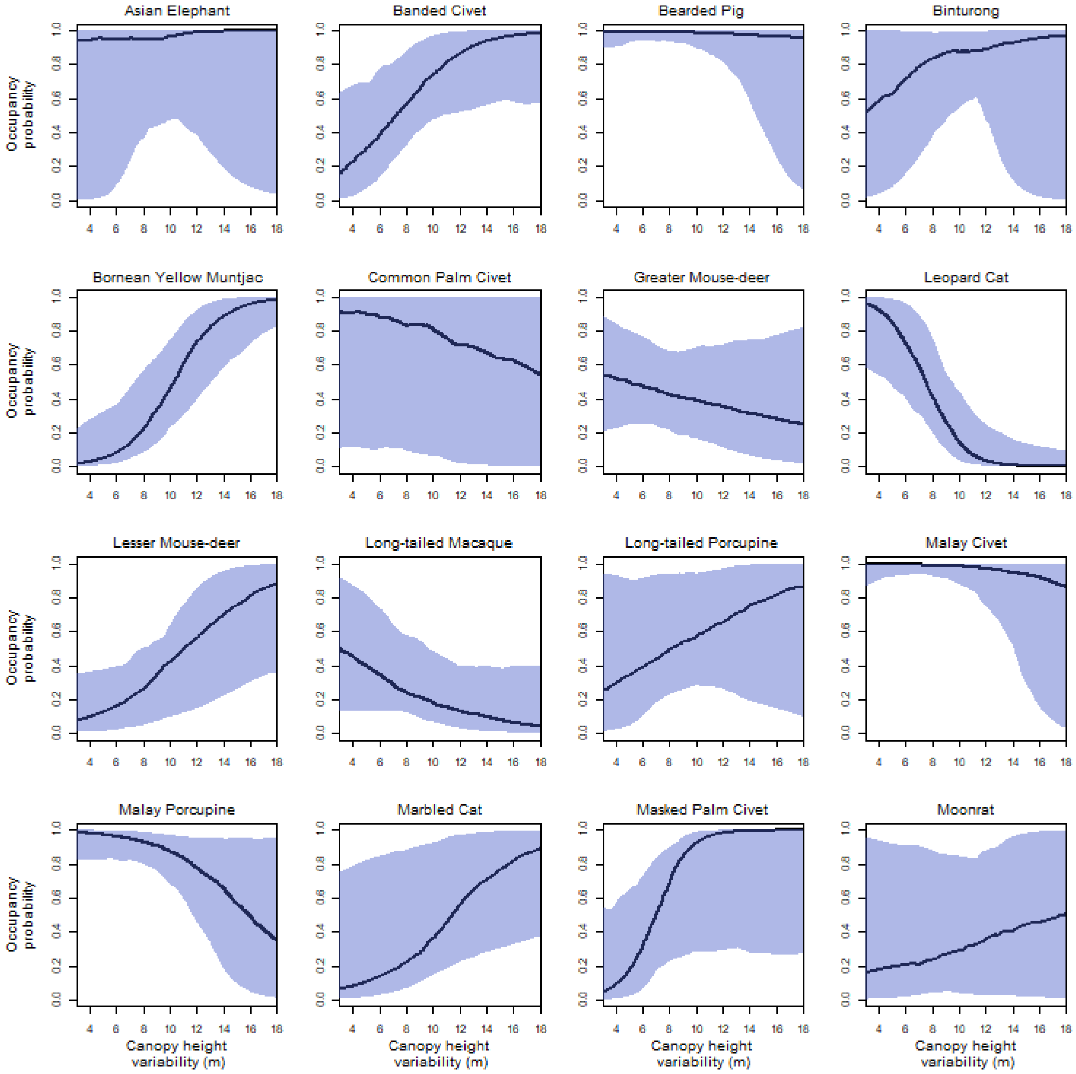

Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Occupancy probability
0.0
0.2
0.4
0.6
0.8
1.0
Forest cover (proportion)

Figure S2.2: Occupancy (second order habitat selection) relative to forest quality. Forest quality was defined using canopy height variability (m), with greater variability indicating better quality forest habitat. Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.



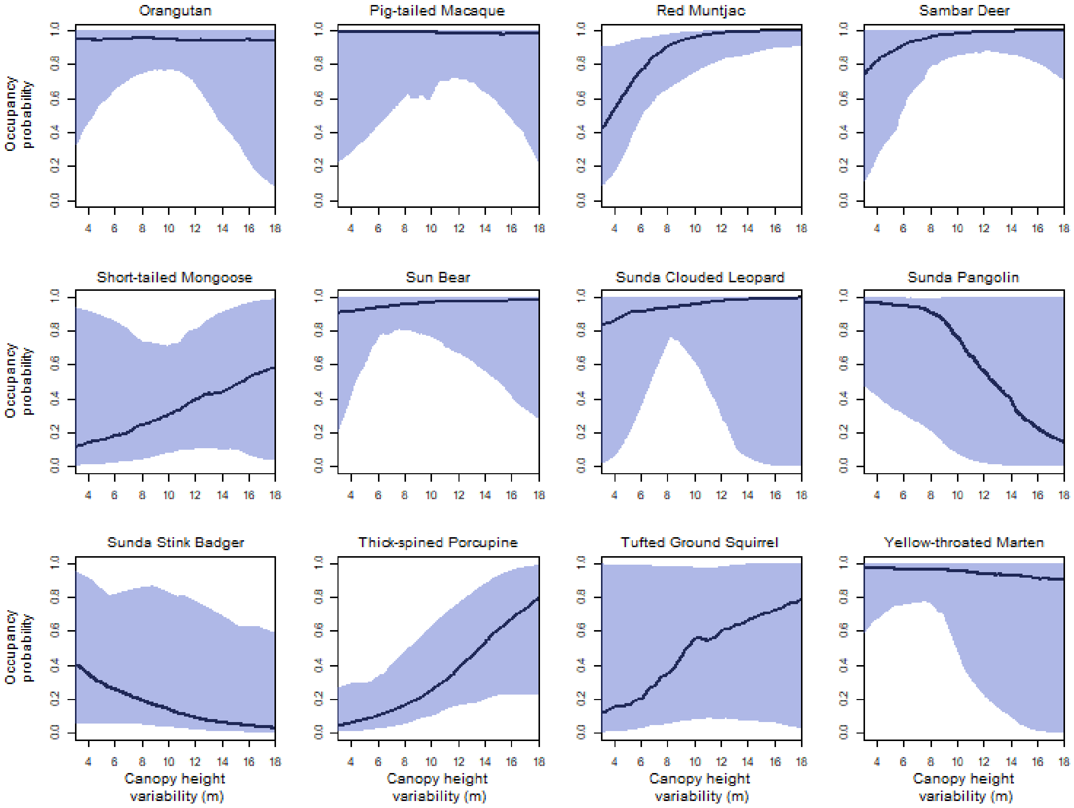
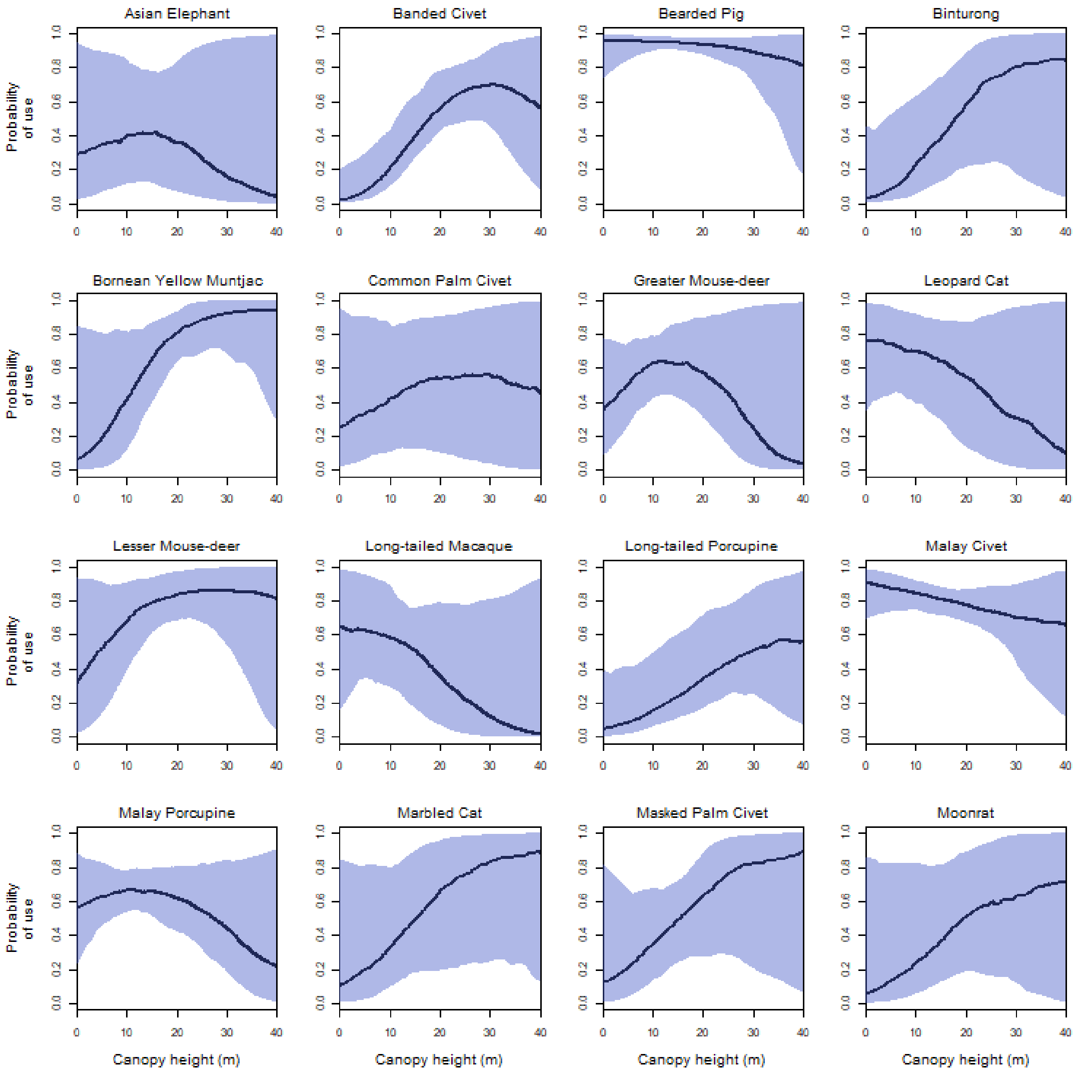

Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Occupancy probability
0.0
0.2
0.4
0.6
0.8
1.0
4
6
8
10
12
14
16
18
Canopy height variability (m)

Figure S2.3: Probability of habitat use (third-order habitat selection) relative to canopy height (m). Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.



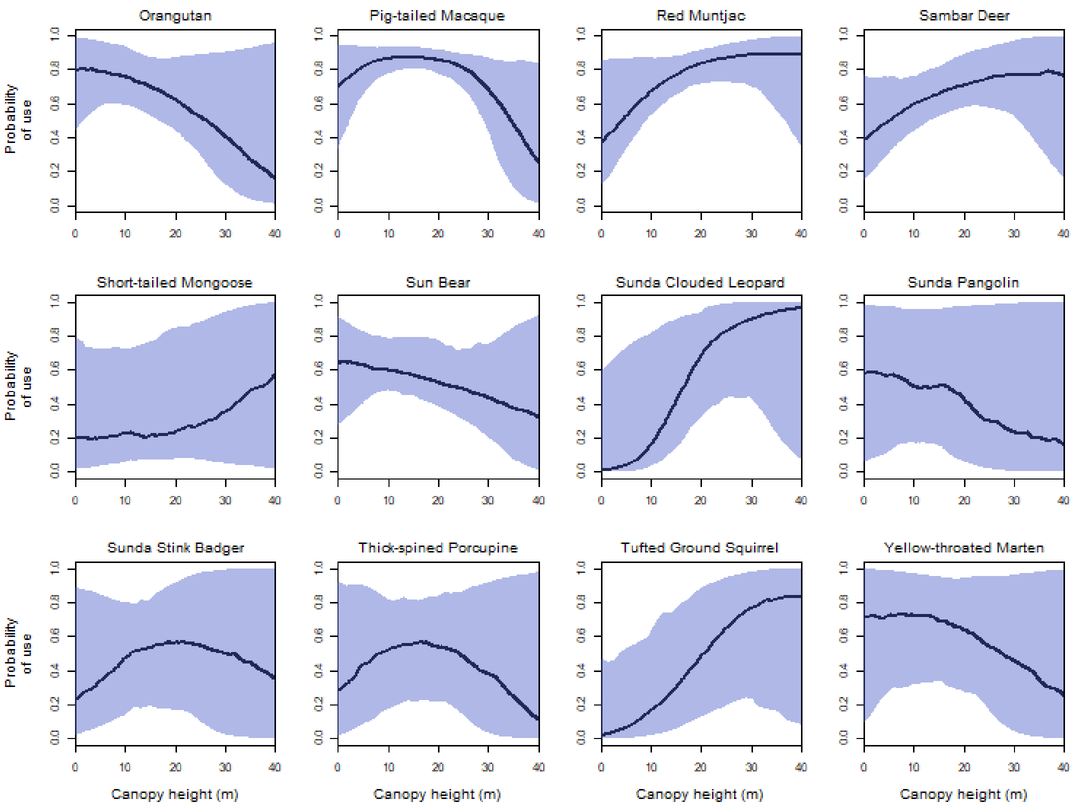
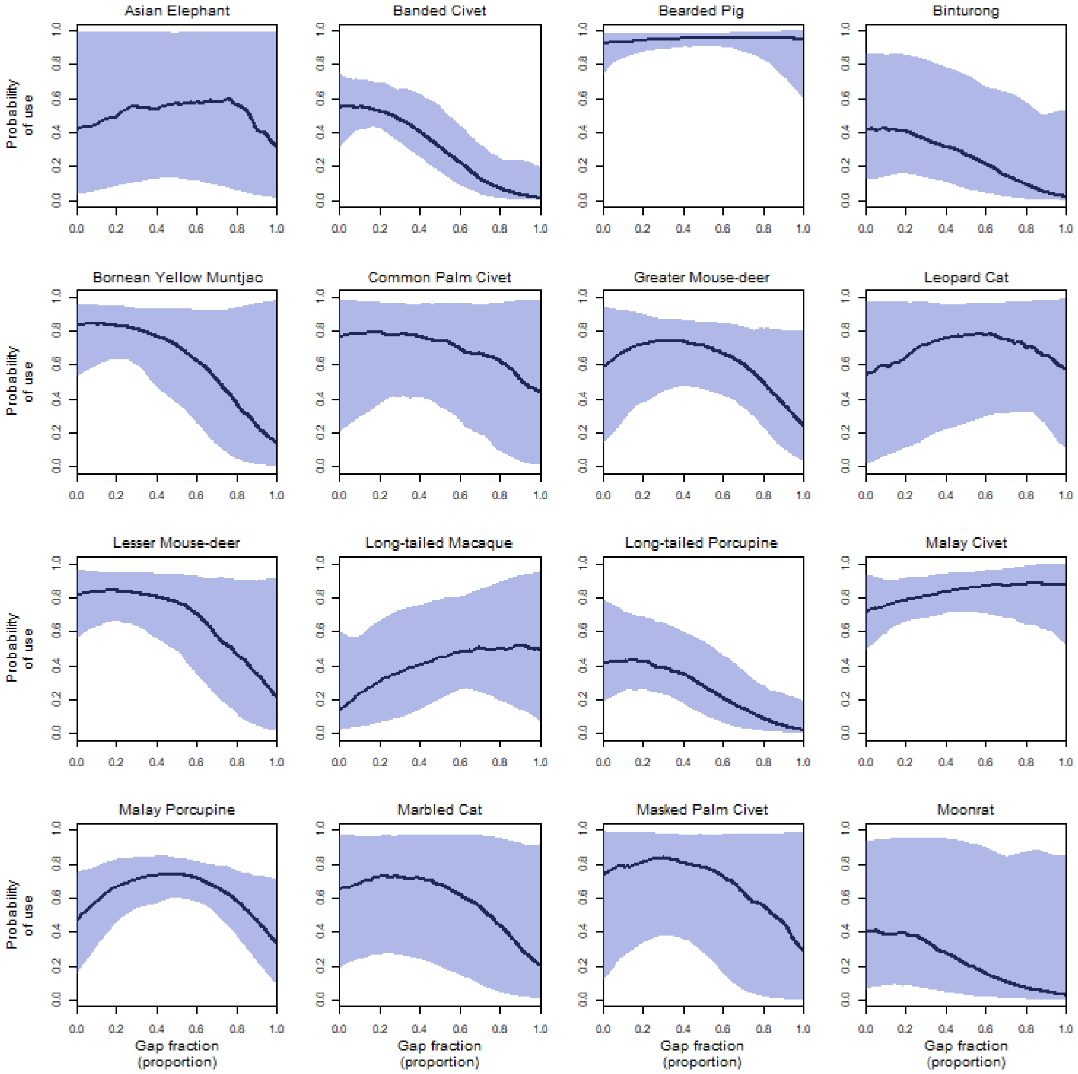

Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Probability of use
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
Canopy height (m)

Figure S2.4: Probability of habitat use (third-order habitat selection) relative to gap fraction. We quantify gap fraction as the proportion of canopy gaps (< 5 m in height) within a 250 m radius of the camera trap. Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.



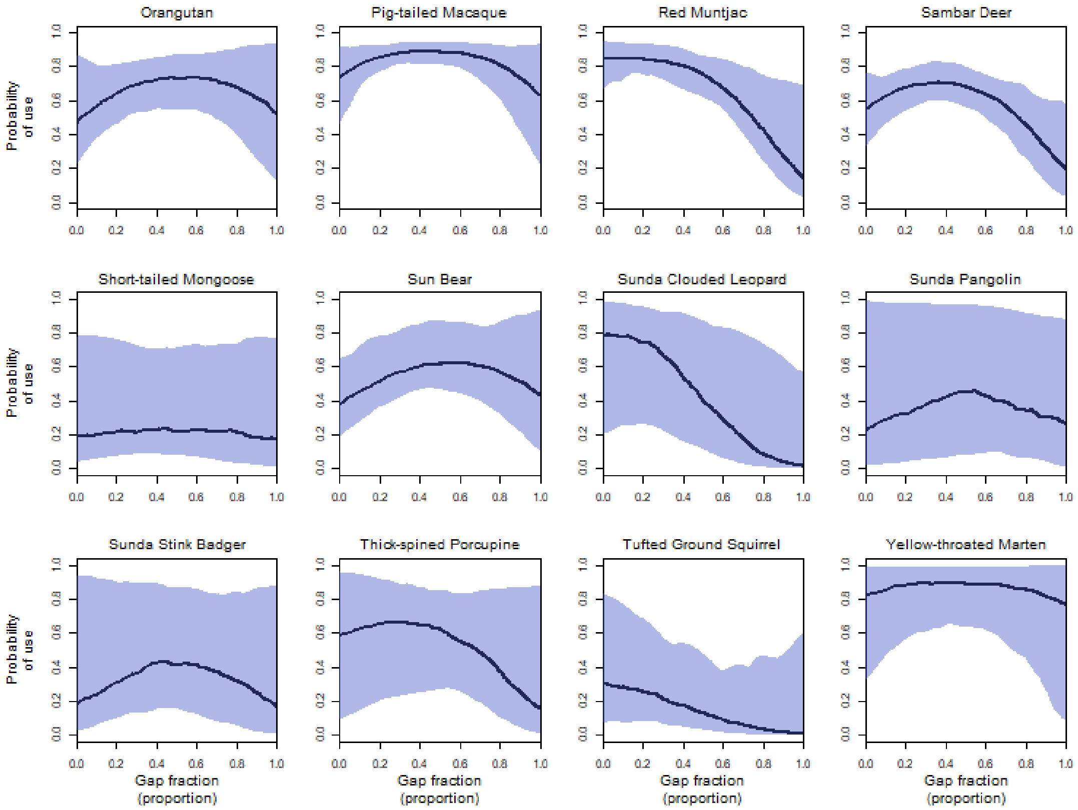
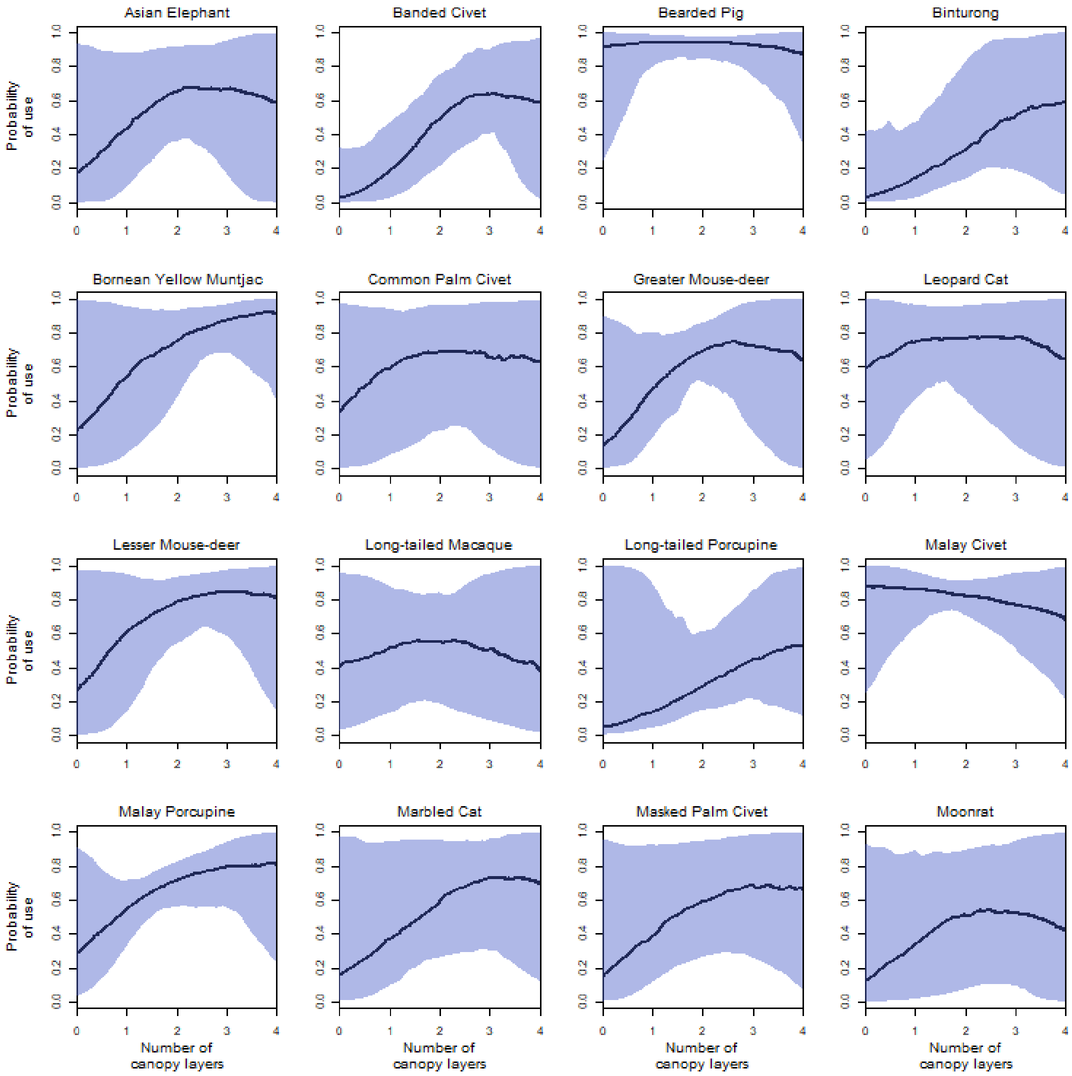

Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Probability of use
0.0
0.2
0.4
0.6
0.8
1.0
Gap fraction (proportion)

Figure S2.5: Probability of habitat use (third-order habitat selection) relative to the number of contiguous layers of vegetation within the canopy. Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.



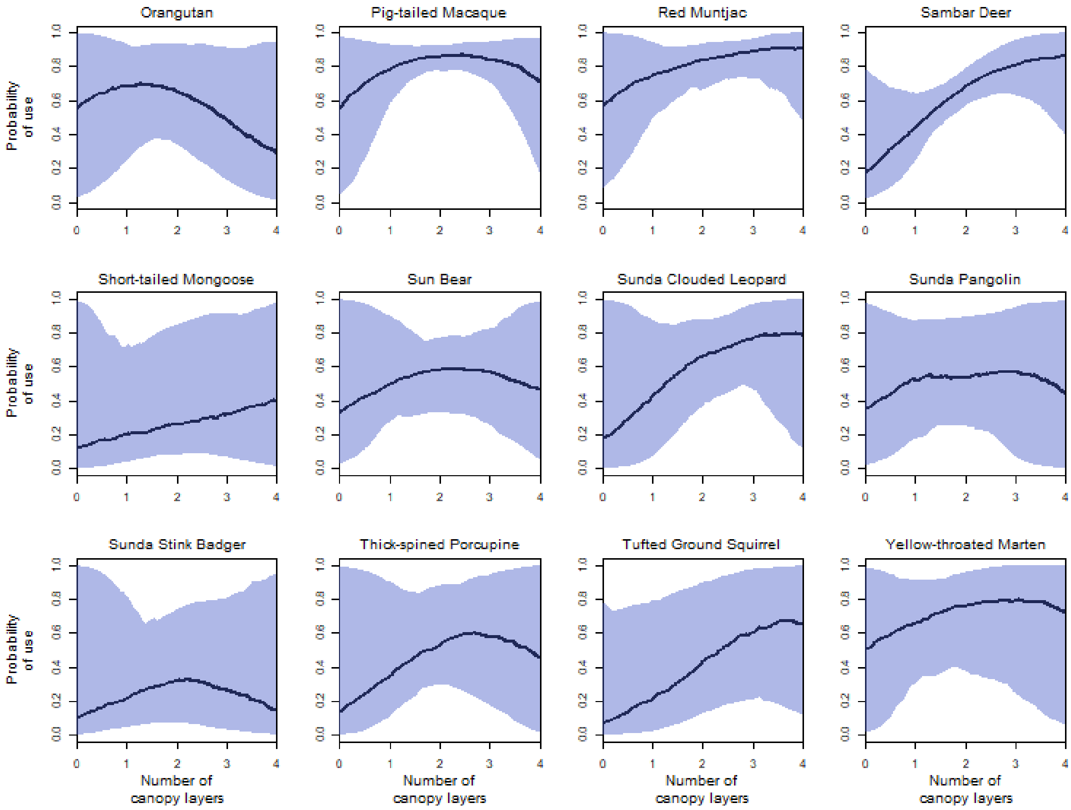
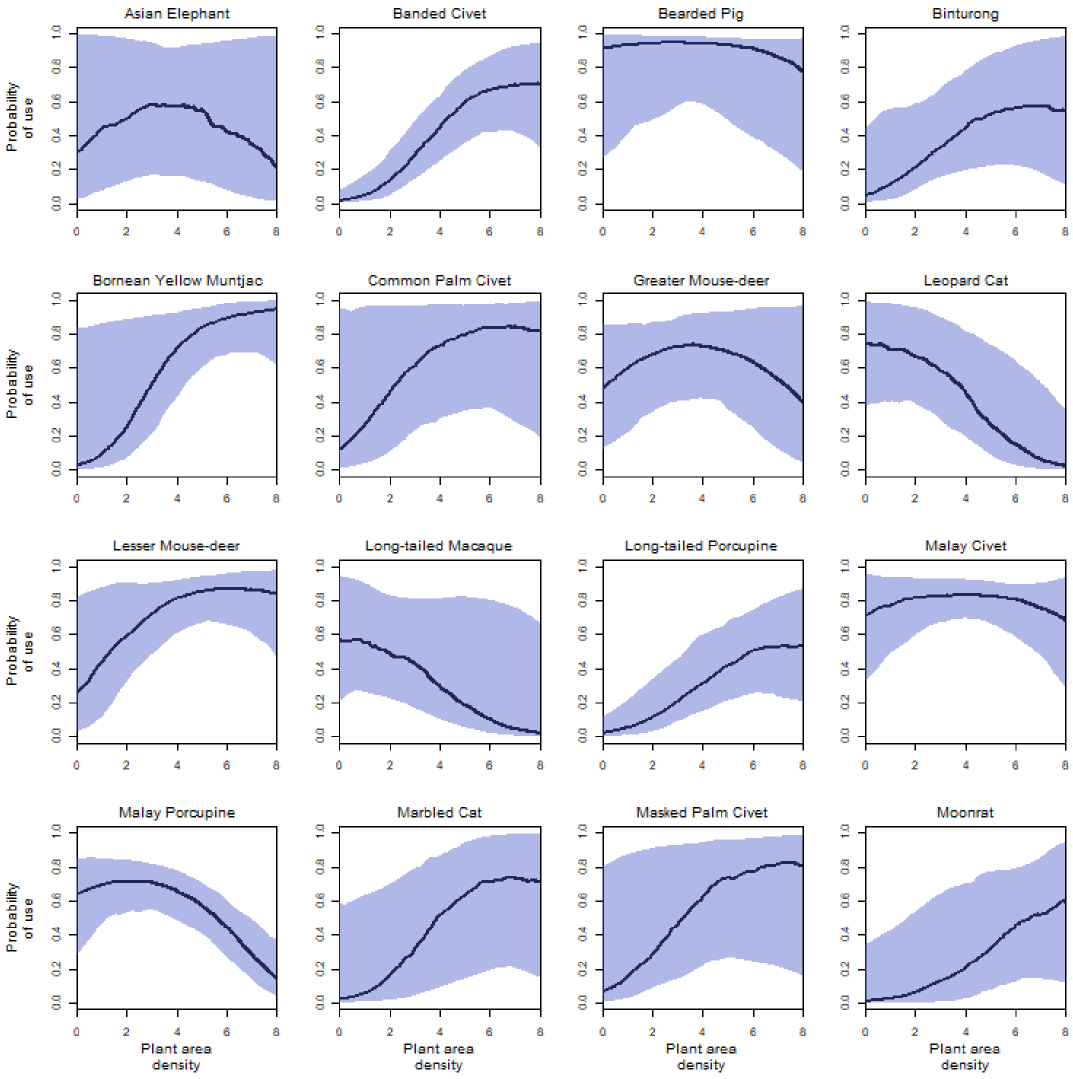

Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Probability of use
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
4
Number of canopy layers

Figure S2.6: Probability of habitat use (third-order habitat selection) relative to plant area density. Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.



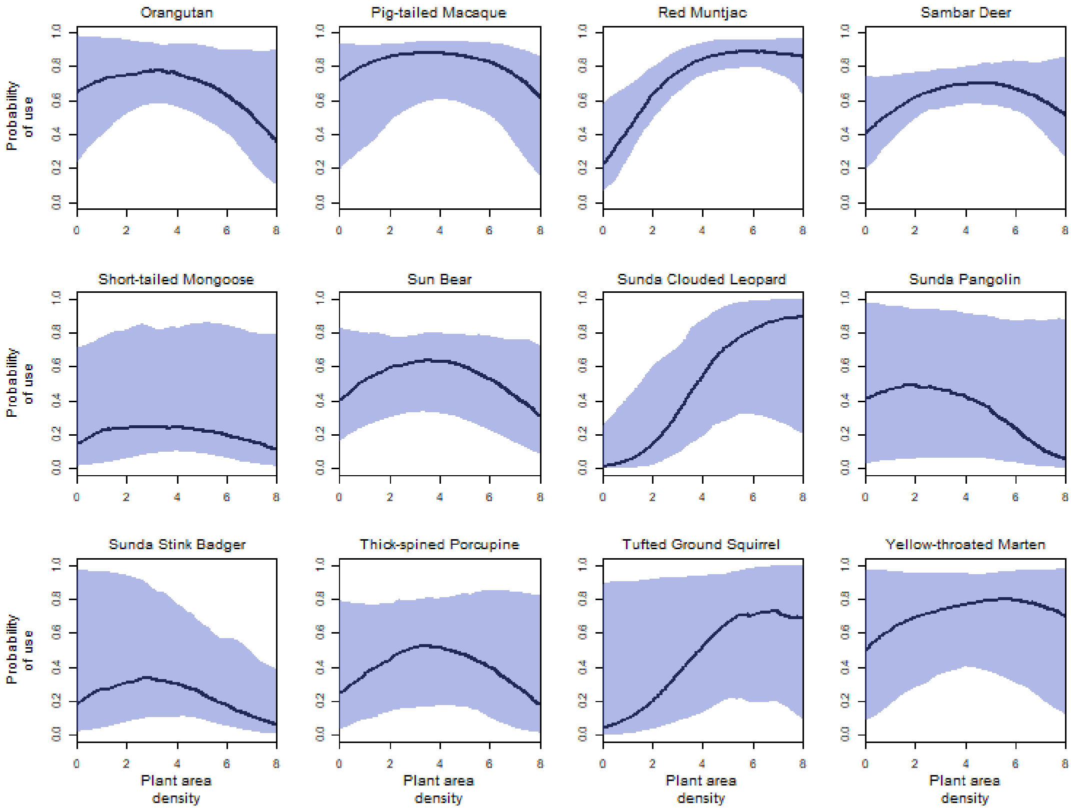
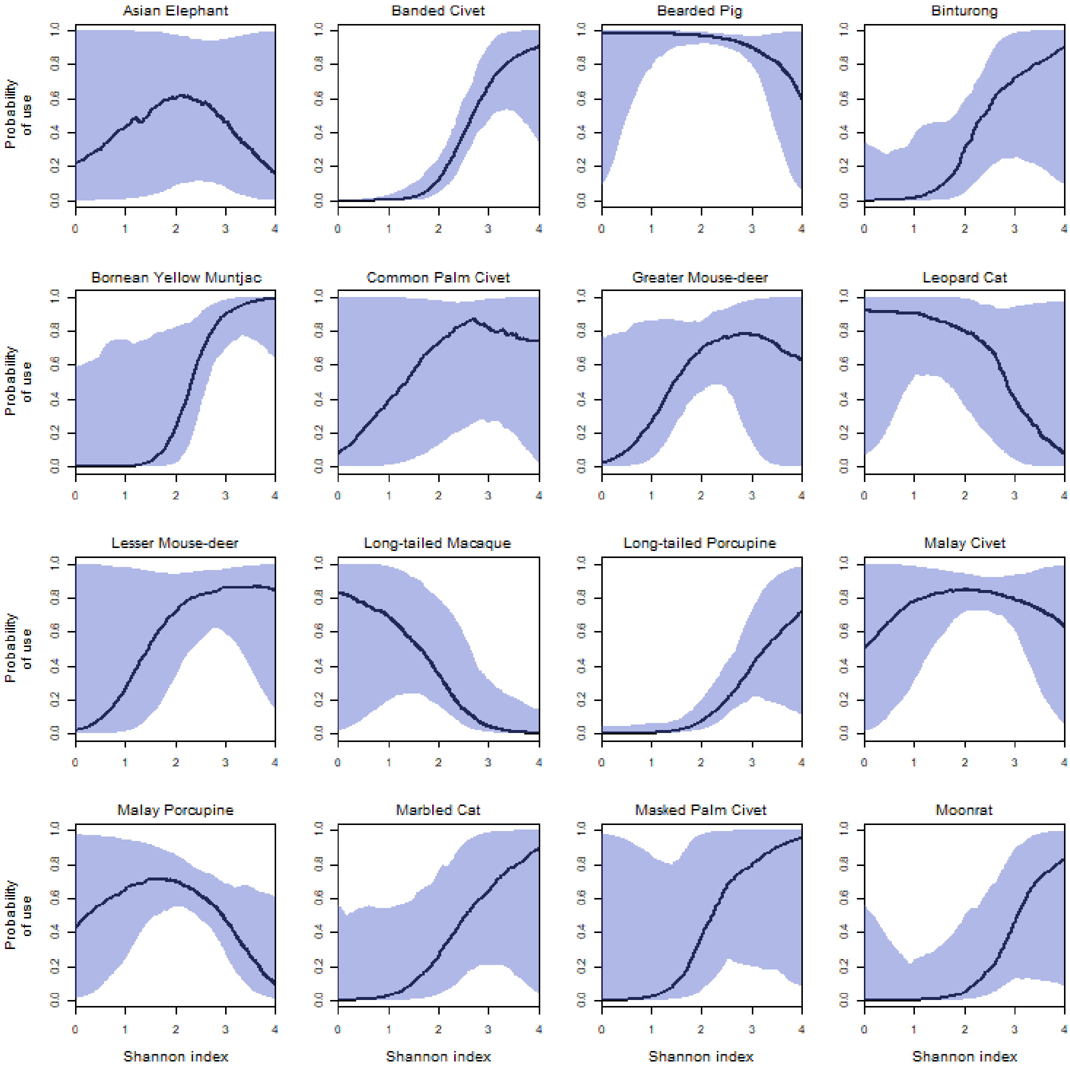

Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Probability of use
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
Plant area density

Figure S2.7: Probability of habitat use (third-order habitat selection) relative to niche availability. We quantify niche availability as the Shannon Index of the plant area distribution. Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.



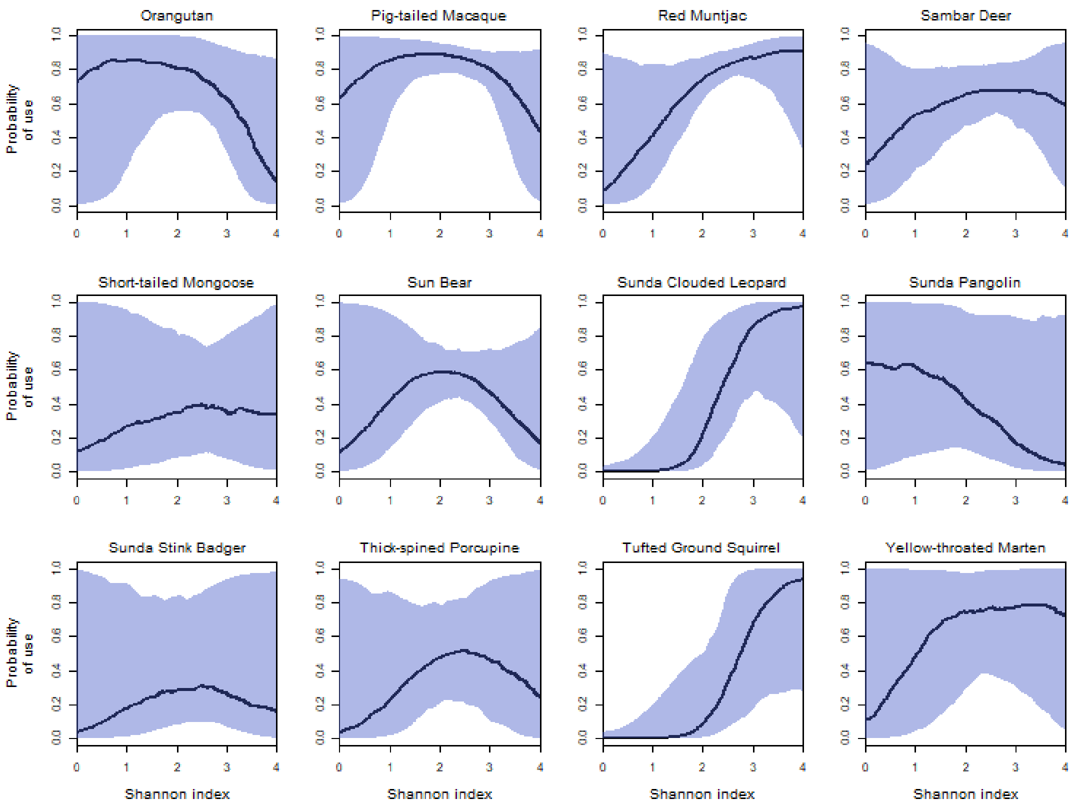
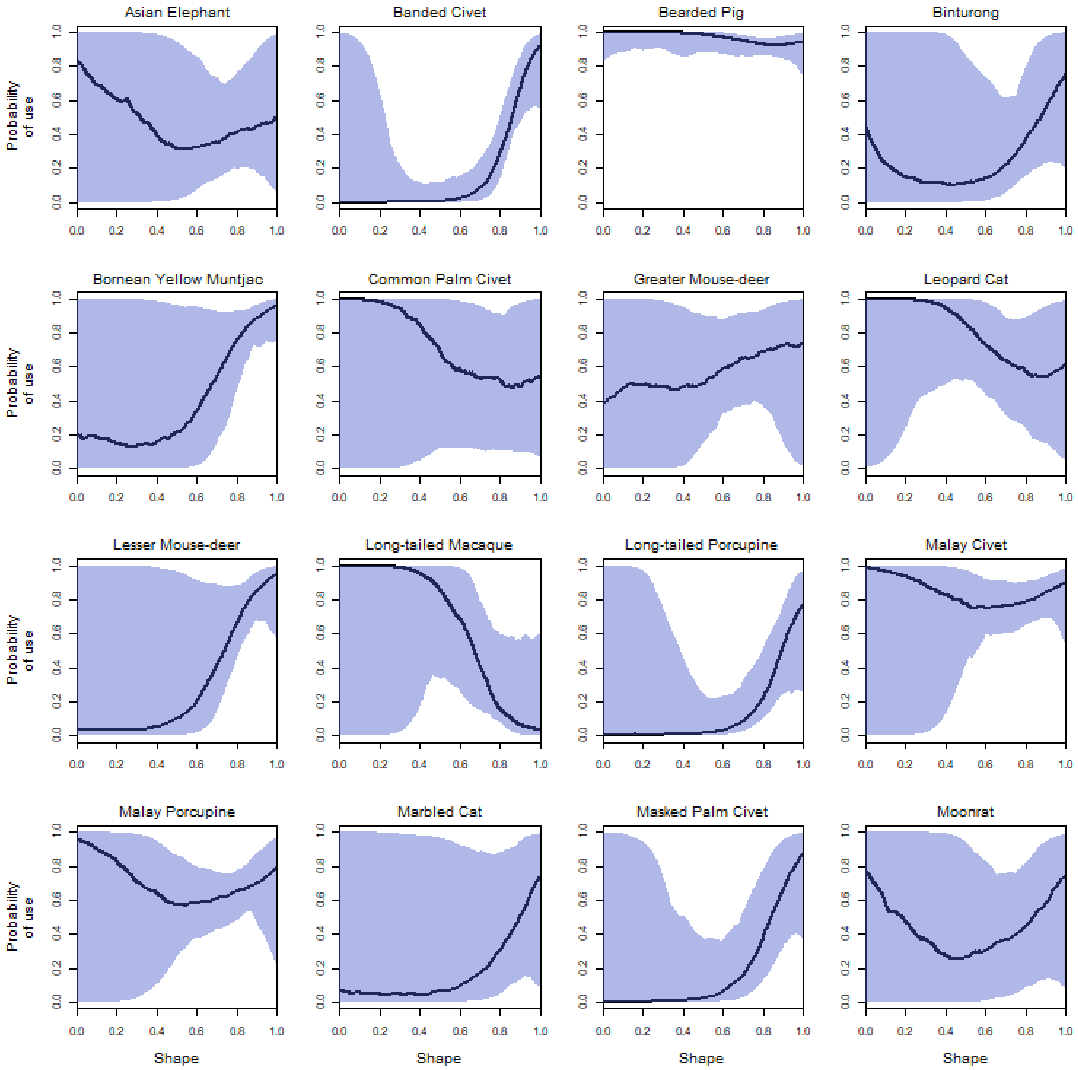

Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Probability of use
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
4
Shannon index

Figure S2.8: Probability of habitat use (third-order habitat selection) relative to shape. We define shape as the distribution of vegetation throughout the vertical column. Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.



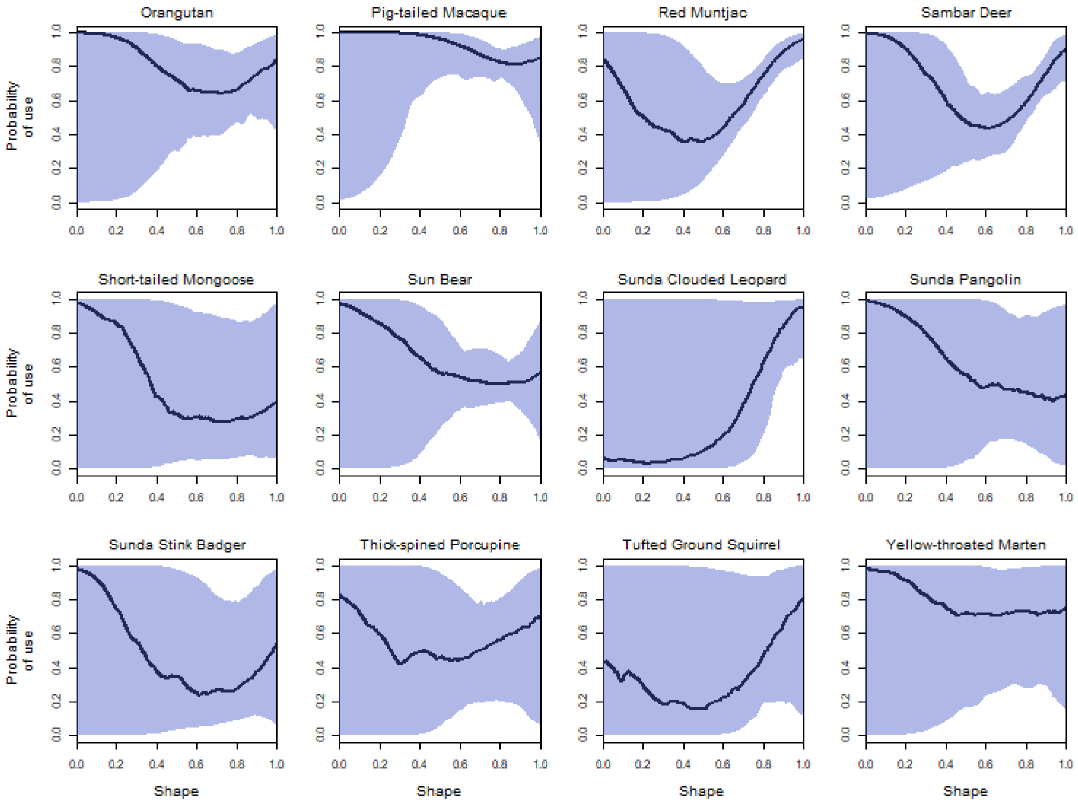

Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Probability of use
0.0
0.2
0.4
0.6
0.8
1.0
Shape

Figure S2.9: Environmental and sampling covariates influencing detection probability. Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Effect sizes are presented as posterior means (points) and 95% Bayesian credible intervals (BCI). Effects were considered substantial if the 95% BCI did not overlap zero (vertical dashed line). Responsive species are presented in blue.

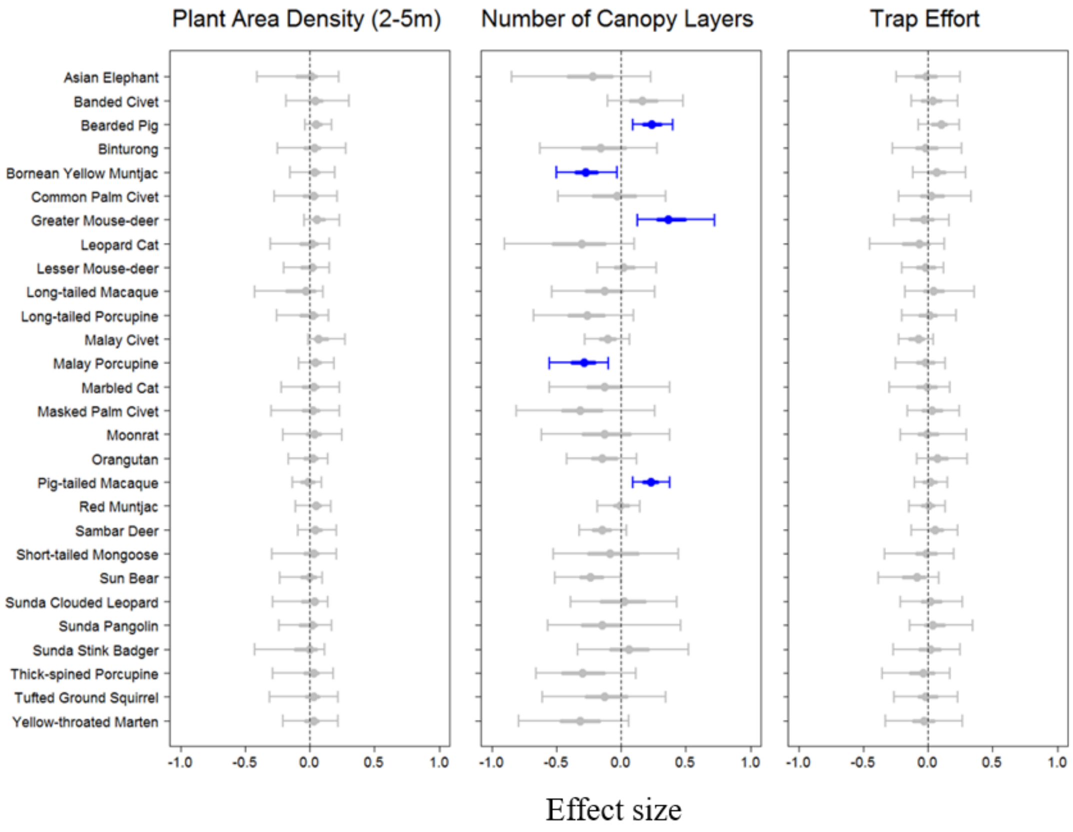
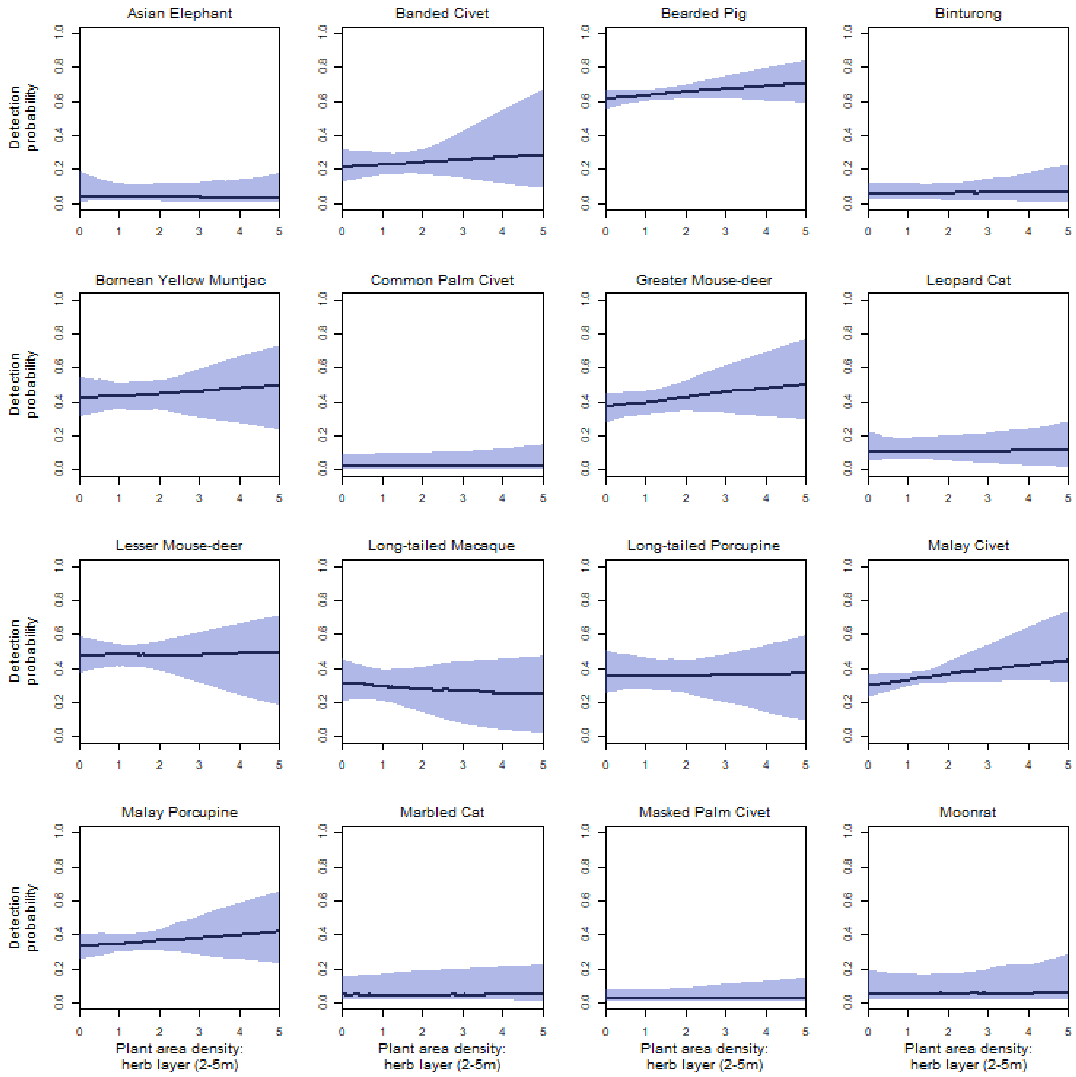


Figure S2.10: Detection probability relative to plant area density in the herbaceous layer (2-5 m). Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.



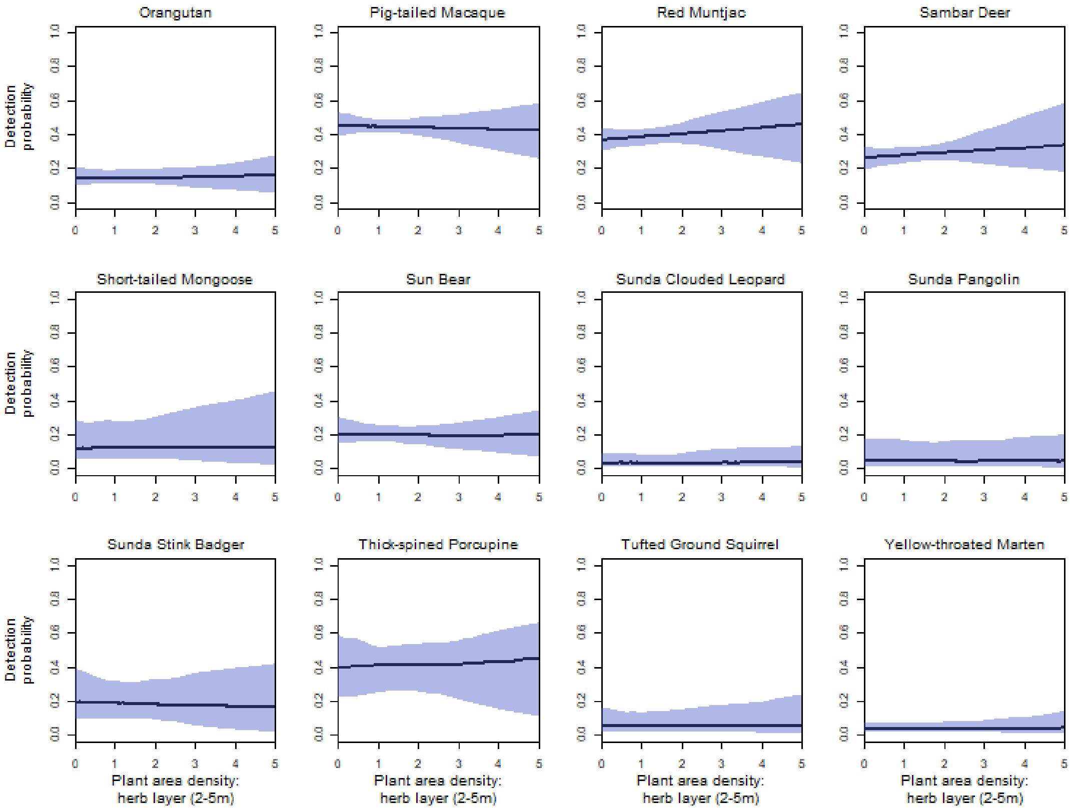
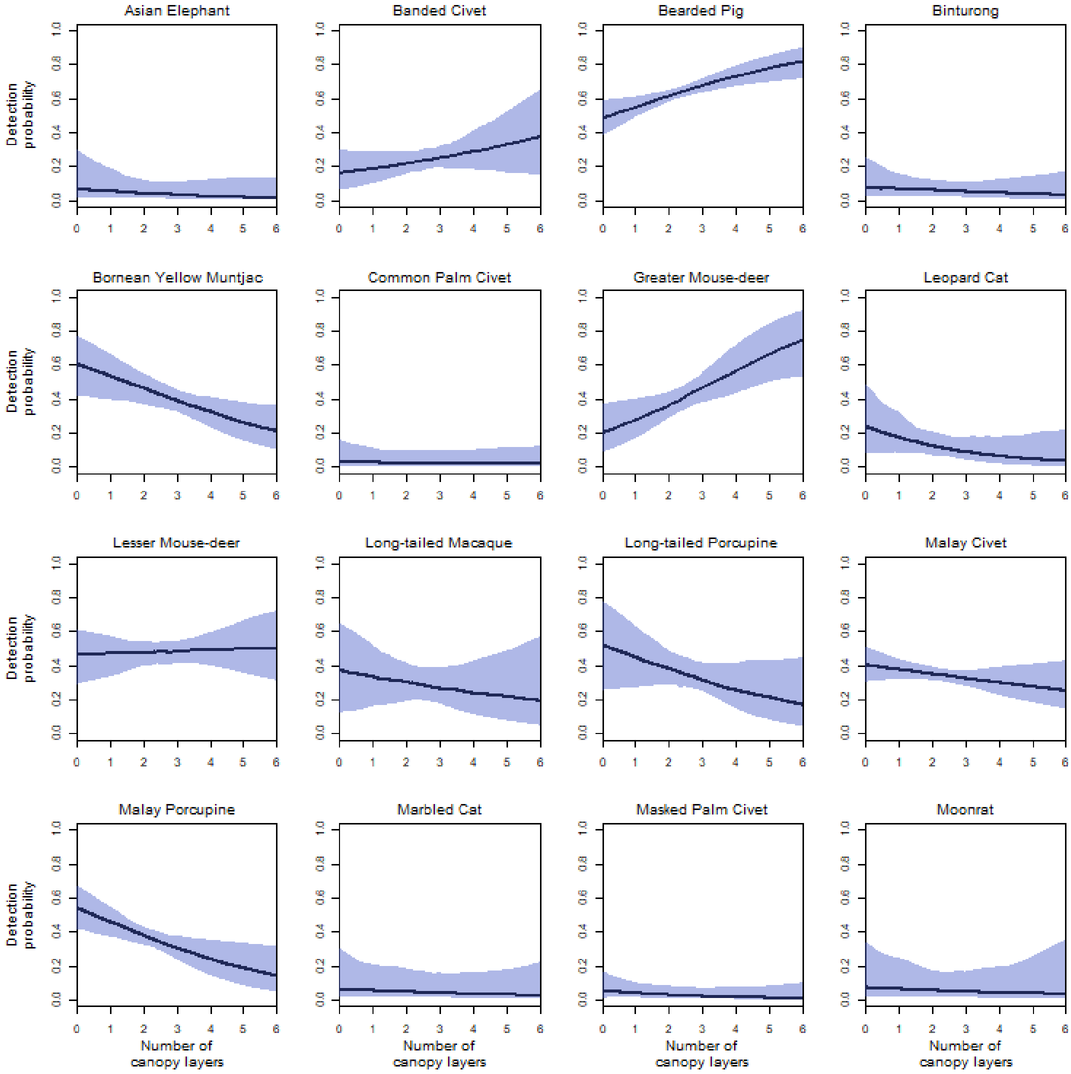

Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
4
5
Plant area density: herb layer (2-5m)

Figure S2.11: Detection probability relative to the number of contiguous layers of vegetation in the canopy. Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.



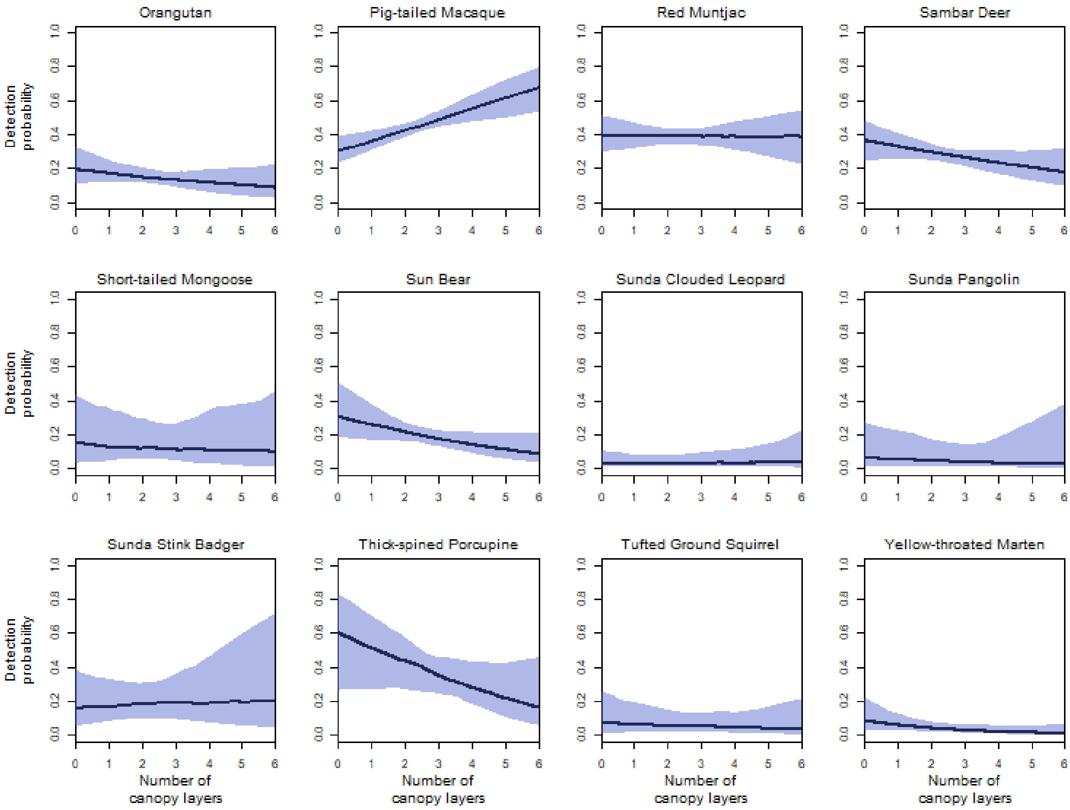
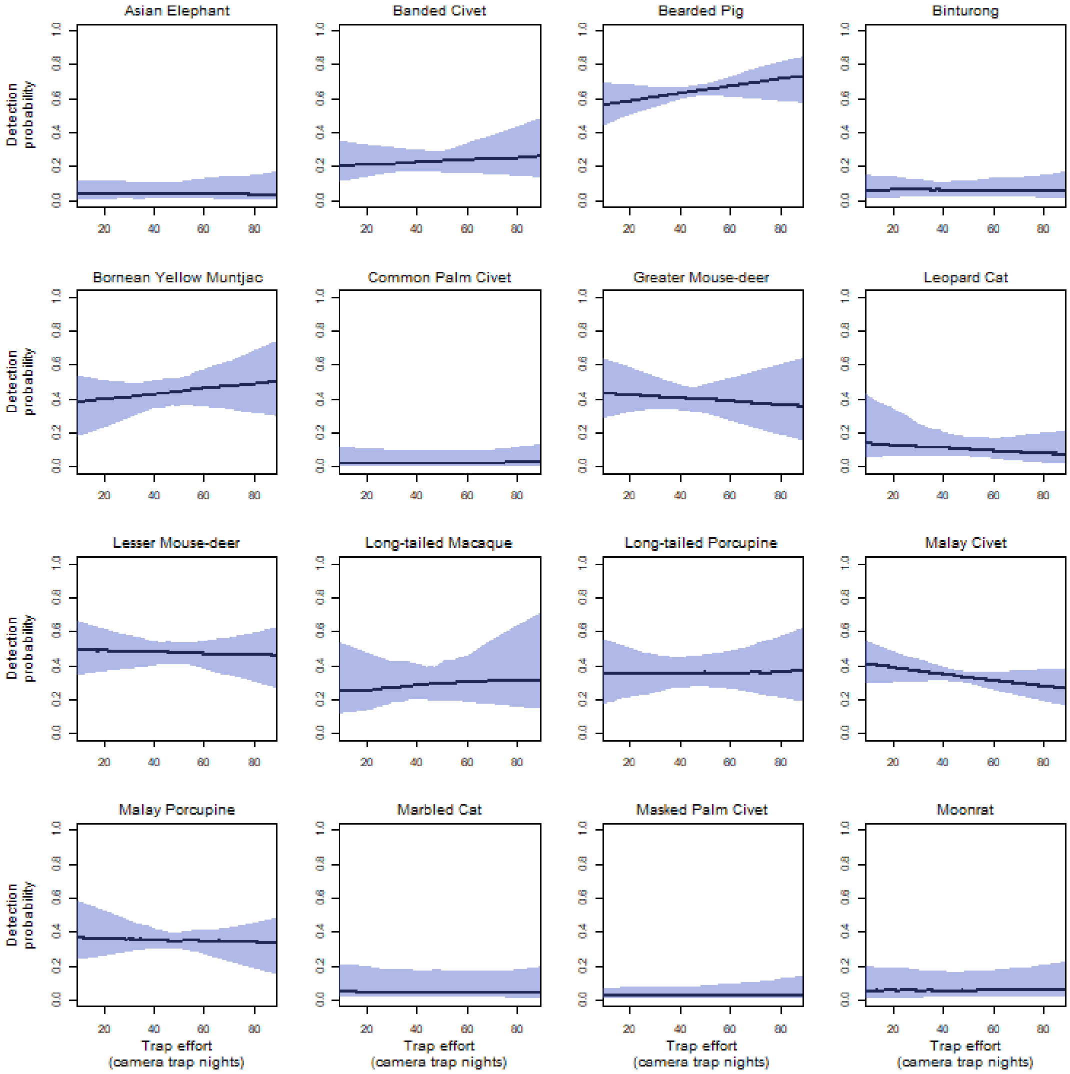
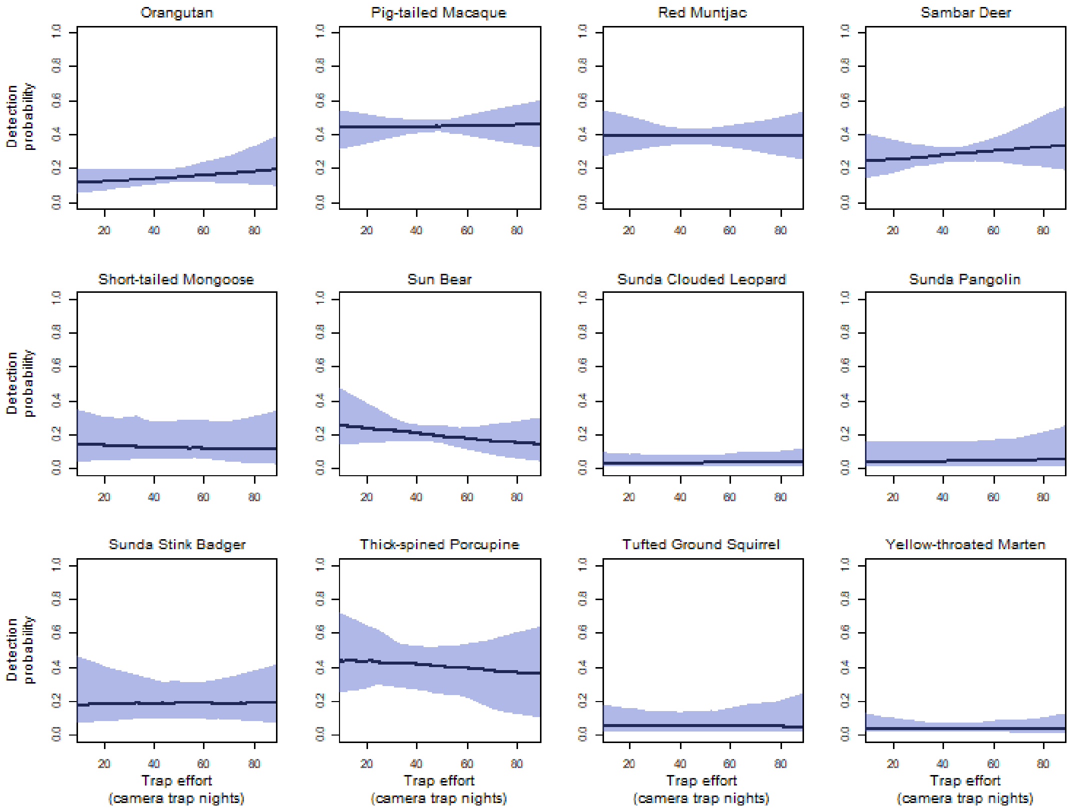

Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
4
5
6
Number of canopy layers

Figure S2.12: Detection probability relative to sampling effort. We define sampling effort based on the number of nights each camera-trap unit was operational. Outputs are presented for the 28 medium-large terrestrial mammals encountered during our sampling. Predicted posterior mean distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals is visualised in light blue.




Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
20
40
60
80
Trap effort (camera trap nights)

S2.1: Model code

We provide model code for the hierarchical Bayesian multi-species, multi-scale occupancy model, written in the BUGS language and implemented in JAGS called through R.

```
model {
   # Hyper-priors for occupancy, habitat use and detection intercepts
   #==============================================
   mu.alpha.psi ~ dnorm(0, 0.01)
   sigma.alpha.psi ~ dunif(0, 10)
   tau.alpha.psi <- pow(sigma.alpha.psi, -2)

   mu.alpha.theta ~ dnorm(0, 0.01)
   sigma.alpha.theta ~ dunif(0, 10)
   tau.alpha.theta <- pow(sigma.alpha.theta, -2)

   mu.alpha.p ~ dnorm(0, 0.01)
   sigma.alpha.p ~ dunif(0, 10)
   tau.alpha.p <- pow(sigma.alpha.p, -2)

   # Hyper-priors for occupancy, habitat use and detection covariate coefficients
   #=====================================================
   mu.beta1.psi ~ dnorm(0, 0.01)
   sigma.beta1.psi ~ dunif(0, 10)
   tau.beta1.psi <- pow(sigma.beta1.psi, -2)

   mu.beta2.psi ~ dnorm(0, 0.01)
   sigma.beta2.psi ~ dunif(0, 10)
   tau.beta2.psi <- pow(sigma.beta2.psi, -2)

   mu.beta1.theta ~ dnorm(0, 0.01)
   sigma.beta1.theta ~ dunif(0, 10)
   tau.beta1.theta <- pow(sigma.beta1.theta, -2)

   mu.beta2.theta ~ dnorm(0, 0.01)
   sigma.beta2.theta ~ dunif(0, 10)
   tau.beta2.theta <- pow(sigma.beta2.theta, -2)

   mu.beta1.p ~ dnorm(0, 0.01)
   sigma.beta1.p ~ dunif(0, 10)
   tau.beta1.p <- pow(sigma.beta1.p, -2)

   mu.beta2.p ~ dnorm(0, 0.01)
   sigma.beta2.p ~ dunif(0, 10)
```

```
   tau.beta2.p <- pow(sigma.beta2.p, -2)

   mu.beta3.p ~ dnorm(0, 0.01)
   sigma.beta3.p ~ dunif(0, 10)
   tau.beta3.p <- pow(sigma.beta3.p, -2)

   # Hyperprior for half-Cauchy scale parameter for occupancy and habitat use
models

#======================================================================
   xi.sd.psi ~ dunif(0, 10)
   xi.tau.psi <- pow(xi.sd.psi, -2)
   xi.sd.theta ~ dunif(0, 10)
   xi.tau.theta <- pow(xi.sd.theta, -2)

   # Species-specific parameters drawn as realisations from the community
distributions

#======================================================================
=
   for(i in 1:n.sp){
      alpha.psi[i] ~ dnorm(mu.alpha.psi, tau.alpha.psi)
      alpha.theta[i] ~ dnorm(mu.alpha.theta, tau.alpha.theta)
      alpha.p[i] ~ dnorm(mu.alpha.p, tau.alpha.p)

      beta1.psi[i] ~ dnorm(mu.beta1.psi, tau.beta1.psi)
      beta2.psi[i] ~ dnorm(mu.beta2.psi, tau.beta2.psi)
      beta1.theta[i] ~ dnorm(mu.beta1.theta, tau.beta1.theta)
      beta2.theta[i] ~ dnorm(mu.beta2.theta, tau.beta2.theta)
      beta1.p[i] ~ dnorm(mu.beta1.p, tau.beta1.p)
      beta2.p[i] ~ dnorm(mu.beta2.p, tau.beta2.p)
      beta3.p[i] ~ dnorm(mu.beta3.p, tau.beta3.p)
      }

   # Hyperpriors/priors for temporal random effect
   #=====================================
   for(i in 1:n.sp){
      # Random year effects for psi component
      for(year in 1:n.year){
         eps.psi[year, i] ~ dnorm(0, eps.tau.psi[i])
         eps.theta[year, i] ~ dnorm(0, eps.tau.theta[i])
         }

      eps.tau.psi[i] ~ dgamma(0.5, 0.5)
      xi.psi[i] ~ dnorm(0, xi.tau.psi)
      sigma.cauchy.psi[i] <- abs(xi.psi[i]) / sqrt(eps.tau.psi[i])

      eps.tau.theta[i] ~ dgamma(0.5, 0.5)
      xi.theta[i] ~ dnorm(0, xi.tau.theta)
```

```
    sigma.cauchy.theta[i] <- abs(xi.theta[i]) / sqrt(eps.tau.theta[i])
    }

  # Ecological model for occurrence of species i in site j
  #==========================================
  for(i in 1:n.sp){
    for(j in 1:n.sites){
      logit(psi[j,i]) <- alpha.psi[i] + beta1.psi[i]*ForCov[j] +
beta2.psi[i]*CH_SD.psi[j] +
                    xi.psi[i]*eps.psi[year.counter.psi[j],i]
      z[j,i] ~ dbern(psi[j,i])

  # Sub-unit model, occurence of species i within spatial replicate l
      for(l in 1:n.spatial[j]){
        logit(theta[j,l,i]) <- alpha.theta[i] + beta1.theta[i]*Structure1[j,l] +
                    beta2.theta[i]*Structure2[j,l] +
xi.theta[i]*eps.theta[year.counter.theta[j,l],i]
        mu.a[j,l,i] <- z[j,i] * theta[j,l,i]
        a[j,l,i] ~ dbern(mu.a[j,l,i])

  # Detection model for replicated detection/non-detection observations
        for(k in 1:n.temporal[j,l]){
          logit(p[j,l,k,i]) <- alpha.p[i] + beta1.p[i]*PAI_Herb.p[j,l] +
beta2.p[i]*Nlay.p[j,l] +
                          beta3.p[i]*TrapEffort[j,l]
          mu.p[j,l,k,i] <- a[j,l,i] * p[j,l,k,i]
          y[j,l,k,i] ~ dbern(mu.p[j,l,k,i])

  # Calculate Pearson's Chi-squared residuals to assess goodness of fit
  # Based on Kery and Royle: Applied hierarchical modelling in ecology, pp. 235
  # Calculate the observed and expected residuals
  # Add small value to prevent division by zero
  #================================
          y.sim[j,l,k,i] ~ dbern(mu.p[j,l,k,i])
          chi2.obs[j,l,k,i] <- pow(y[j,l,k,i] - mu.p[j,l,k,i], 2)/ (mu.p[j,l,k,i] +
0.0001)
          chi2.sim[j,l,k,i] <- pow(y.sim[j,l,k,i] - mu.p[j,l,k,i], 2)/ (mu.p[j,l,k,i] +
0.0001)
        }
        chi2.obs.sum[j,l,i] <- sum(chi2.obs[j,l,1:n.temporal[j,l],i])
        chi2.sim.sum[j,l,i] <- sum(chi2.sim[j,l,1:n.temporal[j,l],i])
      }
      chi2.obs.sum2[j,i] <- sum(chi2.obs.sum[j,1:n.spatial[j],i])
      chi2.sim.sum2[j,i] <- sum(chi2.sim.sum[j,1:n.spatial[j],i])
    }

  # Calculate chi-squared discrepency for each species
  #====================================
    fit.sp.obs[i] <- sum(chi2.obs.sum2[,i])
```

```
      fit.sp.sim[i] <- sum(chi2.sim.sum2[,i])
      c.hat.sp[i] <- fit.sp.obs[i]/fit.sp.sim[i]
      bpv.sp[i] <- step(fit.sp.sim[i] - fit.sp.obs[i])
   }

   # Calculate model discrepency measure and fit statistics
   #=================================================
   fit.obs <- sum(chi2.obs.sum2[1:n.sites, 1:n.sp])
   fit.sim <- sum(chi2.sim.sum2[1:n.sites, 1:n.sp])
   c.hat <- fit.obs/fit.sim
   bpv <- step(fit.sim - fit.obs)

   # Derived quantities
   # Number of occupied sites
   #======================
   for(i in 1:n.sp) {
      Nocc.fs[i] <- sum(z[,i])
      }

   # Number of species occurring at each site
   #====================================
   for(j in 1:n.sites) {
      Nsite[j] <- sum(z[j,])
      }
}
```

Chapter 3. High carbon stock forests provide co-benefits for tropical biodiversity

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5. South East Asia Rainforest Research Partnership (SEARRP), Danum Valley Field Centre, PO Box 60282, 91112 Lahad Datu, Sabah, Malaysia.
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Manuscript published as:

Deere, N.J., Guillera-Arroita, G., Baking, E.L., Bernard, H., Pfeifer, M., Reynolds, G., . . . Struebig, M.J. 2018. High Carbon Stock forests provide co-benefits for tropical biodiversity. *Journal of Applied Ecology*, 55**,** 997-1008.

Abstract

1. Carbon-based policies provide powerful opportunities to unite tropical forest conservation with climate change mitigation. However, their effectiveness in delivering biodiversity co-benefits is dependent on high levels of biodiversity being found in high carbon areas. Previous studies have focussed solely on the co-benefits associated with Reducing Emissions from Deforestation and forest Degradation (REDD+) over large spatial scales, with few empirically testing carbon-biodiversity correlations at management unit scales appropriate to decision-makers. Yet, in development frontiers, where most biodiversity and carbon loss occurs, carbon-based policies are increasingly driven by commodity certification schemes, which are applied at the concession-level.

2. Working in a typical human-modified landscape in Southeast Asia, we examined the biodiversity value of land prioritised via application of REDD+ or the High Carbon Stock (HCS) Approach, the emerging land-use planning tool for oil palm certification. Carbon stocks were estimated via low- and high-resolution datasets derived from global or local-level biomass. Mammalian species richness was predicted using hierarchical Bayesian multi-species occupancy models of camera-trap data from forest and oil palm habitats.

3. At the community level, HCS forest supported comparable mammal diversity to control sites in continuous forest, while lower carbon HCS strata exhibited reduced species occupancy.

4. No association was found between species richness and carbon when the latter was estimated using coarse-resolution data. However, when using high-resolution,

locally-validated biomass data, diversity demonstrated positive relationships with carbon for threatened and disturbance-sensitive species, suggesting sensitivity of co-benefits to carbon data sources and the species considered.

5. *Policy implications.* Our work confirms the potential for environmental certification and Reducing Emissions from Deforestation and forest Degradation (REDD+) to work in tandem with conservation to mitigate agricultural impacts on tropical forest carbon stocks and biodiversity. Successful implementation of both approaches could be used to direct development to low carbon, low biodiversity areas in topical countries.

Keywords: Agriculture, Borneo, camera-trapping, certification, High Carbon Stock; land-use planning, mammals, occupancy modelling, oil palm, REDD+, tropical forest.

Introduction

Agricultural expansion has emerged as a pervasive threat to tropical forests and biodiversity (Wilcove et al., 2013), and has been implicated in the loss of ~150 million ha of tropical forest over the last three decades (Gibbs et al., 2010, Hansen et al., 2013). A key driver of recent deforestation has been rising demand for cheap vegetable oil such as that from oil palm (*Elaeis guineensis*), which now covers 16 million ha across 43 countries, often at the expense of tropical forest (Pirker et al., 2016).

The potential economic and social benefits associated with oil palm (Potter, 2015) contrast with severe and well-documented ecological impacts. Conversion of forest to oil palm plantation results in major biodiversity decline, which disproportionately affects forest specialists and species of conservation concern, resulting in assemblages dominated by disturbance-tolerant generalists (Fitzherbert et al., 2008, Yaap et al., 2010). With around 19% of land suitable for oil palm coinciding with areas of high biodiversity (Pirker et al., 2016), across forested Asia, Africa and South America, the full ecological impact of this commodity crop is yet to be fully realised. Mitigation measures that reconcile environmental sustainability, biodiversity conservation and production of crops such as oil palm are therefore essential in tropical regions.

Retaining native habitat in oil palm estates is known to enhance the biological value of plantation landscapes by providing ecological refugia and improved connectivity (Gillies and St Clair, 2010, Struebig et al., 2011). However, in practice, the designation of conservation set-asides can be hindered by agricultural profitability, with income exceeding US$11,240 ha^{-1} over a 25 year growing cycle (Fisher et al., 2011a). Thus, conservation efforts seeking to preserve forest within plantations may be more successful when economic incentives are provided to offset the opportunity costs associated with foregoing development. Amongst several mitigation tools available, two incentive-driven policies based on carbon stocks have gained traction in tropical regions: (1) REDD+ (United Nations Reducing Emissions from Deforestation and forest Degradation) and related carbon credit schemes, and (2) improved land-use planning via commodity certification (Yaap et al., 2010).

REDD+, a payment for ecosystem services tool to mitigate climate change, aims to compensate stakeholders in developing nations for conservation initiatives and sustainable management practices that protect and restore the carbon sequestered by forests (Venter and Koh, 2012). If REDD+ were to achieve its economic potential, payments generated could make forest conservation financially competitive compared to oil palm cultivation (Butler et al., 2009). REDD+ is also attractive to conservation because it may deliver co-benefits, whereby safeguarding high carbon areas also protects biodiversity at no additional cost (Gardner et al., 2012). However, this assumes spatial congruence between areas of high carbon and biodiversity. In reality it is difficult to generalise on the nature, strength and extent of these co-benefits because outcomes vary both within and between spatial scales (e.g. global: Naidoo et al., 2008, Strassburg et al., 2010, national: Egoh et al., 2009, Murray et al., 2015, local: Ruiz-Jaen and Potvin, 2010, Kessler et al., 2012). The extent to which carbon-biodiversity co-benefit assumptions hold at management unit scales appropriate to decision-makers remains an open question.

REDD+ is largely implemented at sub-national levels. While an increasing number of studies are recognising the importance of fine-scale assessments (e.g.

Beaudrot et al., 2016b, Magnago et al., 2015, Sollmann et al., 2017), most information on biodiversity co-benefits is derived from global- and national-scale studies that demonstrate overreliance on coarse-grained, secondary data sources. Carbon data are typically derived from global maps (e.g. Avitabile et al., 2016, Baccini et al., 2012), which have limited application at local-scales pertinent to management (Mitchard et al., 2014). Furthermore, field-based species data are widely underrepresented in the co-benefits literature due to the costs associated with biodiversity surveys in the tropics (Gardner et al., 2008). Researchers predominantly rely on coarse species range delineations, which are fraught with uncertainty (Rodríguez-Castañeda et al., 2012) and may not account for localised extirpation due to anthropogenic pressure (Harrison et al., 2016). Despite statistical advances that account for imperfect detection in biodiversity indices (Royle and Dorazio, 2008), these methods have received relatively limited application in a co-benefits context (but see Gilroy et al., 2014, Sollmann et al., 2017), resulting in possible underestimates of species assemblages. Consequently, biodiversity co-benefits assessments at local-scales, using primary, fine-grained data would provide valuable policy insights.

While the potential importance of REDD+ cannot be overstated, agricultural certification schemes show promise to ensure sustainable practices as companies benefit from greater access to environmentally conscious markets and increased price premiums of certified products (Yaap et al., 2010). The Roundtable on Sustainable Palm Oil (RSPO) is often seen as an exemplar scheme within the agricultural sector, currently certifying 21% of the global palm oil market across 2.48 million ha of land (RSPO, 2015). RSPO certification prohibits the conversion of high conservation value habitat in oil palm estates. However, associated assessment procedures have attracted criticism, raising concerns that current methodologies do not afford adequate biodiversity protection (Edwards et al., 2012, Yaap et al., 2010).

The High Carbon Stock (HCS) Approach has emerged as a land-use planning tool to demarcate conservation priority areas based on carbon value, and is being explored within the RSPO architecture and that of other certification schemes. The HCS methodology seeks to conserve biodiverse and ecologically functional forest networks within agricultural concessions by directing conversion towards heavily degraded land of low carbon value (Rosoman, 2017). This is achieved by stratifying land into discrete classes according to vegetation density and structure, which are then adopted as proxies for above-ground carbon stocks and assumed to support varying levels of biodiversity. These strata are subsequently validated using field-derived above-ground carbon estimates, before land parcels are prioritised for conversion based on area and connectivity (Rosoman, 2017).

The HCS Approach has attracted widespread interest amongst agricultural industries with 10 million ha of land being evaluated across five oil palm producing countries (Rosoman, unpublished data). As a model scheme, the successful integration of the HCS Approach within the RSPO framework may encourage uptake across other certifiable agricultural commodities, such as rubber and soya. Nevertheless, the extent to which HCS strata correspond to areas of high biodiversity value is dependent on the accurate partitioning of vegetation classes according to their carbon value, as well as the underlying association between carbon and biodiversity. Before the HCS Approach is formally adopted within certification standards, these assumptions should be tested to understand the conservation merit of the tool.

Here, we determine the effectiveness of incentive-driven carbon-based mechanisms to safeguard biodiversity, and provide the first validation of both the carbon and biodiversity credentials of the HCS land-use planning tool. Our appraisal focuses on a landscape undergoing conversion from forest to oil palm in Borneo, a region characterised by high deforestation and forest degradation (Gaveau et al., 2014, Struebig et al., 2015) that is typical of most HCS applications. First, we validate the accuracy of the HCS classification procedure and quantify the biodiversity value of the vegetation strata. We then assess the potential for REDD+ to deliver biodiversity co-benefits using primary and high-resolution data sources. To assess the influence of spatial grain on the nature of co-benefit relationships, we compare global- and local-scale measures of carbon. Throughout, we employ biodiversity indices that explicitly account for imperfect detection to provide a more accurate representation of species assemblages than simple species counts. Our work evaluates the extent to which policy options that attach greater economic significance to conservation protect vulnerable tropical forests and safeguard biodiversity.

Materials and methods

Study system

The study was conducted over a 13,153 ha development area comprising the Stability of Altered Forest Ecosystems project (SAFE; www.safeproject.net) and surrounding plantations in Kalabakan Forest Reserve, Sabah, Malaysian Borneo (4^{0} 46’N, 116^{0} 57’ E; Fig. 3.1). SAFE is a landscape-scale forest modification experiment (Ewers et al., 2011) comprising highly disturbed lowland and hill dipterocarp forest that was logged multiple times between 1978 and 2008. The wider landscape includes near-pristine forest in Brantian-Tatulit Virgin Jungle Reserve, twice-logged forest in Ulu Segama Forest Reserve, and plantations (primarily oil palm).

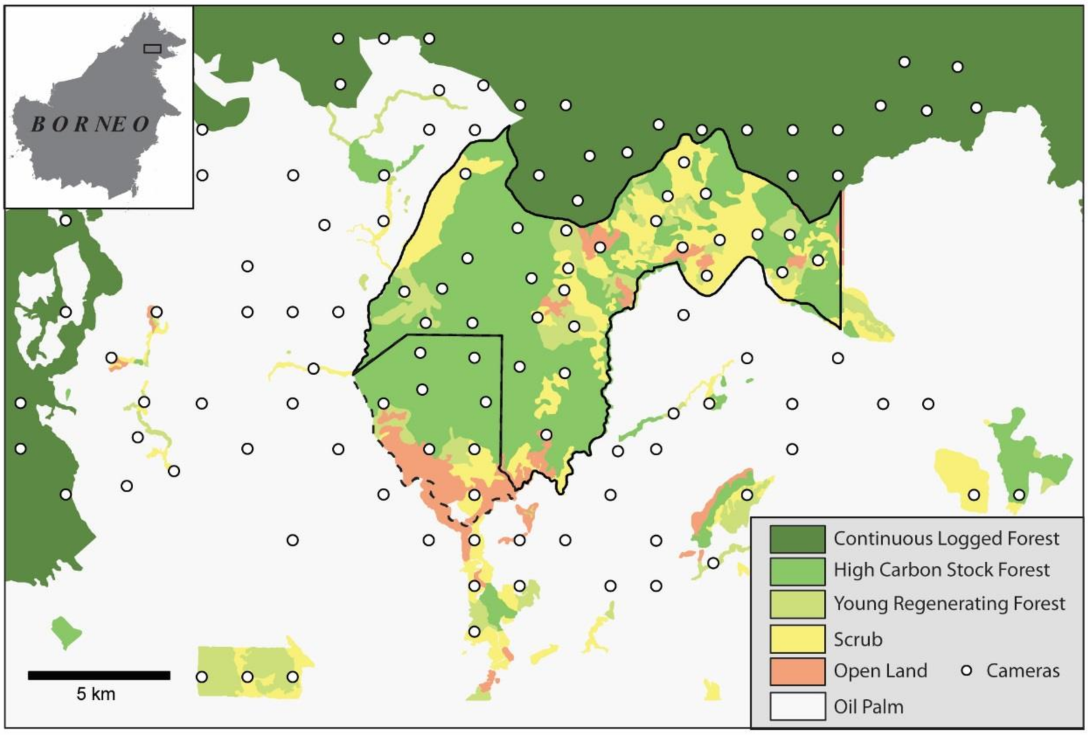


Figure 3.1: Study site, HCS stratification and camera-trap design. HCS classification of the study landscape in Sabah, Borneo. Forest cover was delineated into four strata on the basis of vegetation density (Dense Forest, Young Regenerating Forest, Scrub, Open Land) and supplemented with two reference classes (Continuous Logged Forest, Oil Palm) to act as forest and agricultural controls. Points indicate camera-trap locations (N=115).

HCS classification and validation

The HCS Approach uses high-resolution remotely-sensed images to stratify concessions into six vegetation classes, each with unique structural characteristics (in descending order of carbon value): (1) 'High Density Forest'; (2) 'Medium Density Forest'; (3) 'Low Density Forest'; (4) 'Young Regenerating Forest'; (5) 'Scrub'; and,

(6) ‘Open Land’ (see supplement S3.1). In practice, the High, Medium and Low Density Forest strata are aggregated as ‘Dense Forest’ and earmarked for conservation. Young Regenerating Forest can also comprise valuable carbon stocks and is also spared from development. The threshold for allocating land for production rests on distinguishing these strata from heavily-degraded Scrub and Open Land. Therefore, we mapped Dense Forest, Young Regenerating Forest, Scrub and Open Land as separate classes.

All spatial data processing was implemented in ArcGIS 10.2.1 (ESRI). We used Landsat 8 and SPOT5 satellite imagery (15 m and 2.5 m resolution respectively; temporal range: 2012-2014) to stratify forest habitat using HCS assessment protocols (see supplement S3.1). Multiple data sources were chosen to minimise classification difficulties associated with cloud cover and haze. We undertook a supervised classification of satellite images, supplemented with visual interpretation techniques to correct for the potentially confounding effects of topographic shadow (Wulder et al., 2004). The resulting classes were then calibrated using above-ground carbon values derived from forest inventory data (N=139), collected as part of the core SAFE monitoring programme. These data conform to standardised forest inventory protocols (http://www.rainfor.org), calculating carbon as a function of above-ground biomass (trees >10 cm DBH) using an established pantropical algorithm (Chave et al., 2014). Resulting HCS classes were validated using independently derived carbon estimates (Pfeifer et al., 2016; see supplement 3.7.2).

Camera-trap sampling of medium-large mammals

We delineated terrestrial mammal diversity as these taxa are consistently prioritised in policy, land-use planning and certification schemes. Remotely-operated digital cameras (HC500 Hyperfire, Reconyx, Wisconsin, U.S.A.) were deployed at 130 locations across the landscape between May and September 2015 (Fig. 3.1). These locations were separated by a mean distance of 1.4 km and distributed across an elevational gradient (mean=376 m.a.s.l.; range=64-735 m.a.s.l.). Accounting for theft, vandalism and malfunction, data were retrieved from 121 locations. We stratified our sampling according to HCS strata, while capturing the broader heterogeneity of the landscape using reference classes (protected 'Continuous Logged Forest' and well-established 'Oil Palm Plantation') for comparative purposes. As the extent of Scrub and Open Land was relatively low compared to the other classes, these strata were pooled into a single class, 'Developed Land', for biodiversity analyses: Continuous Logged Forest, *N*=27; Dense Forest, *N*=23; Young Regenerating Forest, *N*=16; Developed Land, *N*=26; and, Oil Palm Plantation, *N*=23.

Due to the number of cameras available, data collection was completed over two rotations, each comprising 65 locations. Single units were deployed for 42 consecutive nights per location, yielding a total survey effort of 4,669 camera nights. Cameras were positioned at a standardised height of 30 cm, on low resistance travel routes (e.g. riparian areas, logging roads, skid trails) and off-trail to account for inter- and intra-specific differences in habitat use.

Prior to analyses, all images that could not be identified to species level were discarded (blurred images and photos of non-target species, equating to 17.6% of 142,294 images). Species encounters were considered independent events if they contained different individuals or were separated by a period of >60 minutes. A detection matrix was developed for each species, whereby 42-day sampling periods were divided into six, seven-day temporal replicates. Any camera site active for fewer than seven days was excluded from analysis, leaving 115 analytical units each with 2-6 replicates.

Modelling framework

We employed hierarchical Bayesian multi-species occupancy modelling (Dorazio and Royle, 2005) to estimate species diversity from camera data. Hierarchical models permit the separation of ecological and sampling processes that may influence the data (Gelman and Hill, 2007). In the context of occupancy, this means that true absences can be differentiated from non-detection by explicitly defining models for occurrence and detection.

Multi-species occupancy models take single-species occupancy detection models as building units (Guillera-Arroita, 2017). Following Zipkin et al. (2010), we denote the occurrence of species i at site j by the binary variable $z_{i,j}$ (1=species presence; 0=species not detected). The occurrence state is described as the outcome of a Bernoulli process, $z_{i,j} \sim Bern(\psi_{i,j})$, where $\psi_{i,j}$ denotes the occurrence probability. The true occurrence state is imperfectly observed, so the model includes a second Bernoulli process, $x_{i,j,k} \sim \text{Bern}(p_{i,j,k}*z_{i,j})$, where $x_{i,j,k}$ is the observed detection/non-detection data, k is the survey replicate and $p_{i,j,k}$ represents the corresponding detection probability conditional to species presence. The product $p_{i,j,k}*z_{i,j}$ reflects that detection at sites where the species is present ($z_{i,j}$=1) happens with detection probability $p_{i,j,k}$, and that detection is not possible at sites where the species is absent ($z_{i,j}$=0). We assume that variation in the abundance of a species across sampling sites does not affect species detection probabilities $p_{i,j,k}$ (Royle and Dorazio, 2008).

Occurrence and detection models for individual species were linked via a hierarchical component that modelled regression coefficients as realisations from a common community-level distribution with hyperparameters. Under this approach, species are assumed to respond to environmental conditions in a similar, but not identical, manner. Derived species estimates are, therefore, a compromise between individual response and the average response of the community. This results in shrinkage (the borrowing of information by individuals across the community), which has been shown to improve estimation precision, particularly for rare or elusive species that are infrequently detected during surveys (Pacifici et al., 2014). We report hyperparameters to provide an indication of community-level responses to covariates.

Spatial concordance between HCS classes, carbon and biodiversity

To assess how mammal community representation could vary according to policy relevant carbon variables, we described occupancy and detectability using three models:

Model 1: $\text{logit}(\psi_{i,j}) = \mu_{(i)HCS\ Class(j)}$

$\text{logit}(p_{i,j,k}) = \upsilon_{(i)HCS\ Class(j)}$

Model 2: $\text{logit}(\psi_{i,j}) = \mu_i + \alpha_{1i}CC1000_j + \alpha_{2i}CC1000^2_j$

$\text{logit}(p_{i,j,k}) = \upsilon_{(i)HCS\ Class(j)}$

Model 3: $\text{logit}(\psi_{i,j}) = \mu_i + \alpha_{1i}CC25_j + \alpha_{2i}CC25^2_j$

$$\text{logit}(p_{i,j,k}) = \upsilon_{(i)HCS\ Class(j)}$$

Occupancy and detection probabilities were modelled with intercepts on the logit scale, specific for each species and HCS class (Model 1). Continuous measures of carbon, including quadratic terms, were incorporated into occurrence models alongside species-specific intercepts to determine the potential for REDD+ to deliver biodiversity co-benefits (Models 2 and 3). These carbon data were from two sources: coarse-grained 1 km resolution global maps ('CC1000'; Avitabile et al., 2016), and 25 m resolution maps derived from biomass estimates from the study site linked to Rapideye^{TM} satellite imagery ('CC25'; Pfeifer et al., 2016; for a subset of sites not obscured by cloud cover, N=66). HCS-specific intercepts were retained in the detection components of Models 2 and 3 as they broadly describe the influence of habitat type. We chose to model HCS, CC1000 and CC25 separately due to strong evidence of collinearity between these variables ($|r|\geq0.7$). Continuous carbon and HCS covariates were calculated as average values extracted from a 100 m buffer (ca. 3.1 ha area) around each camera location. Covariates were centred and standardised prior to analysis. We found no evidence of spatial autocorrelation in the detection dataset (Moran's $I=0.08\leq P\leq0.92$), indicating that assumptions of independence in occupancy modelling were met (Royle and Dorazio, 2008).

The models were fitted to include inference about the number of potential species not observed during sampling (Dorazio and Royle, 2005). To achieve this, detection data were augmented with 50 hypothetical species, with all-zero encounter histories, following Royle *et al.* (2007). Predicted species richness was calculated for each camera location allowing for post-hoc comparison between HCS classes.

We compared mammal richness between HCS classes using a Bayesian linear model. We follow a two-stage analytical approach described by Kéry & Royle (2015), whereby estimation uncertainty associated with predicted species richness is propagated by the inclusion of an additional residual component into the model (standard deviation of richness estimates from the hierarchical Bayesian multi-species occupancy models). In principle, parameter estimates could be derived directly from a single model, but this resulted in lower precision. Since land-use change disproportionately affects species of conservation concern and disturbance-sensitive forest specialists, we report our findings for: (1) all species; (2) threatened species (IUCN red-listed as vulnerable, endangered or critically endangered); (3) non-threatened species (IUCN least concern or near-threatened); (4) disturbance-sensitive species (listed as medium-high sensitivity according to Wilson et al., 2010), and; (5) disturbance- tolerant species (low sensitivity; see Table S3.1 for species-specific group assignment).

Biodiversity co-benefits of REDD+

To assess the potential biodiversity co-benefits of REDD+, we extracted predicted species richness values from the hierarchical occurrence model and explored their association with carbon. To determine if these relationships were grain-dependent, we derived carbon data from coarse- (CC1000, 1 km) and fine-grained (CC25, 25m) satellite-derived datasets. Associations between levels of mammal species richness and carbon at the two different spatial resolutions, and for *a priori* groupings, were assessed via Bayesian two-stage linear models incorporating quadratic terms.

All analyses were conducted in WinBUGS version 1.4.3 through R version 3.3.0 using the package "R2WinBUGS" (Sturtz et al., 2005); see supplement S3.3 for further information on model specification and predictive performance checks.

Results

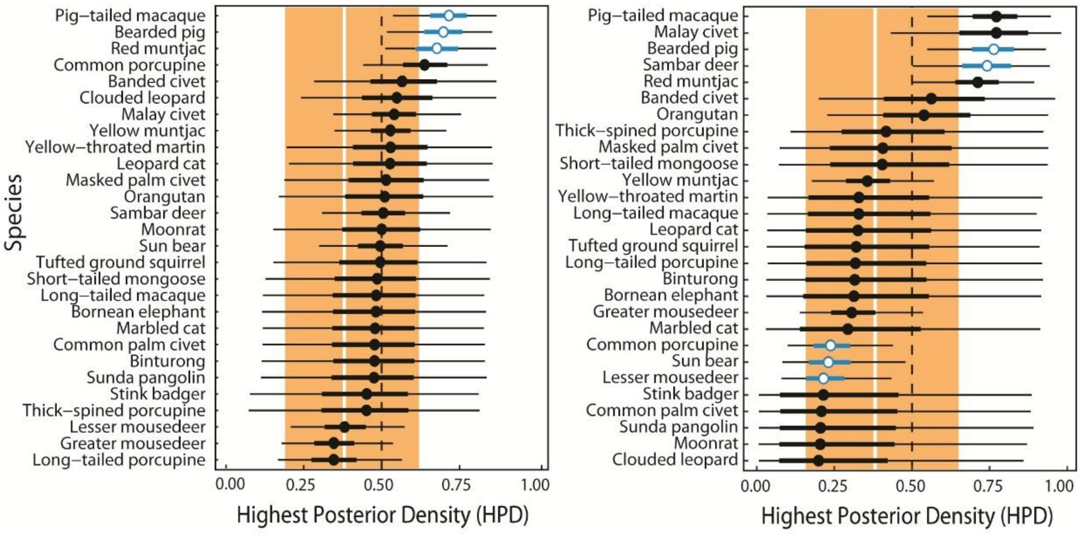
Camera-trapping yielded 3,237 independent capture events of 28 species, comprising 24 genera distributed across 16 families. In contrast, our models predicted 30.6 species across the landscape (95% Bayesian Credible Interval, BCI=28.0-37.0), suggesting that few mammal species were missed by our sampling. The effect of imperfect detection was more pronounced at the camera-trap level, where predicted richness was consistently greater than observed richness (mean=4.35, range=0.02-12.26).

Spatial concordance between biodiversity and HCS classes

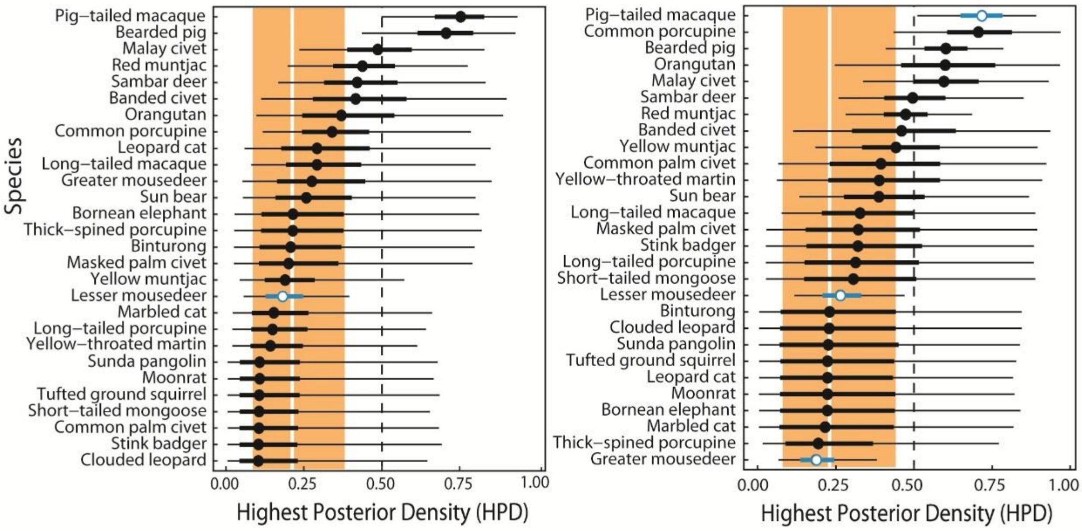
Hierarchical Bayesian multi-species models indicated reduced mammalian occupancy in the low carbon strata (Fig 3.2). Community hyperparameters revealed comparable estimates of mean occupancy between Continuous Logged Forest (mean=0.49, BCI=0.32-0.63), Dense Forest (0.36, 0.17-0.60) and Developed Land (0.32, 0.12-0.56). However, community occupancy was low in Young Regenerating Forest (0.23, 0.11-0.45) and Oil Palm plantation (0.05, 0.01-0.31).

Our models demonstrated species-specific associations with HCS classes (Fig. 3.2). For example, occupancy estimates indicate that bearded pig (*Sus barbatus*) and southern pig-tailed macaque (*Macaca nemestrina*) were common in Continuous Logged Forest (bearded pig: 0.71, 0.53-0.85; pig-tailed macaque: 0.71, 0.53-0.86) and Dense Forest (bearded pig: 0.74, 0.53-0.90; pig-tailed macaque: 0.74, 0.52-0.92), with occupancy of the pig-tailed macaque also high in Developed Land (0.71, 0.51-0.87). Conversely, species such as the lesser mouse-deer (*Tragulus kanchil*) (0.20, 0.08-0.40) and sun bear (*Helarctos malayanus*) (0.21, 0.08-0.44) were rare in Dense Forest. In the Oil Palm plantation five species demonstrated low occupancy, four of which were threatened taxa (Fig. 3.2e). Species-specific detection summaries for the HCS model are available in supplementary figures S3.1-3.4.

(a) Continuous Logged Forest (b) High Carbon Stock Forest



(c) Young Regenerating Forest (d) Developed Land



(e) Oil Palm

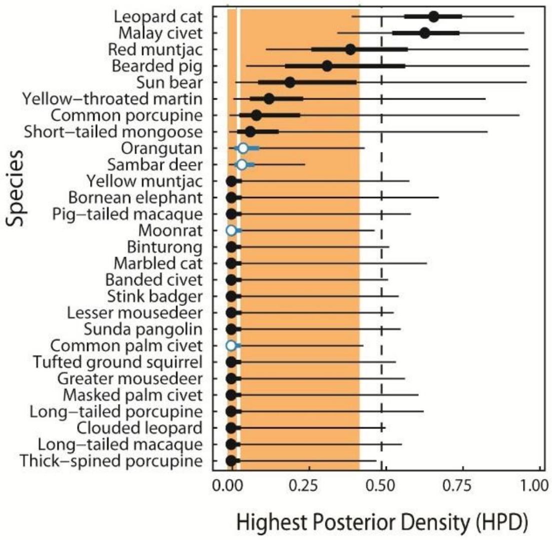


Figure 3.2: Species-specific outputs from the Bayesian hierarchical model. Caterpillar plots of outputs from the hierarchical Bayesian multi-species occupancy model. Graphs show species-specific baseline occupancy estimates (including 95% Bayesian Credible Interval) relative to habitat class (a-e). Mean community hyperparameter occupancy values and their associated credible intervals are represented in the shaded (orange) background to each plot. Species exhibiting deviations from a baseline occupancy of 0.5 are shown with shaded (blue) bars.

Extremes in predicted species richness were identified between the reference habitat classes (Fig. 3.3); Continuous Logged Forest was found to have the highest richness (14.12, 13.20-15.07), while Oil Palm plantation supported the most depauperate community (4.54, 3.58-5.52). Estimates of total richness were similar between Dense Forest (11.38, 10.30-12.51) and Developed Land (10.63, 9.52-11.02), while the number of species found in Young Regenerating Forest was significantly lower (8.15, 7.13-9.27). These patterns were consistent across groupings.

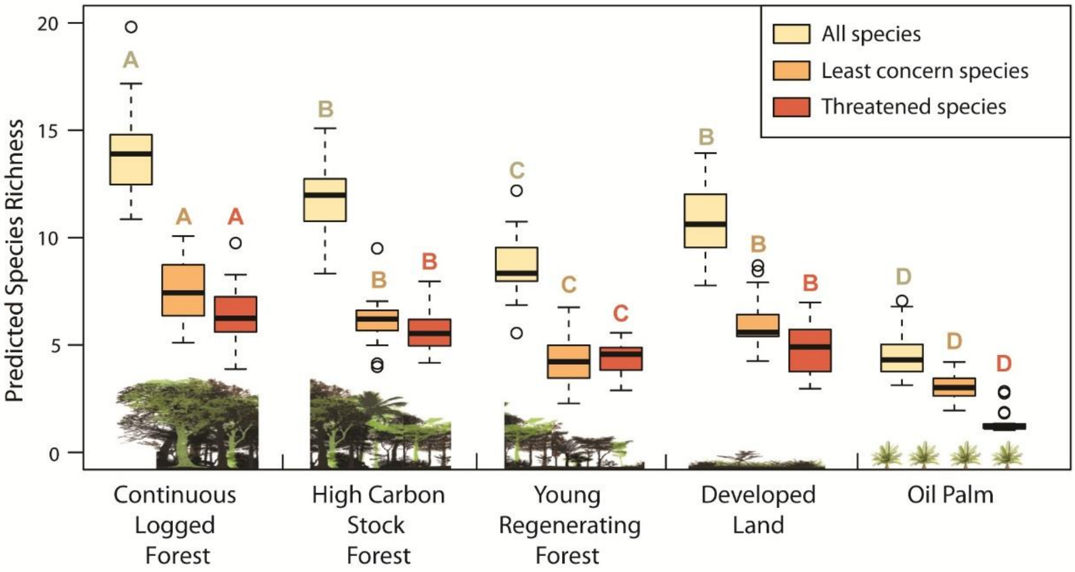


Figure 3.3: Species richness relative to HCS-delineated forest strata. Boxplots demonstrating species richness in relation to habitat class for: (1) all species; (2) threatened species (IUCN red-listed as vulnerable, endangered or critically endangered); (3) disturbance sensitive species. Boxes delineate median and interquartile range of species richness values, vertical dashed lines outline the 2.5th and 97.5th percentiles of the data and transparent circles represent outlying data points. Letters indicate significant differences between habitat classes within broader species groupings (different letters suggest significance while identical letters indicate non-significance).

Biodiversity co-benefits of REDD+

The global- versus local-scale carbon values at camera locations were inconsistent. The 1 km resolution global data tended to produce much higher carbon estimates compared to those derived from higher resolution imagery (global mean=152.23 t C ha^{-1}, range=50.39-236.53; local mean=22.95t C ha^{-1}, range= 0.31-94.98). Carbon values from the global- and local-scale maps corresponded broadly with biomass values derived from field inventories (N=164; r_s=0.55 global; r_s=0.51; local-scale). However, local-scale carbon estimates were found to be more precise (RMSE: local=29.05 t C ha^{-1}; global=130.94 t C ha^{-1}). We found no influence of continuous measures of carbon on mammalian occupancy using either global- or local-scale carbon data (see supplementary figures S3.1-3.4). Species-specific detection summaries for the continuous carbon models are available in supplementary figures S3.1-3.4.

Grain-dependency between the association of carbon and mammal richness was evident. Using global carbon data no relationship between the two variables was apparent, regardless of the species grouping (Figs. 3.4a,c,e). However, at the local-scale, positive associations with carbon were identified for threatened and disturbance-sensitive species (Figs. 3.4d,f). This trend was not consistent across groupings with all species, non-threatened and disturbance-tolerant taxa demonstrating no relationship with carbon (Fig. 3.4b).

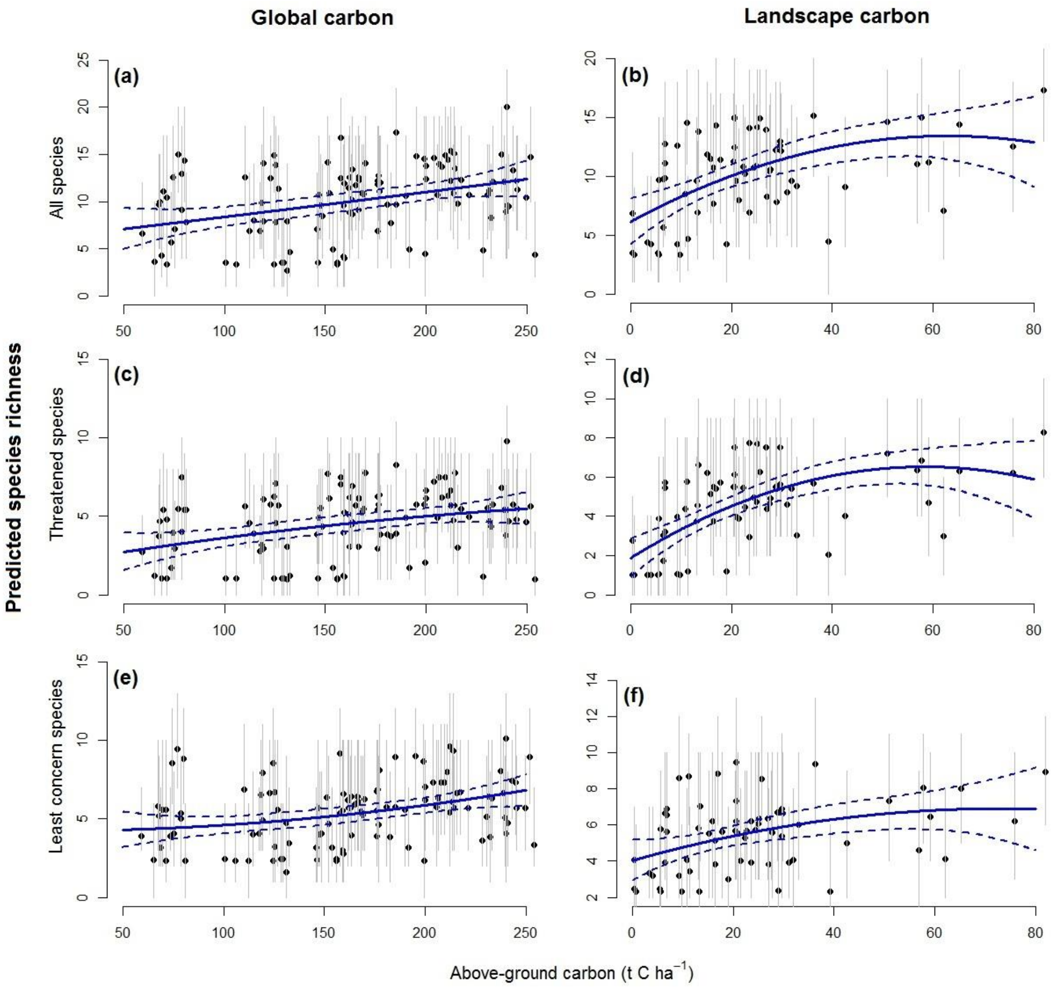


Figure 3.4: Species richness relative to continuous metrics of carbon. Bayesian linear model outputs demonstrating significant positive relationships between predicted species richness and carbon stock estimates derived from a 25 m resolution local dataset (d: threatened species; f: disturbance-sensitive species). All other associations presented were found to be non-significant. Solid (blue) lines indicate predicted mean posterior distribution values, dashed lines refer to predicted 95% Bayesian Credible

Intervals and vertical grey lines highlight the error associated with each estimated species richness value.

Discussion

The extent to which biodiversity and carbon spatially align is fundamental to our understanding of whether carbon-based policies can deliver positive results for conservation in human-modified landscapes. Among the few studies that assess biodiversity and carbon covariance using primary and/or high-resolution data (Magnago et al., 2015, Sollmann et al., 2017), ours is the first to verify an association within a tropical landscape mosaic undergoing certification. We show that the strength, nature and extent of biodiversity co-benefits are dependent on how carbon stocks are characterised (i.e. categorical or continuous), the spatial resolution of the carbon data employed, and the species considered.

Contribution of the HCS approach to biodiversity conservation

When evaluating community-level responses to HCS classes, we found comparable levels of mammalian occupancy between Continuous Logged Forest, Developed Land and Dense Forest, while occupancy was reduced in Young Regenerating Forest and Oil Palm. Occupancy can be a viable surrogate for abundance under certain conditions (Efford and Dawson, 2012). Our results could therefore suggest the persistence of certain mammal species at lower densities within carbon-poor classes, which confirms previous reports of reduced mammalian abundance in impoverished forest habitats (Bicknell et al., 2014).

Occupancy and species richness estimates for the total mammal community highlight comparable levels of biodiversity between the Dense Forest and Developed Land classes, supporting previous studies that demonstrate the conservation value of heavily degraded forest for a range of taxonomic groups (Edwards et al., 2014, Struebig et al., 2013, Wearn et al., 2016). However, we advise caution when interpreting the biodiversity value of Developed Land, which may not be fully realised for long-lived mammal species until extinction debts, owed to a legacy of disturbance, are repaid (Rosa et al., 2016). The biodiversity value of Developed Land that we found is also crucially dependent on the low levels of hunting at our study site. Hunting has been shown to have substantial impacts on mammal communities elsewhere in the region (Harrison et al., 2016). Our study adds to the growing body of evidence that shows oil palm plantations to have depauperate mammalian communities, comprised of few generalist species occurring at low densities (Wearn et al., 2016, Yue et al., 2015). While our data generally conform to the pattern of declining biodiversity relative to structural complexity, Young Regenerating Forest demonstrated comparably lower biodiversity value regardless of the metric examined. Given the difficulties in differentiating between the Young Regenerating Forest and Scrub strata (see supplement S3.2), we believe this finding reflects ambiguities in the HCS classification process.

While our analyses demonstrate differences in conservation value between the HCS strata, the ability of land parcels to support biodiversity will also be limited by habitat fragmentation effects. This process is pervasive in human-modified landscapes, and has contributed to species richness declines of up to 75% (Haddad et al., 2015). While efforts to account for habitat fragmentation in the HCS prioritisation process are underway, a definitive toolkit is still in development. Therefore, while we have not explicitly accounted for the independent and interactive effects of fragmentation metrics (e.g. patch size, isolation and connectivity) on biodiversity in our analyses, it warrants further consideration as the HCS Approach gains traction across the agricultural sector.

Contribution of REDD+ to biodiversity conservation

Our results indicate that spatial concordance between biodiversity and carbon can be overlooked if the latter is calculated via low-resolution data. Using carbon information from a commonly utilised global dataset, no association with mammal diversity was identified, suggesting that REDD+ initiatives would not provide biodiversity co-benefits in heavily degraded landscapes. However, when high-resolution carbon maps were employed, a positive relationship with species richness was found for threatened and disturbance-sensitive taxa, demonstrating the value of REDD+ to those species most vulnerable to land-use change. When all species were considered these relationships were obscured by non-threatened, generalist species that are resilient to disturbance. Our findings provide further support for biodiversity co-benefits in agricultural land-use mosaics, as previously demonstrated for a range of taxonomic groups (birds and dung beetles: Gilroy et al., 2014; amphibians: Basham et al., 2016), while highlighting important nuances in the carbon-biodiversity relationship. We advocate the use of fine-grained, field-validated carbon data when determining the extent and nature of biodiversity co-benefits and suggest an emphasis on species of conservation concern.

Our detailed landscape appraisal is the first to identify biodiversity co-benefits for mammals, a taxonomic group that occupies key trophic positions in tropical forest ecosystems and is frequently prioritised by conservation. Previous studies have proved less convincing. Across a pantropical network of sites, Beaudrot *et al.* (2016b) found no association between forest carbon and three measures of mammalian diversity. However, by aggregating fine-scale biomass data at the site level, the authors compromised the resolution of their data, potentially obscuring intra-site relationships that would be more representative of a REDD+ management unit. Similarly, Sollmann *et al.* (2017) found little correspondence between above-ground biomass and mammal occupancy in a certified forest reserve in Malaysian Borneo, despite adopting a comparable methodology to the present study. Contrasting findings may be attributed to spatial variability in hunting pressure.

Implications for HCS implementation

Given that RSPO members have little obligation to protect highly disturbed forest of uncertain conservation value, the HCS Approach is a useful tool to designate high carbon, high biodiversity land in areas that would otherwise be converted to plantation. High Carbon Stock areas can also contribute to national and regional spatial planning initiatives that mitigate the effects of environmental change on tropical biodiversity by promoting connectivity in human-modified landscapes (Struebig et al., 2015).

Under current HCS guidelines, 62% (8,150 ha) of the remaining forest in the study system would qualify for protection from agricultural conversion, equating to a net gain of 15.72 t C ha^{-1} (see Appendix S2) at an annual opportunity cost of US$3.7 million (based on Fisher et al., 2011a). The success of certification depends on financial returns from sustainable production offsetting the economic losses associated with sustainable practices. While the zero deforestation principle of the HCS Approach reduces reputational risk by aligning with consumer goods forum calls to eliminate deforestation from global commodity supply-chains, it has been considered economically restrictive for nations with extensive pristine forests (Senior et al., 2015), indicating that current guidelines may be too stringent. Strata such as Young Regenerating Forest might, therefore, end up being earmarked for conversion rather than conservation in some circumstances. However, with the conservation value of this stratum likely to increase as forests regenerate, the impact of such a policy change needs to be fully evaluated. Carbon neutral conversion represents an alternative to the current emphasis on zero deforestation. While the specific carbon threshold for delineating forest has proved contentious, Pirker et al. (2016) demonstrated that protecting areas exceeding 100 t C ha^{-1} would safeguard 73% of the climatically suitable area for oil palm expansion. Ultimately, compromise begets progression, and while the industry should still strive for zero deforestation, carbon neutral conversion may be more viable in specific countries and circumstances, if agricultural expansion, economic development and forest conservation are to be reconciled.

Implications for REDD+ implementation

The considerable enthusiasm for biodiversity co-benefits often obscures the fact that REDD+ is fundamentally a carbon-orientated mechanism with limited scope for increasing biodiversity conservation (Venter and Koh, 2012). While we provide further evidence to verify biodiversity co-benefits in human-modified landscapes, it is unlikely that REDD+ will be economically viable in carbon-poor environments. Given current economic pressures and weak carbon markets, REDD+ projects currently prioritise carbon gains at low operating costs. Acting optimally for carbon will therefore place increasing agricultural pressure on secondary or degraded forests that are comparatively low in carbon value but retain appreciable levels of biodiversity (Edwards et al., 2014). Conservationists must ensure that safeguards are in place to support vulnerable species in disturbed habitats that fall beyond the remit of carbon-financing mechanisms.

The viability of REDD+ in human-modified landscapes is further hindered by the profitability of oil palm. Under current voluntary markets, avoided deforestation through REDD+ was found to have an opportunity cost of $3221–8636 ha^{-1} over a 30 year period when compared to potential profits generated from oil palm (Butler et al., 2009). For REDD+ to be an economically competitive alternative to oil palm cultivation, climate change policies must legitimise REDD+ carbon credits to facilitate their trade on financially lucrative compliance markets (Butler et al., 2009).

Conclusions

Our work highlights the potential for environmental certification and REDD+ financing mechanisms to work in tandem with conservation to mitigate the effects of agricultural expansion on tropical forest carbon stocks and biodiversity. REDD+ is well placed if it prioritises large tracts of contiguous forest, especially if commitments to carbon stock enhancement safeguard degraded forest of biological value.

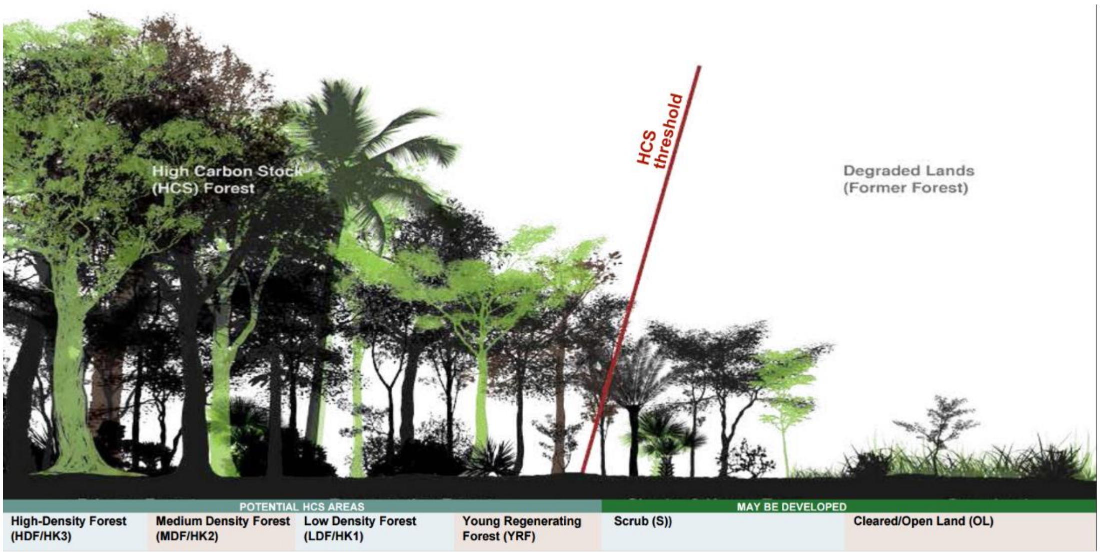
Certification schemes, coupled with land-use planning tools such as HCS, can help secure sizeable forest patches of high conservation value in agricultural estates, and offer a further safeguard to minimise encroachment. Conservationists should capitalise on both types of carbon-based policy to maximise the potential for developed lands to provide ecological stepping stones for threatened wildlife between a network of high-carbon, high-biodiversity areas.

Acknowledgements

This study was funded by the UK Natural Environment Research Council (NERC) (NE/K016407/1; http://lombok.hmtf.info/) and a NERC EnvEast PhD studentship to NJD. GGA is the recipient of a Discovery Early Career Research Award from the Australian Research Council (DE160100904). We thank the Sabah Biodiversity Council, Sabah Forest Department, Yayasan Sabah, Sime Darby and Benta Wawasan for permitting access. We are indebted to Jamiluddin Jami, Arnold James, Mohd. Mustamin, Ampat Siliwong, Sabidee Mohd. Rizan, Najmuddin Jamal and Lois Kinneen for field assistance. We also thank Rob McWilliam, Tri Agus Sugiyanto (both The Forest Trust), Grant Rosoman and Sapta Ananda (both Greenpeace) for training on HCS techniques.

Supplementary information

S3.1: Definitions of strata delineated by the High Carbon Stock (HCS) Approach



The High Carbon Stock (HCS) methodology seeks to conserve biodiverse and ecologically functional forest networks within agricultural concessions by directing conversion towards heavily degraded land of low carbon value (Rosoman, 2017). This is achieved by using high resolution satellite imagery to stratify the landscape into discrete strata according to vegetation density and structure, which are then adopted as proxies for above-ground carbon stocks and assumed to support varying levels of biodiversity. The HCS Approach recognises six distinct vegetation classes (detailed below), each with unique structural characteristics.

Habitat Classes		**Analytical Classification**
	**Continuous Logged Forest** contains similar structural properties to Dense Forest. This class is not considered for development due to its protected status. This class was incorporated as a control against which carbon and biodiversity of other strata could be compared.	Continuous Logged Forest
	**Dense Forest** comprises three classes, high/medium/low density forest, and refers to closed-canopy natural forest characterised by: • >50% canopy cover; • Significant proportion of trees >30cm dbh; • Dominated by climax community tree species. Development status: **Conserved**	Dense Forest
	**Young Regenerating Forest** is highly disturbed remnant forest characterised by: • 30-40% canopy cover; • Significant proportion of trees between 10 and 30cm dbh; • Dominated by pioneer tree species. Development Status: **Conserved**	Young Regenerating Forest

	**Scrub** refers to land that has previously been cleared but experienced some regeneration. It is characterised by: • <25% canopy cover; • Dominated by tall grasses and ferns but containing some pioneer species. Development status: **Converted**	Developed Land
	**Open Land** represents a post-clearance habitat dominated by grass or crops with few woody plants. Development status: **Converted**	
	**Oil palm** (*Elaeis guineensis*) represents the final phase of land-use change in the study system when natural forest habitat has been displaced by commodity agriculture. This class was incorporated as a control against which carbon and biodiversity of other strata could be compared.	Oil Palm Plantation

S3.2: Validating the carbon credentials of the High Carbon Stock (HCS) Approach

Rationale

The High Carbon Stock (HCS) land-use planning tool is gaining traction in oil palm certification as companies seek to honour their commitments to sustainable production. However, there is a paucity of information in the scientific literature to validate the accuracy of the HCS stratification process to delineate high carbon conservation priority areas. Here, we provide an assessment of the carbon credentials of the HCS toolkit.

Methods and Materials

HCS classes were delineated across the Stability of Altered Forest Ecosystems (SAFE) Project study site using standardised protocols (Rosoman, 2017). These strata were validated using independent high-resolution satellite data of above-ground biomass (RapidEye, 5 m resolution; temporal coverage 2012-2013; Pfeifer et al., 2016), across cloud-free areas of the study landscape. Carbon stocks were calculated using a conversion factor of 0.47 (Martin and Thomas, 2011), and values were extracted from 200 random points per HCS class (N=800) separated by a minimum distance of 50 m. A Bayesian linear model was employed to determine the distribution of carbon values across classes, thus testing the accuracy of the classification process.

Results

Following our land-cover stratification, 62 % of the remaining forest in the study landscape, comprising 6,031 ha of High Carbon Stock forest and 2,120 ha of Young Regenerating Forest, would qualify for conservation under current HCS guidelines (Fig. 1). The classes appropriately reflected modelled carbon content, which was greatest for Dense Forest (45.86 t C ha^{-1}, 95% BCI=42.32-49.44) and significantly lower in the other classes (Young Regenerating Forest: 31.30t C ha^{-1}, 27.85-34.80; Scrub: 29.62 t C ha^{-1}, 26.19-33.05; Open Land: 16.09t C ha^{-1}, 12.59-19.62). Pairwise comparisons of carbon content revealed significant differences between all habitat classes with the exception of Young Regenerating Forest and Scrub. On average, land earmarked for conservation contained 41% more carbon than that designated for development (i.e. Scrub and Open Land strata combined) under the HCS Approach, equating to a net value of 15.72 t C ha^{-1} across the landscape.

Discussion

There is a general consensus in the scientific literature that field-derived carbon estimates are laborious, costly and time consuming to implement over large spatial scales (Gibbs et al., 2010, Petrokofsky et al., 2012). Consequently, there is a need for cost-effective, efficient protocols that can be followed to delineate high carbon stock areas. Our results provide empirical support for the prioritisation of high carbon stock areas for conservation in the humid tropics via the HCS Approach. High Carbon Stock Forest (Dense Forest and Young Regenerating Forest combined) was estimated to store 45.86 t C ha^{-1}, which falls within the range of estimates for highly degraded forest habitat in Borneo (40-100 t C ha-1; Lucey et al. Lucey et al., 2014), but is considerably lower than pristine lowland tropical forest (477 t C ha-1; Budiharta et al., 2014b).

Our analyses demonstrate that carbon stocks are similar between land classified as Young Regenerating Forest and Scrub, suggesting that the HCS toolkit cannot reliably distinguish between these strata. This has direct implications for conservation, as Young Regenerating Forest should be retained within the landscape, yet Scrub can be developed. This reflects the concerns of Annisa (2014), who stressed the difficulties associated with partitioning heterogeneous vegetation into categorical carbon classes, as habitat transitions are gradual and not discrete. While the initial version of the HCS toolkit offered a clear carbon threshold value (35 t C ha^{-1}) with which to differentiate between strata suitable for development and conservation, it has been omitted in subsequent revisions, introducing subjectivity and misinterpretation into the classification process. We recommend the adoption of explicit carbon threshold values defining each HCS stratum, to improve calibration and thus classification accuracy. Threshold values would make the HCS methodology more transparent, objective and comparable across concessions. In practice, the thresholds should be regionally-specific, accounting for the recognised geographic variation in standing carbon stock across tropical forests globally (Avitabile et al., 2016, Banin et al., 2014).

Table S3.1: Species assignment to grouping categories

Species	Threat Status	Disturbance Response
Asian elephant	Threatened	Sensitive
Banded civet	Threatened	Sensitive
Bearded pig	Threatened	Tolerant
Binturong	Threatened	Sensitive
Clouded leopard	Threatened	Sensitive
Common palm civet	Non-threatened	Tolerant
Greater mousedeer	Non-threatened	Sensitive
Leopard cat	Non-threatened	Tolerant
Lesser mousedeer	Non-threatened	Sensitive
Long-tailed macaque	Non-threatened	Tolerant
Long-tailed porcupine	Non-threatened	Tolerant
Malay civet	Non-threatened	Tolerant
Malay porcupine	Non-threatened	Tolerant
Marbled cat	Threatened	Sensitive
Masked palm civet	Non-threatened	Tolerant
Moonrat	Non-threatened	Sensitive
Orangutan	Threatened	Sensitive
Pig-tailed macaque	Threatened	Tolerant
Red muntjac	Non-threatened	Tolerant
Sambar deer	Threatened	Sensitive
Short-tailed mongoose	Non-threatened	Tolerant
Stink badger	Non-threatened	Tolerant
Sun bear	Threatened	Sensitive
Sunda pangolin	Threatened	Tolerant
Thick-spined porcupine	Non-threatened	Tolerant
Tufted ground squirrel	Threatened	Sensitive
Yellow muntjac	Non-threatened	Sensitive
Yellow-throated marten	Non-threatened	Tolerant

S3.3: Model Specification and predictive performance checks

All analyses were conducted in WinBUGS version 1.4.3 called through R version 3.3.0 using the package “R2WinBUGS” (Sturtz et al., 2005). All statistical models were constructed using uninformative priors. Unless stated otherwise, parameter estimates are presented as means alongside 95% Bayesian Credible Intervals (BCIs) and considered statistically significant if their 95% BCIs did not overlap zero. For the hierarchical Bayesian multi-species occupancy model, three parallel chains were run for 75,000 iterations, 25,000 of which were discarded during the burn-in; posterior chains were thinned by 10. For all Bayesian two-stage linear models, three parallel chains were run for 12,000 iterations, following a burn-in of 2,000; posterior chains were thinned by 5. Convergence was assessed using visual inspection of trace plots and the Gelman-Rubin statistic, values ≥ 1.1 indicate failure to converge (Gelman and Hill, 2007). Model fit was assessed statistically using a posterior predictive check, which compares model fit for the actual data against a simulated, idealised dataset (Gelman et al., 1996). Bayesian *p*-values were extracted as a numerical summary of the posterior predictive distribution, with quantities close to 0.5 indicating adequate model fit. We identified quantitative and visual support for convergence in all models presented, while obtained Bayesian *p*-values did not provide evidence of lack of fit ($0.43 \leq p \leq 0.52$).

WinBUGS code for hierarchical Bayesian community occupancy model used to assess spatial concordance between biodiversity and HCS classes.

```
model{

  #Define prior distributions for community-level model parameters
  #=====================================================
  omega ~ dunif(0,1)
  sigma.vCLF <- 1/sqrt(tau.vCLF)
  sigma.vHCS <- 1/sqrt(tau.vHCS)
  sigma.vYRF <- 1/sqrt(tau.vYRF)
  sigma.vDEV <- 1/sqrt(tau.vDEV)
  sigma.vOP <- 1/sqrt(tau.vOP)

  for (i in 1:(n+nzeroes)) {
  # Create priors for species i from the community hyperparameters
  #====================================================
     w[i] ~ dbern(omega)

     u[i] ~ dnorm(a, tau1)
     alpha1[i] ~ dnorm(mu.alpha1, tau.alpha1)
     alpha2[i] ~ dnorm(mu.alpha2, tau.alpha2)

     v.CLF[i] ~ dnorm(mu.vCLF, tau.vCLF)
     v.HCS[i] ~ dnorm(mu.vHCS, tau.vHCS)
     v.YRF[i] ~ dnorm(mu.vYRF, tau.vYRF)
     v.DEV[i] ~ dnorm(mu.vDEV, tau.vDEV)
     v.OP[i] ~ dnorm(mu.vOP, tau.vOP)

  #Create a loop to estimate the Z matrix (true occurrence for species i
  #at point j
  #======================================================
     for (j in 1:J) {
        logit(psi[j,i]) <- u[i] + alpha1[i]*carbon1[j] + alpha2[i]*carbon2[j]
        mu.psi[j,i] <- psi[j,i]*w[i]
        Z[j,i] ~ dbern(mu.psi[j,i])

  #Create a loop to estimate detection for species i at point j during
  #sampling period k
  #====================================================
           for (k in 1:K[j]) {
              logit(p[j,k,i]) <- v.CLF[i]*Ind1[j] + v.HCS[i]*Ind2[j] +
                                 v.YRF[i]*Ind3[j] +  v.DEV[i]*Ind4[j] +
                                 v.OP[i]*Ind5[j]

             mu.p[j,k,i] <- p[j,k,i]*Z[j,i]
```

```
                X[j,k,i] ~ dbern(mu.p[j,k,i])
                Xnew[j,k,i] ~ dbern(mu.p[j,k,i])

# Create simulated dataset to calculate Bayesian p value
#==========================================
          d[j,k,i]<-  abs(X[j,k,i] - mu.p[j,k,i])
          dnew[j,k,i]<- abs(Xnew[j,k,i] - mu.p[j,k,i])
          d2[j,k,i]<- pow(d[j,k,i],2)
          dnew2[j,k,i]<- pow(dnew[j,k,i],2)
          }

    dsum[j,i]<- sum(d2[j,1:K[j],i])
    dnewsum[j,i]<- sum(dnew2[j,1:K[j],i])
    }
 }

# Calculate discrepency measure
#=========================
    p.fit<-sum(dsum[1:J,1:n])
    p.fitnew<-sum(dnewsum[1:J,1:n])
}

# Sum all species observed (n) and unobserved species (n0) to find the
# total estimated richness
#=====================================================
n0 <- sum(w[(n+1):(n+nzeroes)])
N <- n + n0

# Create a loop to determine point level richness estimates for the
# whole community and for threatened, non-threatened, disturbance-tolerant
# and disturbance-sensitive species
#=========================================================
for(j in 1:J){
    Nsite[j]<- inprod(Z[j,1:(n+nzeroes)],w[1:(n+nzeroes)])
    Nleast[j]<- inprod(Z[j,1:n],least.concern[1:n])
    Nthreat[j]<- inprod(Z[j,1:n],threatened[1:n])
    Ntolerant[j]<- inprod(Z[j,1:n],tolerant[1:n])
    Nsensitive[j]<- inprod(Z[j,1:n],sensitive[1:n])
    }
}
```

Figure S3.1: Mammal occupancy relative to HCS-delineated forest strata. Species-specific posterior summaries for occupancy as a function of HCS class (Continuous Logged Forest: CLF; Dense Forest: DF; Young Regenerating Forest: YRF; Developed Land: DEV; Oil Palm: OP). We visualise mean predicted posterior distribution values (horizontal lines), accompanied by 95% Bayesian Credible Intervals (vertical lines).

Figure S3.2: Mammal detection probability relative to HCS-delineated forest strata. Species-specific posterior summaries of detection probability as a function of HCS class (Continuous Logged Forest: CLF; Dense Forest: DF; Young Regenerating Forest: YRF; Developed Land: DEV; Oil Palm: OP). We visualise mean predicted posterior distribution values (horizontal lines), accompanied by 95% Bayesian Credible Intervals (vertical lines).

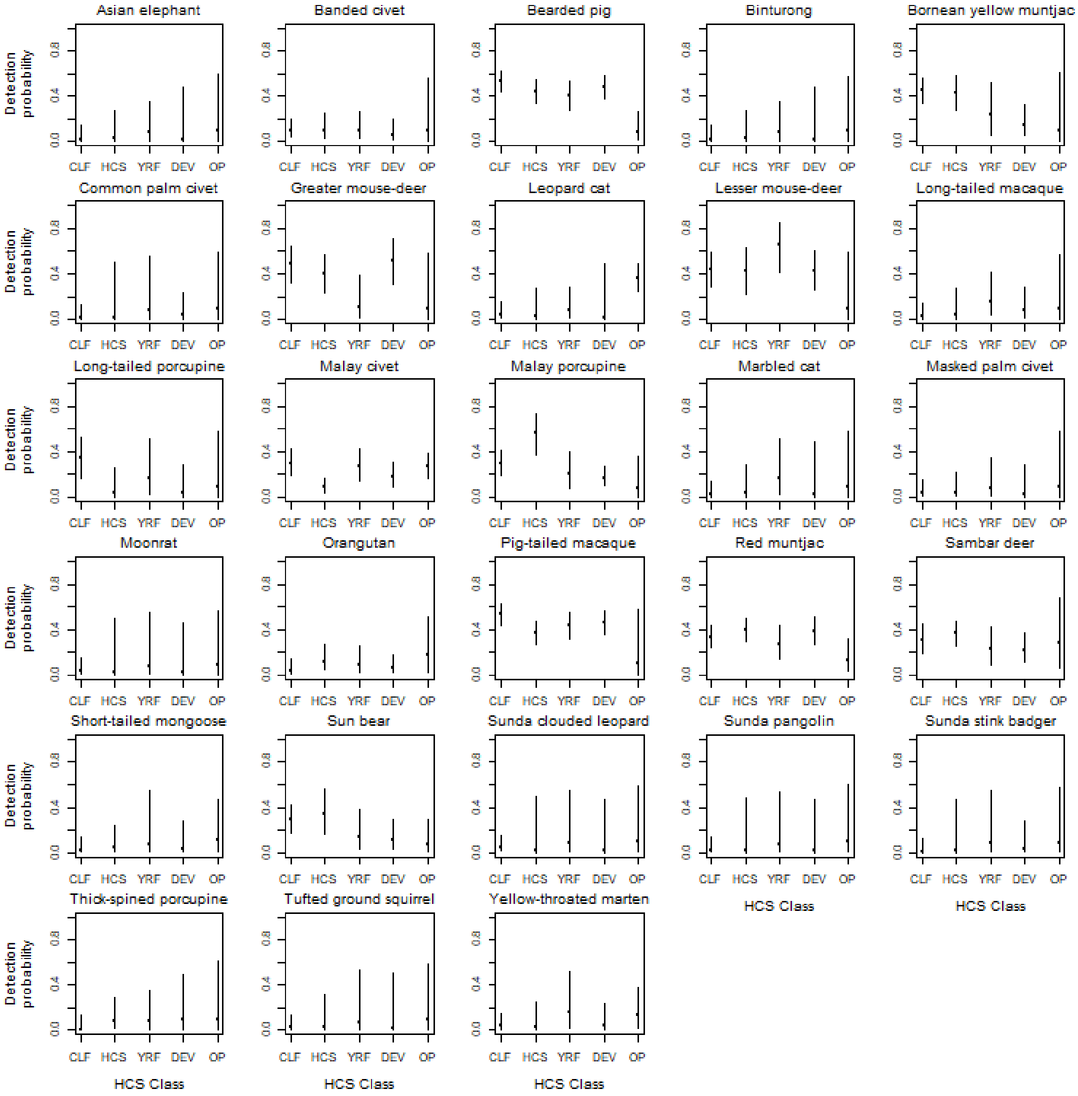


Figure S3.3: Mammal occupancy relative to continuous carbon (coarse-scale). Species-specific posterior summaries of occupancy as a function of continuous carbon derived from a 1 km resolution dataset (Avitabile *et al.* 2016). We present predicted mean posterior distribution values (blue line) and 95% Bayesian credible intervals (blue shaded region).

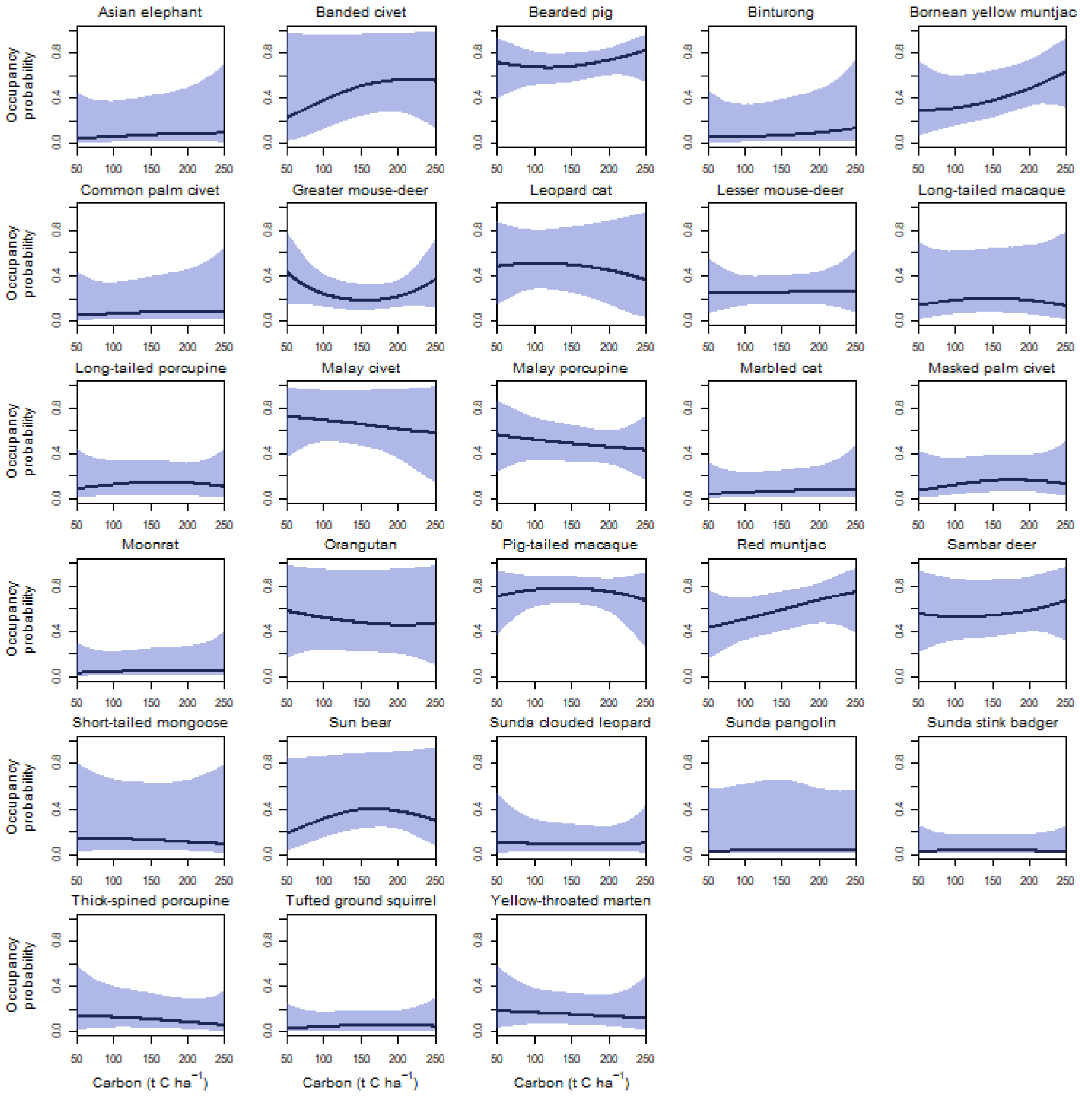
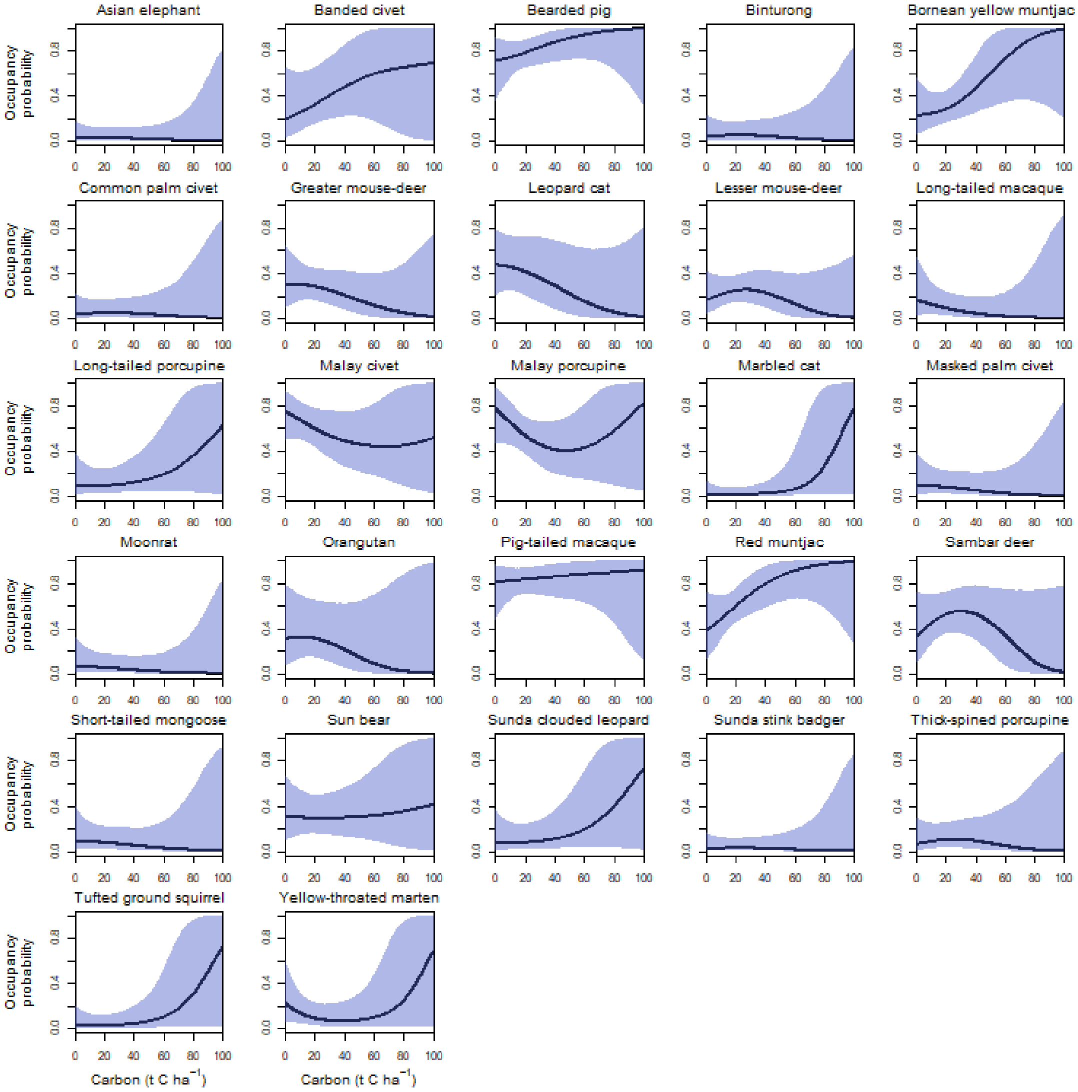


Figure S3.4: Mammal occupancy relative to continuous carbon (fine-scale). Species-specific posterior summaries of occupancy as a function of continuous carbon derived from a 25 m resolution dataset (Pfeifer *et al.* 2016). We present predicted mean posterior distribution values (blue line) and 95% Bayesian credible intervals (blue shaded region).



Chapter 4. Secondary disturbance limits mammal persistence in human-modified landscapes: implications for zero-deforestation commitments

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Manuscript in preparation

Abstract

Zero-deforestation commitments have emerged as a way for production companies to disassociate agricultural expansion from forest loss in the tropics. However, the success of these policies is dependent on effective methodologies that translate corporate commitment into actual implementation on the ground. The High Carbon Stock (HCS) Approach is the dominant tool used to implement zero-deforestation commitments, yet the efficacy of the methodology to design ecologically functional forest networks in production landscapes has not been assessed. In a highly-fragmented tropical forest landscape dominated by oil palm, we test the capacity for HCS designations of conservation-priority to sustain mammal diversity in forest remnants. Our results found that forest patches afforded the highest conservation priority by HCS protocols were indeed important refugia for IUCN-threatened species and megafauna. Moreover, large, less isolated fragments were found to support larger mammal populations, though the conservation value of a remnant was moderated by forest quality and hunting pressure. Disturbance synergies are rarely accounted for in fragmentation assessments, but we identify greater empirical support for models that included habitat quality and hunting measures together. We find that current HCS core area criteria conserve only a fraction of the mammal community and estimate that an area of 3,199 ha would be required to sustain the full complement of mammal species. This figure increased by an order of magnitude when hunting effects were accounted for. Maintaining strategically configured large forest remnants should be the primary objective for medium-large mammal conservation. Where this is not feasible a greater emphasis on landscape-connectivity is essential. To this end, we advocate greater recognition of the importance of low-medium conservation priority patches and encourage their integration into restoration objectives.

Keywords: Habitat fragmentation; High Carbon Stock Approach; hunting; land-use planning; tropical mammals; N-mixture modelling; Southeast Asia; zero-deforestation.

Introduction

Tropical forests support a large proportion of global biodiversity, but are compromised by anthropogenic activities (Barlow et al., 2018). Indeed, 227 million ha of tropical forest area has been lost since 1950 (Rosa et al., 2016). The remaining forest exists as 130 million fragments (Taubert et al., 2018), 70% of which is edge habitat (Haddad et al., 2015). Cumulatively, the processes of tropical forest loss and fragmentation erode biodiversity by reducing effective habitat area and quality, as well as increasing exposure to anthropogenic disturbance (Barlow et al., 2016). If biodiversity collapse is to be averted in tropical regions, deforestation must be curbed.

Agricultural conversion accounts for up to 78% of tropical deforestation (Curtis et al., 2018), and is widely recognised as the primary threat to terrestrial vertebrates (Tilman et al., 2017, Curtis et al., 2018). The pantropical expansion of oil palm (*Elaeis guineensis*) is at the forefront of conservation concerns. Driven by high productivity and accelerating demand for palm oil derivatives, oil palm currently occupies 18.7 million hectares of land (Meijaard et al., 2018). Conversion of tropical forests to oil palm is associated with precipitous biodiversity declines and biotic homogenization (Fitzherbert et al., 2008, Wearn et al., 2016). Since 1970, global palm oil production has doubled every decade, a trend which is forecast to continue (Austin et al., 2017). Much of the ecologically suitable land identified to meet future agricultural expansion currently comprises highly biodiverse ecosystems (Pirker et al., 2016). We therefore need to capitalise on all opportunities to reconcile production and conservation, if we are to safeguard biodiversity against the proliferation of commodity agriculture.

Growing public awareness of the environmental impacts of oil palm, and associated demand for more sustainable production, has prompted the emergence of voluntary standards that aim to eliminate deforestation from commodity supply-chains. These “zero-deforestation” pledges feed into corporate social responsibility strategies that align societal expectations with company development (Lyon and Maxwell, 2008). Such strategies reduce reputational risk, generate a favourable brand image, maintain consumer loyalty and circumvent import restrictions to environmentally conscious markets (Lambin et al., 2018). In the oil palm industry, 80% of producers with dominant market shares and land allocations have committed to zero-deforestation (Lyons-White and Knight, 2018, Meijaard et al., 2018). Zero-deforestation initiatives have the potential to uncouple oil palm expansion and deforestation, though their success is dependent on effective methodologies that translate corporate commitment into environmentally sustainable expansion.

The High Carbon Stock (HCS) Approach has emerged as the dominant mechanism to realise zero-deforestation commitments in the oil palm sector. For example, signatories of the Sustainable Palm Oil Manifesto, representing five of the largest palm oil producers, have committed to implementing HCS protocols (Padfield et al., 2016). HCS directs agricultural conversion towards degraded land of low carbon and biodiversity value, where production would be independent of deforestation (Rosoman, 2017). HCS comprises two components. Phase one protocols identify biodiverse forest areas for conservation based on tree density and structure (Deere et al., 2018). However, the long-term fate of biodiversity in remnant forest depends on the spatial configuration of remnant habitat. Phase two HCS protocols, therefore, aim to ensure that the remaining forest extent is ecologically functional, based on criteria such as specific patch sizes, level of connectivity and an assessment of quality (Rosoman, 2017). The role these criteria may (or may not) play in protecting biodiversity are yet to be fully evaluated, despite this being fundamental to confirming whether meeting zero deforestation commitments is compatible with conservation objectives.

Synergies between the impacts of anthropogenic disturbance and fragmentation on biodiversity are rarely addressed, potentially introducing significant systematic bias into conservation recommendations if multiple drivers of biodiversity loss cannot be decoupled. Hunting by humans is ubiquitous within tropical forest ecosystems, resulting in widespread defaunation (Harrison, 2011). Despite recognition that forest fragmentation increases its accessibility to hunters, few studies integrate hunting indices into fragmentation assessments (but see Michalski and Peres, 2007, Peres, 2001), due to difficulties detecting and quantifying the spatial signature of human pressure. Additionally, geographic and taxonomic bias in fragmentation research limits the scope of generalisations, due to divergent species responses within and between biogeographic realms (Deikumah et al., 2014, Keinath et al., 2017).

Here we quantify forest fragmentation impacts on biodiversity to inform the HCS methodology underpinning zero-deforestation commitments. Our study area in Sabah, Malaysian Borneo, has been subject to some of the highest deforestation rates in the tropics (Hansen et al., 2013), and remaining forest is distributed across 7.6 million fragments (Brinck et al., 2017). Malaysia is at the forefront of oil palm cultivation, contributing to 34% of global palm-oil production at the expense of 2.1 million hectares of forest in Malaysian Borneo alone (Gaveau et al., 2016a). Despite experiencing vast and rapid land-use change, Southeast Asia has been underrepresented in global fragmentation assessments (Deikumah et al., 2014), hindering the development of conservation measures for the region's vulnerable biodiversity. We develop a modelling framework to understand the impacts of HCS-relevant fragmentation metrics on biodiversity, while accounting for potential disturbance synergies. Our appraisal focuses on tropical forest mammals because they are sensitive to habitat fragmentation (Crooks et al., 2017), regionally threatened, and consistently prioritised by conservation policies (Schipper et al., 2008).

Materials and methods

Study System

We conducted fieldwork within the Stability of Altered Forest Ecosystems (SAFE) project and surrounding oil palm estates in Sabah, Malaysian Borneo. The study area is nested within Kalabakan Forest Reserve (KFR; 4°33'N, 117°16'E) comprising lowland and hill dipterocarp forest. KFR is a highly heterogeneous mosaic of near pristine old-growth forest, secondary forest at varying stages of recovery and oil palm plantations. Within the SAFE experimental area, isolated replicate forest fragments of standardised sizes (1, 10 and 100 ha) have been retained within an agricultural matrix to better understand the long-term ecological consequences of fragmentation (Ewers et al., 2011).

We established 128 sampling locations across the study landscape, partitioned into continuous forest controls (N=60) and fragmented forest sites (N=68; Fig. 4.1). Sampled fragments ranged in size between 1 and 590 ha, thus broadly capturing the dominant size classes of Southeast Asian forest remnants (average fragment size = 52 ha, 13-213 ha depending on forest cover data source; Brinck et al., 2017).

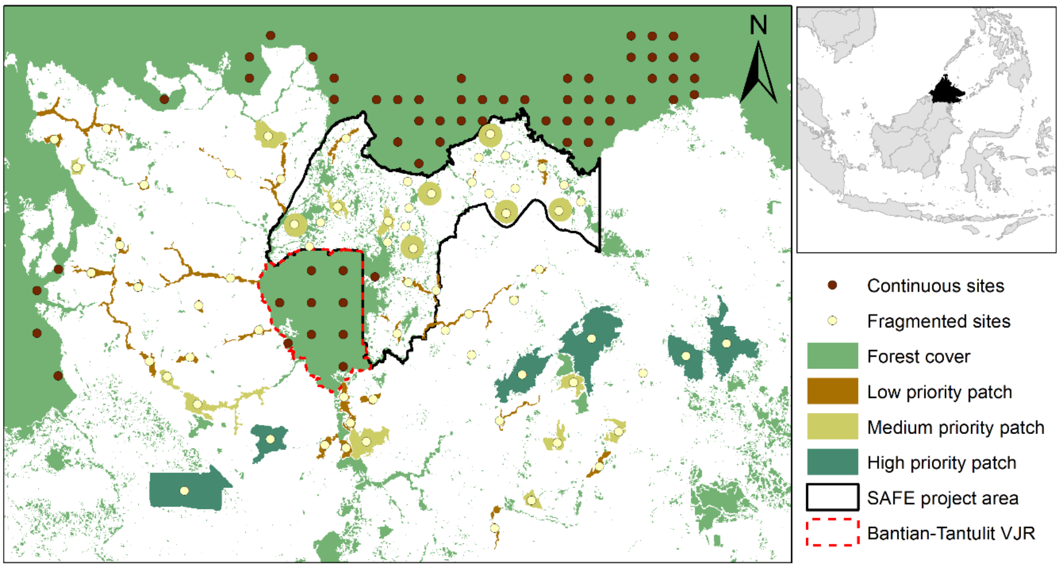


Figure 4.1: Map of study site, HCS patch prioritisation and camera-trap design. Map of study area (inset shows broader geographic context), highlighting camera-trap sampling locations partitioned across continuous- and fragmented forest sites. Sampled forest fragments are colour coded to reflect their HCS conservation priority designation.

Mammal sampling

To characterise the mammal community, we obtained detection/non-detection data from remotely operated digital camera-traps (Reconyx HC500, Wisonsin, USA) between June 2015 and December 2017. Camera-traps were deployed at 128 locations (Fig. 1, mean distance between sites, 1.4 km; elevation range, 89 –708 m). We adopted a paired design to capture a greater breadth of environmental conditions and maximise survey effort in topographically challenging terrain. Paired camera-trap units were positioned up to 250 m apart (mean distance=207.3 m; range=23.3–231.7 m). After malfunction and theft, we retrieved data from 214 units across all 128 sampling locations, equating to 83.6% of the 256 deployed camera-traps. Units were deployed for a minimum of 42 consecutive nights and were continuously active, providing a total sampling effort of 10,097 camera-trap nights.

Determinants of mammal persistence in fragmented landscapes

We compiled spatially-explicit fragmentation metrics at the patch-scale to capture key criteria from the HCS prioritisation decision tree (Rosoman, 2017): core area, shape and isolation. These forest metrics were quantified for all patches with a threshold carbon value of 35 t C ha^{-1}, using LiDAR-derived above-ground carbon maps (Asner et al., 2018), as per HCS protocols. We also derived measures of forest quality and hunting pressure. Forest quality was quantified using two metrics, biomass (t ha^{-1}; derived from Asner et al., 2018) and a HCS-specific patch-scale measure of the proportion of dense forest (>75 t C ha^{-1}). We developed a bespoke hunting variable based on modified population pressure surfaces conceived by Platts et al. (2012). We derived hunting pressure using travel-time cost surface models, which integrate proximity to infrastructure (roads and villages), landcover, topography and human population density (see supplementary section S4.1 for further methodological details of covariate processing). We retained commonly adopted hunting proxies (proximity to infrastructure and population density) to gauge the value of our metric compared to the disaggregated component variables. We deemed collinearity amongst predictors confounding if Pearson's correlation coefficients were $|r|>0.7$ and variance inflation factors were VIF>3. Prior to analysis, continuous covariates were centred on their mean values and standardised to one-unit standard deviation.

Modelling framework

Data from paired camera-traps were combined into single analytical units prior to analysis to mitigate issues of Markovian dependence (Hines et al., 2010). Species-specific detection histories for each analytical unit were pooled into six-day sampling occasions (3-7 temporal replicates site^{-1}), which we summarised for each species across sites. We excluded two species with fewer than five detections from the modelling process (banded linsang, *Prionodon* linsang; smooth-coated otter, *Lutrogale perspicillata*) as it is difficult to uncouple ecological and observation processes when detection data are sparse (Brodie et al., 2015b).

We employed hierarchical multi-species Bernoulli/Poisson *N*-mixture models to estimate mammal abundance from detection/non-detection data (Royle and Nichols, 2003, Yamaura et al., 2011). Throughout, we interpret abundance as a relative measure and restrict inference to spatial comparisons (Wearn et al., 2017). Our hierarchical models consisted of two components, describing the ecological and observation processes underpinning the data (see supplementary sections S4.2 and S4.3 for further information on model formulation). Using temporally-replicated samples of detection/non-detection data, our models explicitly accounted for imperfect detection, allowing differentiation between true absence and non-detection (MacKenzie et al., 2017).

To determine the influence of HCS-relevant fragmentation metrics and secondary disturbance impacts on patterns of mammal abundance, we specified models of the form.

$$\log(\lambda_{ij}) = \alpha_{0i} + \alpha_{1i} Forest\ Cover_j + \alpha_{2i} Fragmentation_j + \alpha_{3i} Quality_j + \alpha_{4i} Hunting_j + \varepsilon(Year_j)_i$$

$$\text{logit}(r_{ij}) = \beta_{0i} Habitat_j + \beta_{1i} Survey\ Effort_j$$

Abundance (λ_{ij}) and detection (r_{ij}) were modelled using log and logit link functions respectively, incorporating species-specific slopes and intercepts. Species-specific random effects were drawn from a common distribution with estimable hyper-parameters (Guillera-Arroita, 2017). This formulation permits community-level inference and provides robust parameter estimates for cryptic species rarely detected during sampling (Zipkin et al., 2009).

Eleven models were constructed to explore the independent and additive effects of fragmentation, forest quality and hunting metrics on mammal abundance (Table 1). To decouple fragmentation effects from habitat loss (Fahrig, 2017), we incorporated a forest cover covariate across all models to quantify habitat availability in the vicinity of the sampling location. Scale optimisation methods were used to ascertain the optimal spatial extents for covariates (buffers of radii: 50, 100, 250, 500, 1000, 2500 and 5000 m). Covariates were aggregated across their best-fitting buffers and calculated as weighted averages between paired units, based on the proportion of survey effort each pair contributed to the sampling location. We incorporated temporal random effects (ε) in the abundance component of the model to account for inter-annual variation due to multi-year sampling, assuming population and demographic closure over a 12-month period. We modelled detection probability as a function of categorical habitat-specific intercepts and survey effort (number of camera-trap nights). We define three distinct habitat classes for the detection model, which were objectively defined using HCS stratification protocols (dense forest; >75 t C ha-1; young regenerating forest: 35-75 t C ha-1; non-forest habitat: 0-15 t C ha-1; Rosoman, 2017).

To inform scale-optimisation methods and rank competing models, we calculated Watanabe-Akaike Information Criterion (WAIC), a within-sample model selection tool analogous to AIC (Broms et al., 2016, Watanabe, 2010). We consider substantial support for models with ΔWAIC<2 (Burnham and Anderson, 2003), and calculate evidence ratios to compare the explanatory power of competing models (Burnham et al., 2011). We only present findings for models deemed to have substantial support, containing covariates derived from optimal scales (see supplementary tables S4.1 and S4.2).

To investigate trait-mediated responses to HCS patch prioritisation protocols, we assigned conservation designations to forest remnants in accordance with HCS core area criteria (High Priority Patch: >100 ha; Medium Priority Patch: 10-100 ha; Low Priority Patch: <10 ha; Fig. 1) and compared their capacity to support mammal populations. We partitioned species (supplementary Table S4.3) according to their IUCN conservation status (Non-threatened: least concern, near-threatened; Threatened: vulnerable, endangered, critically endangered), ecological specialism (generalist, specialist; Wilson et al., 2010), body size (medium: <5 kg; large: 5-25 kg; mega: >25 kg; derived from the PanTHERIA database, Jones et al., 2009) and trophic guild (carnivore, herbivore, frugivore, insectivore, omnivore; derived from the PanTHERIA database, Jones et al., 2009).

To determine quantitative recommendations for HCS core area criteria, we derived predicted species richness estimates from model outputs, accounting for imperfect detection. Predicted species richness was calculated as the sum of occupancy (Ψ), which is a deterministic function of abundance: $\Psi_{ij} = 1 - exp(-\lambda_{ij})$. To quantify the potential impact of disturbance synergies on core area criteria, we calculate predicted species richness under three scenarios: 1) core area only; 2) core area and hunting; and 3) core area, hunting and forest quality.

Results

Biodiversity value of HCS priority forest remnants

Pairwise comparison identified an 18.5% (95% Bayesian Credible Interval, BCI: 14-20%) increase in mean local mammal abundance in forest remnants compared to continuous forest when all species were considered (Fig. 4.2). This trend was predominantly driven by substantial increases in generalist (53.7% increase, 49.9-64.2%) and omnivorous species (82.5% increase, 66.0-118.0%). When partitioning the results according to HCS designations, High Priority Patches of forest consistently harboured greater levels of abundance than Medium and Low Priority Patches. Specifically, high priority patches were important for threatened (Medium Priority Patches: 37.2% increase, 33.3-37.7%; Low Priority Patches: 45.1% increase, 37.3-47.7%) and mega-bodied species (Medium Priority Patches: 40% increase, 37.4-44.9%; Low Priority Patches: 46.7% increase, 39.9-49.9%). Medium- and Low

Priority Patches supported comparable mammal abundance across all trait groups and guilds.

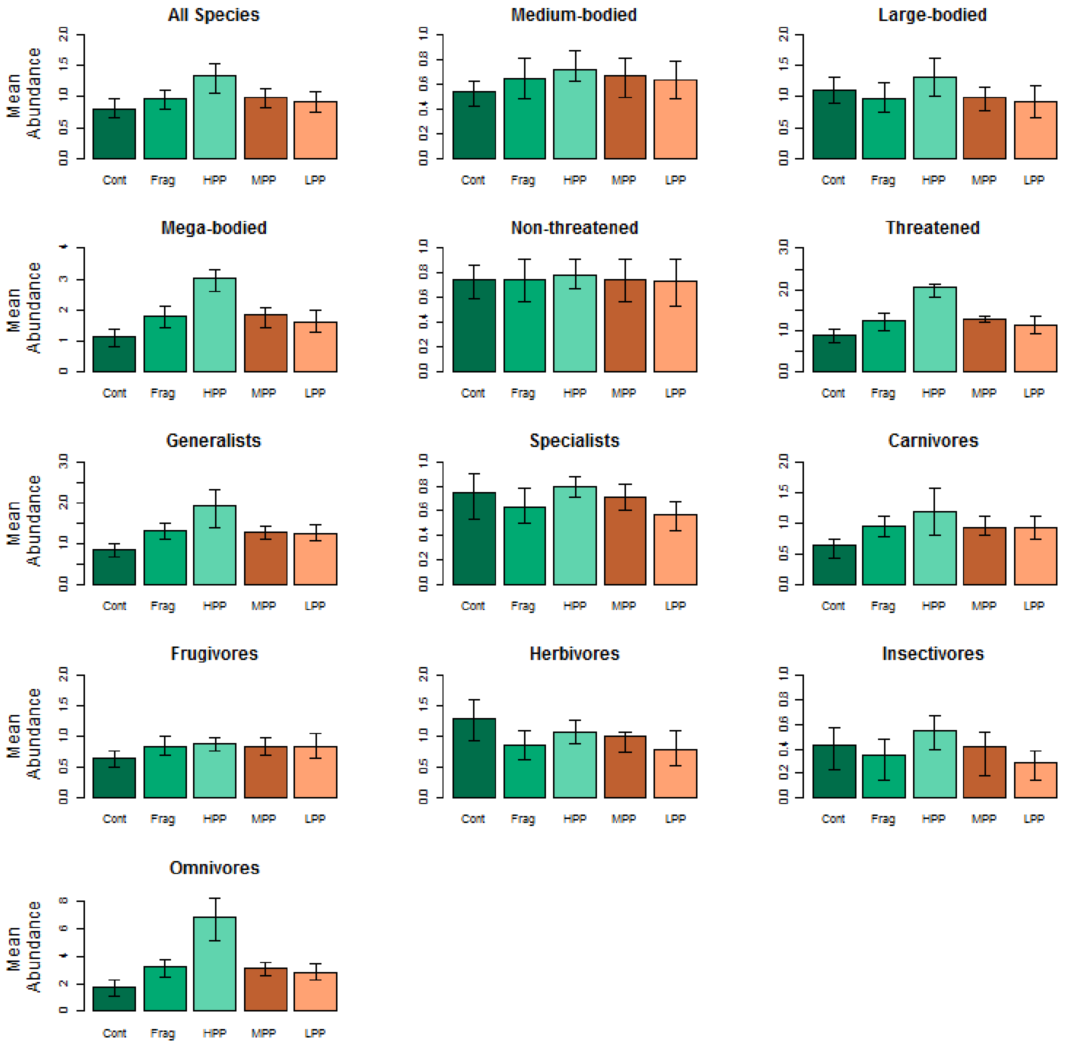


Figure 4.2: Local abundance of tropical forest mammals relative to habitat type and HCS patch priority designation. Abundance is calculated as a relative measure representing the estimated average number of individuals whose home range overlaps with camera-traps deployed in broad habitat classifications. We quantify mammal abundance across continuous (Cont) and fragmented forest (Frag), and HCS designated conservation priority forest patches (HPP: High Priority Patch; MPP: Medium Priority

Patch; LPP: Low Priority Patch). We present findings for all species and partitioned according to body size.

Model performance

We found comparable statistical support for models incorporating fragmentation and quality measures and those supplemented with our hunting pressure metric (Table 4.1). Evidence ratios suggested that these models performed 7.5 and 3.9 times better, respectively, than those limited to fragmentation metrics alone. When considered independently, models containing fragmentation metrics had greater support than those containing hunting or forest quality metrics in isolation (Table 4.1). The hunting pressure model had greater explanatory power than that containing disaggregated hunting proxies (Table 4.1), performing more than 100 times better.

Table 4.1: Performance of Bernoulli/Poisson *N*-mixture models. Performance of models assessing the impact of alternative configurations of fragmentation, hunting and forest quality on mean local mammal abundance. Models are presented in descending order of performance based on Watanabe Akiake Information criterion (WAIC), a measure of the relative quality of statistical models given the data. Δ WAIC indicates variation in WAIC relative to the top-ranking model; WAIC w denotes Akaike weights and further quantifies strength of evidence between competing models.Models were considered to have comparable statistical support if they were within two ΔWAIC (presented in bold). Though not presented, every model contained a forest cover covariate to decouple the effects of forest fragmentation from habitat loss.

Model and covariates	**WAIC**	**ΔWAIC**	**WAIC*w***
Fragmentation + Quality: Core + Shape + Isolation + Biomass + Prop_HCS	**4196.14**	**0.00**	**0.58**

Fragmentation + *Hunting* + *Quality:* Core + Shape + Isolation + Hunt_Press + Biomass + Prop_HCS	**4197.45**	**1.31**	**0.30**
Fragmentation: Core + Shape + Isolation	4200.18	4.04	0.08
Fragmentation + *Hunting:* Core + Shape + Isolation + Hunt_Press	4202.26	6.12	0.03
Fragmentation + *Hunting* + *Quality:* Core + Shape + Isolation + Pop_Density + Dist_Roads + Dist_Village + Biomass + Prop_HCS	4206.00	9.86	0.00
Hunting + *Quality:* Hunt_Press + Biomass + Prop_HCS	4208.25	12.11	0.00
Quality: Biomass + Prop_HCS	4208.69	12.55	0.00
Fragmentation + *Hunting:* Core + Shape + Isolation + Pop_Density + Dist_Roads + Dist_Village	4209.63	13.50	0.00
Hunting: Hunt_Press	4210.13	13.99	0.00
Hunting + *Quality:* Pop_Density + Dist_Roads + Dist_Village + Biomass + Prop_HCS	4216.10	19.96	0.00
Hunting: Pop_Density + Dist_Roads + Dist_Village	4222.68	26.54	0.00

Core: core area of a forest patch (i.e. area within patch after subtracting a 100m internal buffer; ha); Shape: ratio of patch perimeter and perimeter of an optimally compact patch of comparable area; Isolation: distance to nearest continuous forest (defined as patch >10,000 ha; km); Hunt_Press: bespoke hunting pressure metric combining population counts, accessibility, distance from roads and distance to population centres; Pop_Density: population density (people km$^{2\ -1}$); Dist_Roads: distance to the nearest road (km); Dist_Villages: distance to the nearest village (km); Biomass: aboveground live biomass (t ha^{-1}); Prop_HCS: proportion of High Carbon Stock Forest (>35 t C ha^{-1}).

An evidence-base for zero-deforestation support tools

The influence of fragmentation, hunting and habitat quality in shaping mammal abundance was evident at the community-level (Fig. 4.3). We found strong positive associations between mean local abundance and patch core area (posterior mean: 0.11, BCI: 0.05-0.21) and the proportion of HCS forest within remnant forest patches (0.09, 0.02-0.23). Conversely, we found weak evidence of mammal population declines relative to our alternative measure of forest quality, biomass (-

0.09, 90% BCI: -0.18 to -0.01). Moreover, isolation demonstrated a strong negative association with mean abundance (-0.12, -0.24 to -0.01), suggesting that local mammal abundance diminishes in more isolated fragments. There was also weak support for hunting impacts (-0.16, -0.31 to -0.02), highlighting the sensitivity of mammal communities to anthropogenic pressure.

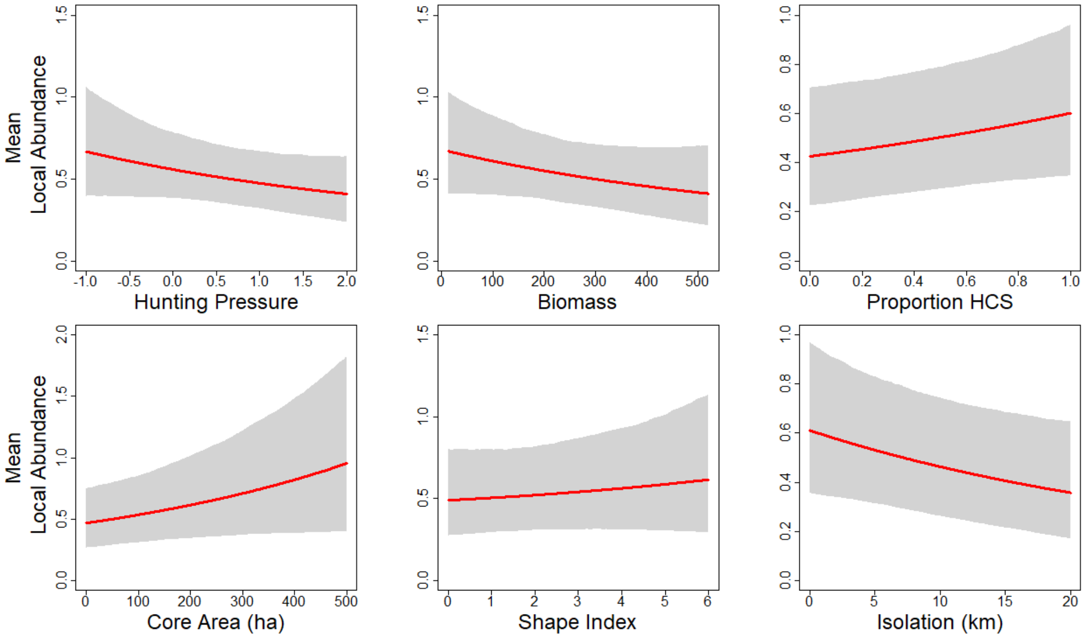


Figure 4.3: Mammal community responses to fragmentation metrics, forest quality and hunting pressure. Response of the medium-large terrestrial mammal community to anthropogenic pressure (hunting), forest quality (biomass and proportion HCS) and fragmentation metrics (core area, shape and isolation). Predicted mean posterior distribution values are presented in red, while the 95% Bayesian credible interval is shaded in grey.

Only modest gains in mammalian species richness were achieved across fragment sizes varying in core area from zero to 500 ha (Fig. 4.4). At the threshold core area of 10 ha, which differentiates Low and Medium Priority Patches, only 13 species (10.7-14.9) of the 38 species sampled, equating to 33% (28.2-39.2%), were estimated to be present. At a core area of 100 ha, the initial criterion for designating patches high priority, predicted richness was 13 species (11.2-15.9). Thus, for a 10-fold increase in core area, no additional species were preserved. Based on extrapolation, a core area of 3,199 ha (2131-5182) would be required to conserve the 38 mammal species constituting our community.

Using the additive influence of habitat area, quality and anthropogenic pressure, we developed quantitative recommendations of patch core area required to support viable mammal assemblages from species richness predictions (Fig. 4.4). Under a range of patch size configurations, variation in hunting pressure limited the conservation gains that can be achieved by increasing patch core area (Fig. 4.4). We predict that in remnant forest patches subjected to hunting pressure, a minimum core area of 27,498 ha would be required to achieve the full complement of mammal species. However, the deleterious impacts of hunting can be offset considerably by habitat quality, reducing the area required to conserve intact communities to 4,531 ha.

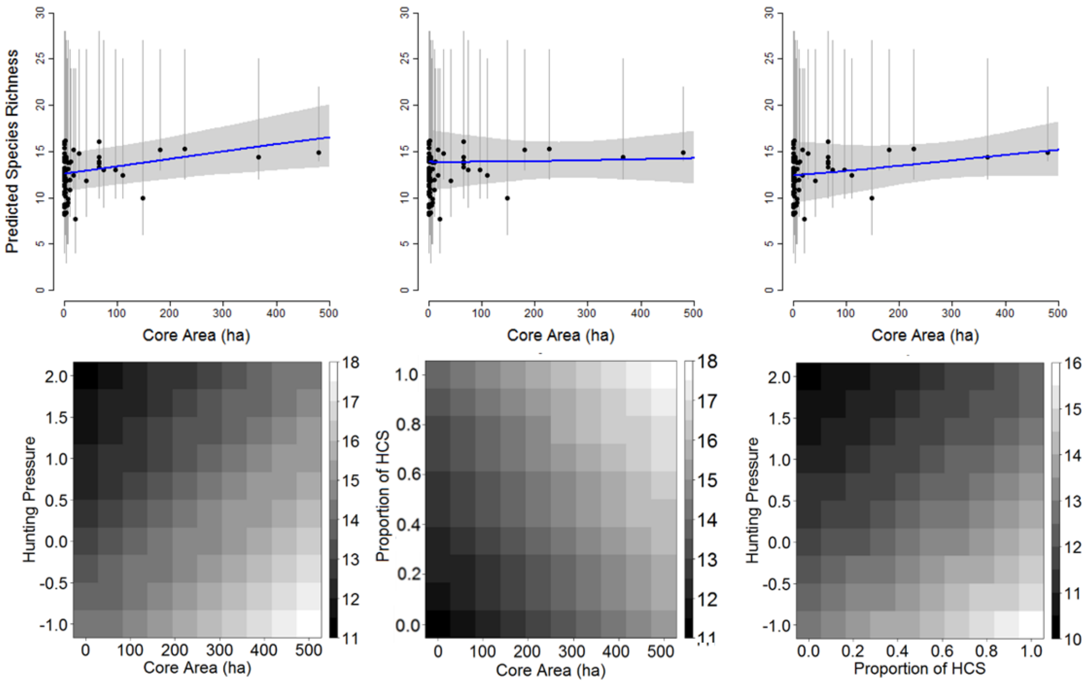


Figure 4.4: Estimated species richness demonstrating secondary disturbance impacts on HCS core area criteria. Total estimated species richness (top row) predicted using core area alone (left), core area and hunting pressure (middle) and core area, hunting pressure and habitat quality (right). Interaction plots (bottom row) demonstrate how hunting pressure (left) and forest quality (middle) modulate the conservation value of forest patches and interface (right).

Discussion

Robust scientific evidence is central to informed environmental decision making (Lucey et al., 2017, Sutherland et al., 2004). Our work identifies challenges and opportunities for HCS implementation in tropical deforestation frontiers. We use empirical evidence of fragmentation impacts on biodiversity to identify HCS-relevant patch and landscape attributes that make forest remnants more hospitable to biodiversity. Moreover, we emphasise the importance of incorporating synergistic disturbance impacts into fragmentation assessments to prevent systematic bias in quantitative recommendations.

The biodiversity value of HCS-delineated forest remnants

At present, HCS is the only available methodology to support oil palm companies meeting their zero-deforestation commitments. Therefore, the extent to which zero-deforestation pledges contribute to biodiversity conservation is dependent on the capacity of the forest remnants prioritised by HCS to sustain wildlife. We identified marked increases in the abundance of generalist and omnivorous species in fragmented forest sites. This homogenisation process whereby specialist species are displaced by a few abundant generalists, is well-documented in forest fragments (Beca et al., 2017, Canale et al., 2012, Magioli et al., 2016). Generalists are able to maintain populations in forest fragments due to their ecological plasticity, which facilitates the exploitation of a greater breadth of resources (Garmendia et al., 2013, Michalski and Peres, 2007). Release from competition and predation in forest fragments can also result in increases in abundance by fragmentation-tolerant species (Laurance, 2008).

When we partitioned forest fragments according to HCS patch criteria, High Priority Patches contained significantly larger concentrations of mega-bodied and threatened species when compared to Low and Medium Priority Patches. Megafauna and threatened species demonstrate traits associated with sensitivity to fragmentation, including large area requirements, slow reproductive rates, rarity and range restriction (Keinath et al., 2017). Therefore, forest remnants designated as the highest priority by HCS protocols have the potential to act as refugia for those species most vulnerable to fragmentation.

Low and medium priority fragments supported comparably modest mammal abundance across all species and guilds. This is an important observation because Low and Medium Priority Patches become viable for conversion within the HCS framework if they are shown to be negligible for biodiversity. Given that Low and Medium Priority Patches were the dominant size class within our study (91.2%), a trend which is representative across the tropics, we advocate greater recognition of the importance of these patches in land-use planning. They play pivotal conservation roles caching genetic diversity, maintaining equilibria in predator-prey systems, sustaining the regional species pool, and protecting relict habitat for local endemics (Huffaker, 1958, Ovaskainen, 2002, Resasco et al., 2017, Saura et al., 2014, Struebig et al., 2011). Consequently, incorporating Low and Medium Priority Patches into long-term restoration strategies could prove a cost-effective conservation strategy in fragmented agricultural landscapes.

A blueprint for ecologically functional forest mosaics

Our multi-modelling framework revealed patch-scale fragmentation metrics to be the strongest determinants of mammalian abundance. These findings explain the underlying mechanisms dictating mammal abundance in HCS-delineated priority patches. At the community-level, mammals were found to be substantially more abundant in forest remnants comprising a large core area and in close proximity to continuous logged forest. Larger fragments have increased carrying capacity to sustain larger animal populations. Moreover, fragments with a greater core area are more robust to edge effects, which can alter the structure and microclimatic conditions of fragments (Laurance, 2008). In a pan-tropical assessment, mammal abundance declined by 57% towards forest edges (Pfeifer et al., 2017). Less isolated fragments experience higher colonisation rates, with immigration providing a demographic safeguard from local extinction (Brown and Kodric-Brown, 1977). Our results echo those from studies elsewhere in Borneo, which identified declines in mammal populations with increasing distance from forest source populations (Yue et al., 2015). We therefore stress the importance of maintaining connectivity in agricultural landscapes for dispersal-limited taxa, particularly specialised species with limited tolerance for matrix conditions.

We demonstrate the potential for anthropogenic stressors to amplify the effects of fragmentation on tropical mammals. We found that models incorporating measures of forest quality and hunting had considerably more support than those containing fragmentation metrics alone, suggesting that mammal abundance is best explained when accounting additively for disturbance effects. We found that mammal communities decreased in abundance in areas predicted to experience high levels of hunting pressure, though variation at the community level obscured pronounced impacts on ungulates and large rodents, which exhibited precipitous declines (see supplementary figures S4.2 and S4.3). Our species-specific results reflect previous research showing that these taxonomic groups are the preferred quarry of hunters (Brodie et al., 2015b, Fa and Brown, 2009). In the few studies that have explored hunting within the context of fragmentation, hunting has demonstrated substantial negative impacts on mammal abundance (Cardinale et al., 2006, Cullen Jr et al., 2000, Kosydar et al., 2014, Peres, 2001, Sampaio et al., 2010). Our study adds to this body of evidence and further emphasises the importance of developing mitigation measures that safeguard vulnerable mammal populations from overexploitation in fragmented landscapes. Moreover, we introduce a valuable spatially explicit hunting metric that can be developed from freely available remote-sensing data to quantify human pressure at scales appropriate to conservation management

We found that forest quality, measured as the proportion of HCS-delineated forest within the patch, demonstrated a positive association with mammal abundance. This provides further evidence of the biodiversity value of forest prioritised for conservation by the HCS approach (Deere et al., 2018). An increasing proportion of HCS forest within remnant patches likely corresponds to increasing structural complexity, resulting in a diverse niche space which can accommodate greater mammal abundance (**Chapter 3**). Maintaining and restoring patch quality should therefore be central to forest management in production landscapes.

Management recommendations

A key obstacle to effective conservation policy in production landscapes is a poor understanding of the optimal patch sizes needed to sustain biodiversity (Lucey et al., 2017). Core area is the principal determinant of conservation designation within the HCS prioritisation process, and current protocols specify a threshold of 100 ha to delineate High Priority Patches of conservation value. We demonstrate that these patches would support only a fraction of the estimated species richness in the mammal community (35%). Mammals occupy key positions in tropical forest ecosystems, exerting top-down control on primary production and consumers which influences the distribution, composition and structure of vegetation (Terborgh et al., 2001). The absence of large mammals can have cascading effects on ecosystem functioning leading to arrested succession (Ripple and Beschta, 2006). Previous meta-analysis has suggested that a core area of 200 ha is required to maintain natural forest regeneration (Lucey et al., 2017), but this would be insufficient to maintain mammal-mediated ecological processes. Given that the average fragment size across Southeast Asia is 52 ha (Brinck et al., 2017), our results suggest the potential for negative feedback loops in forest fragments owing to depauparate mammal communities.

Though an evidence-base for optimal patch size for medium-large mammals is lacking, Magioli et al. (2015) found that functional diversity of mammal populations was maximised in patches exceeding 2,050 ha (total area). Based on the trajectory of our trendline, a core area of 3,198 ha would be necessary to conserve the full complement of mammal species within a forest fragment, although we advise caution when interpreting this figure due to the inherent dangers of extrapolating beyond the bounds of the data. Given the opportunity costs of forgoing development, it is unlikely that these area requirements can be met at the concession-level, therefore enhancing and restoring landscape-level connectivity through a network of small forest patches and riparian margins should be a priority for mammal conservation in production landscapes (Zimbres et al., 2017).

The extent to which multiple disturbance impacts influence the optimal patch size has rarely been explored in the scientific literature. Our results suggest that core area associated gains in species richness are supressed by hunting pressure, increasing the area required to retain an intact mammal community by an order of magnitude. This concurs with Peres (2001), who demonstrated that hunting greatly increases the spatial requirements necessary to sustain viable mammal populations. Thus, without explicit consideration of hunting, the optimal fragment size required to retain appreciable levels of biodiversity can be underestimated by 24,300 ha according to our data. We demonstrate that hunting pressure can be alleviated by the maintenance and restoration of forest quality within forest fragments, which reduces the area required to support intact mammal commiunities to 4,531 ha. Nevertheless, if HCS-designated forest fragments are to avoid functioning as population sinks, preventative measures that effectively prohibit illegal timber extraction and hunting are essential in production landscapes.

Conservation implications

Agricultural land currently occupies 1.53 billion hectares globally, with a projected 18% increase predicted before 2050 (Tilman et al., 2017). Zero-deforestation pledges provide a mechanism to ensure this expansion will not be met at the expense of tropical forests. In Malaysia alone sustainability pledges would safeguard 21.14 million hectares of primary and selectively logged forest (Padfield et al., 2016). Our work highlights the potential for zero-deforestation policies to facilitate environmentally-conscious agricultural expansion across the tropics that aligns with biodiversity conservation objectives. HCS-delineated high conservation priority patches were identified as important refugia for species most at risk from forest fragmentation, but the current core area threshold criterion of 100 ha does not adequately safeguard mammal diversity. Maintaining the largest forest remnants should be the primary objective for medium-large mammal conservation but, given their spatial requirements, a greater emphasis on landscape-connectivity is essential to provide conduits of movement between large tracts of continuous habitat. To this end, patch configuration is paramount and we advocate strategic positioning of fragments within the vicinity of continuous tracts of forest, linked by a network of low priority patches and riparian zones. We present evidence that anthropogenic pressure can moderate the biodiversity value of forest remnants and believe this warrants greater consideration within the HCS framework. Specifically, we strongly recommend the integration of standardised hunting and habitat quality measures into future fragmentation assessments. Conservation practitioners must work closely with plantation managers to develop control measures that limit human influences on residual natural vegetation in production landscapes. While zero-deforestation pledges demonstrate an encouraging trend, failure to mitigate barriers to implementation will ensure that deforestation and agricultural expansion continue in tandem.

Acknowledgements

This study was funded by the UK Natural Environment Research Council (NERC) (NE/K016407/1; http://lombok.hmtf.info/) and a NERC EnvEast PhD studentship to NJD. GGA is the recipient of a Discovery Early Career Research Award from the Australian Research Council (DE160100904). We thank the Sabah Biodiversity Council, Sabah Forest Department, Yayasan Sabah, Sime Darby and Benta Wawasan for permitting access. We are indebted to Jamiluddin Jami, Arnold James, Mohd. Mustamin, Ampat Siliwong, Sabidee Mohd. Rizan and Najmuddin Jamal for field assistance. Special thanks to Philip Platts for advice regarding development of the spatially-explicit hunting surface.

Supplementary information

Developing fragmentation, quality and hunting metrics

Patch size, isolation and shape have demonstrated profound impacts on fragment suitability for biodiversity (Haddad et al., 2015) and are central to the HCS patch prioritisation process. To calculate patch core area, defined as habitat within the remnant impervious to external conditions (Ewers and Didham, 2006), we applied a negative buffer of 100 m to the forest cover layer. This criteria is based on scientific evidence suggesting that 75% of edge effects occur within 100 m the forest boundary (Laurance et al., 2002). We determined isolation as the shortest Euclidean distance between the forest patch and tracts of continuous forest (>50,000 ha; Potapov et al., 2008). In the context of our study site, this corresponded to Ulu Segama Forest Reserve, which forms a part of the 1 million ha Yayasan Sabah forest Management Area (Reynolds et al., 2011), the largest contiguous block of forest remaining in Sabah. Shape is traditionally calculated using the perimeter-area ratio. However, this metric is confounded as it does not reliably decouple shape from area effects (Ewers and Didham, 2006). We therefore employed a shape index to compare patch perimeter (m) to that of an optimally compact Euclidean shape (i.e. a square):

$$\text{Shape Index} = \frac{P_i}{Pmin_i}$$

$$Pmin_i = 4\sqrt{area_i}$$

where P_i is the perimeter of patch *i*, $Pmin_i$ is the perimeter of the corresponding optimally compact patch and $area_i$ is the area of patch *i*.

Forest quality is rarely accounted for in fragmentation assessments, but receives explicit consideration within HCS phase two protocols. Forest quality measures provide an indication as to the structural integrity of forest fragments, which dictates the distribution and concentration of forest resources (Simonson et al., 2014). Moreover, quality measures quantify the extent to which exposure to anthropogenic stressors (i.e. illegal timber harvesting) and edge effects erode habitat suitability for mammals. We adopt two forest quality measures, forest biomass (t ha^{-1}; derived from Asner et al., 2018) and the proportion of classified dense forest contained within the patch. We calculated biomass from carbon, based on the assumption that carbon constitutes 47% of standing biomass (Martin and Thomas, 2011). The proportion of dense forest refers to the area of the forest containing high quality forest habitat, defined under HCS guidelines as that exceeding 75 t C ha^{-1} (Rosoman, 2017).

Hunting is a pervasive threat to tropical biodiversity (Harrison, 2011), yet spatially-explicit measures of hunting pressure are lacking. Previous attempts to quantify hunting have involved coarse comparisons of biodiversity in hunted and non-hunted sites (Cullen Jr et al., 2000, Galetti et al., 2009, Kosydar et al., 2014) or direct/indirect hunter encounters (Brodie et al., 2015b, Sampaio et al., 2010). They therefore overlook spatial variability in pressure and are confounded by imperfect detection. Another approach is to use proxies, with proximity to infrastructure adopted as a surrogate for anthropogenic pressure (Benitez-Lopez et al., 2017, Michalski and Peres, 2007) and it is based on these criteria that HCS patch prioritisation protcols delineate risk of illegal incursion. However, proximity measures are typically based on Euclidean distance which greatly simplifies human movement across a landscape. In Southeast Asia, the pressure hunters exert across a landscape represents the cumulative effect of accessibility and population density (Brodie et al., 2015b, Harrison et al., 2016). Simple proximity measures alone are thus unlikely to capture the complexity of interacting variables. To overcome these limitations, we developed a bespoke hunting pressure variable based on spatially-explicit population pressure surfaces developed by Platts et al. (2012). It assumes that population pressure on location i increases with the human population (*pop*) of remote population centre j, weighted by a distance decay function *w*:

$$Hunting\ pressure_i = \sum_{j=1}^{N} pop_j \cdot w_{ij}$$

where N represents the number of locations across which pressure accumulates.

We modify the weighted distance decay function to impose accessibility constraints on the spread of human pressure. Accessibility was calculated using a travel time cost surface model (TTCSM; Frakes, 2015), implemented in ArcGIS version 10.3. TTCSMs calculate duration of travel from user-defined points to localities while accounting for landscape features (e.g. landcover, elevation, slope) or infrastructure that facilitate or impede human movement. In collaboration with oil palm plantation managers, we identified 26 population centres within the surrounding production estates, for which we retrieved corresponding demographic data. Given the isolated nature of our study site and security gates restricting the influx of hunters from beyond plantation borders, we assumed that these population centres represented the most likely sources of hunting pressure. We specified a default travel speed of 5 kmph, based on the average walking speed of a human (Browning et al., 2006). We specified a non-linear decrease in walking speed with increasing slope, using Tobler's Hiking Function (Tobler, 1993):

$$Tobler's\ Hiking\ function = 6 * exp\left(-3.5\ \cdot abs\left(tan\left(\frac{slope}{57.29578}\right) + 0.05\right)\right)$$

where slope was derived from 30 m resolution Shuttle Radar Topography Mission (SRTM) elevation data (U.S. Geological Survey, 2015). Gradients exceeding 31 degrees were specified as absolute barriers to movement (Kinsella-Shaw et al., 1992). We recognised the potential for landcover to impede speed of travel. Using an extensive transect dataset (22 transects of 2 km, walked four times each), we calculated movement speed for all major habitat types present at our study system, and landcover resistance was parameterised based on proportional differences between average walking speed and landcover specific values.

Our model assumes that an individual will optimise the mode and rate of travel, so roads will take precedence over walking when available. Employing Copernicus high-resolution satellite imagery, we digitised 6,201 km of roads across our study landscape. These were recorded as primary and secondary roads and allocated speed limits of 60 (based on the designated speed limit) and 30 (accounting for speed limitations on secondary roads within oil palm plantations) kmph respectively.

TTCSMs were created for each of the 26 population centres. To convert TTCSMs into weighted distance decay functions (*w*), we inverted each surface to scale travel time high to low with increasing distance from settlement. Substituting each inverted TTCSM for *w* in our equation, hunting pressure was calculated by multiplying each TTCSM by the corresponding population count of that village and summing the resulting surfaces (Fig. S4.1). Given that hunting is predominantly opportunistic across Southeast Asia (Harrison et al., 2016), we expect hunting pressure to be equal across all mammals. For comparative purposes, we retained traditional proxies for anthropogenic pressure (distance to roads, distance to villages, human population density; Gaughan et al., 2013) to determine the value of our bespoke hunting metric compared to risk measures adopted by HCS patch prioritisation protocols.

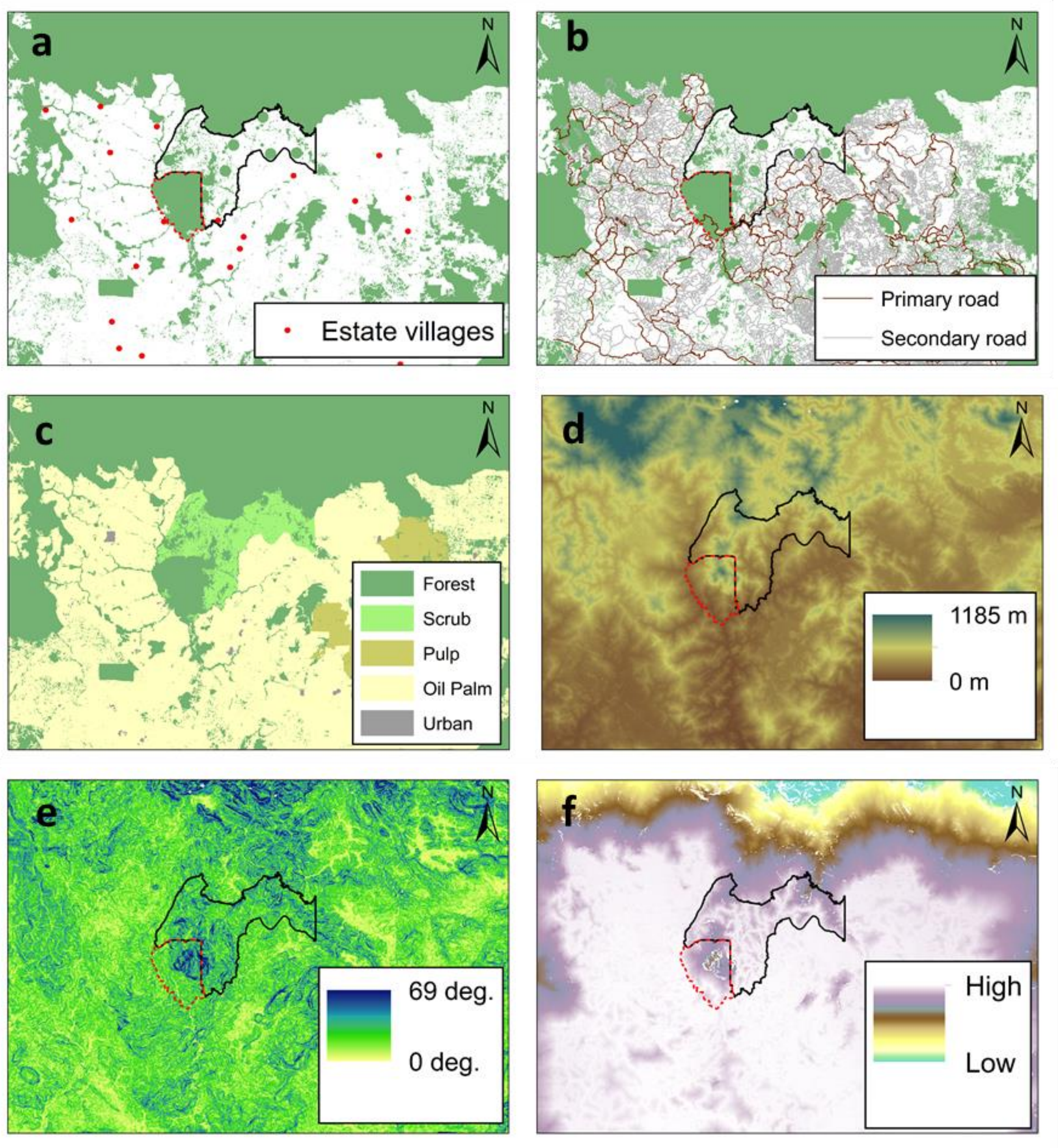


Figure S4.1: Input surfaces for the travel time cost surface model and the final hunting pressure layer. Covariates used to develop the travel time cost surface model (a: human population counts at oil palm estate villages; b: the road network; c: land cover; d: elevation (m); e: slope (degrees) and the resulting spatially-explicit hunting pressure layer (f).

Modelling framework

We modelled the local abundance of species i at sampling location j (a_{ij}) as a Poisson-distributed random variable, described by rate parameter λ_{ij}:

$$\alpha_{ij} \sim Poisson(\lambda_{ij})$$

where λ_{ij} denotes the number of individuals of species i using the habitat surrounding sampling location j. Detection probability (p_{ij}) was assumed to be functionally dependent on local abundance (a_{ij}):

$$p_{ij} = 1 - \left(1 - r_{ij}\right)^{\alpha_{ij}}$$

where r_{ij} represents the detection probability of an individual of species i at sampling location j. The coupling of abundance and per capita detection provides a modelling framework that is robust to spatial heterogeneity in detection probability (Tobler et al., 2015). However, this assumption may be unfounded for rare or territorial species that persist at low densities with negligible heterogeneity in detection probability between sampling locations (Denes et al., 2015). Summarised detection histories (y_{ij}) were described as realisations from a binomial distribution:

$$y_{ij} \sim Binomial(p_{ij}, k_j)$$

where k_j indicates the number of temporal replicates at sampling location j.

We recognise two important assumptions of our modelling framework. The first is independence of detection between sampling occasions, and the second is independence in the observation of individuals within a sampling occasion. While the pooling of paired camera-trap units and summation of detection histories mitigates between occasion non-independence, we acknowledge that the within occasion independence assumption may be violated by gregarious species. We therefore advise caution when interpreting findings for group living species.

Model code for hierarchical multi-species Bernoulli/Poisson N-mixture model, written in the BUGS language for JAGS.

Multi-species *N*-mixture models were implemented in a Bayesian framework, specified in the BUGS language and implemented in the statistical software JAGS (Plummer, 2003). We employ uninformative priors throughout, using flat normal and wide uniform priors for slope and intercept/variance parameters respectively. Variance parameters associated with the temporal random effect were specified using a half-Cauchy distribution to account for potential variance overestimation due to few factor levels (Gelman and Hill, 2006). We ran three Markov chains of 150,000 iterations discarding an initial burn-in of 50,000 and thinned by a rate of 100. Convergence was assessed through visual inspection of trace plots and the Gelman-Rubin statistic, with values <1.1 indicating model convergence (Gelman and Rubin, 1992). Model fit was assessed using a Pearson χ^2 discrepancy measure ($\Pr(\chi^2{}_{obs} > \chi^2{}_{sim})$) and "lack of fit" statistic ($\chi^2{}_{obs}/\chi^2{}_{sim}$), where values 0.05 to 0.95 and equal to one indicate adequate model fit (Kéry and Schaub, 2011) (Table S4.1)

```
model {
# Hyper-priors for abundance and detection intercepts
#==========================================
mu.alpha1.psi ~ dnorm(0, 0.01)
sigma.alpha1.psi ~ dunif(0, 10)
tau.alpha1.psi <- pow(sigma.alpha1.psi, -2)

mu.alpha2.psi ~ dnorm(0, 0.01)
sigma.alpha2.psi ~ dunif(0, 10)
tau.alpha2.psi <- pow(sigma.alpha2.psi, -2)

for(h in 1:4){
   mu.alpha.p[h] ~ dnorm(0, 0.01)
```

```
        sigma.alpha.p[h] ~ dunif(0, 10)
        tau.alpha.p[h] <- pow(sigma.alpha.p[h], -2)
        }

    # Hyper-priors for occupancy and detection covariate coefficients
    #==========================================================
    mu.beta1.psi ~ dnorm(0, 0.01)
    sigma.beta1.psi ~ dunif(0, 10)
    tau.beta1.psi <- pow(sigma.beta1.psi, -2)

    mu.beta2.psi ~ dnorm(0, 0.01)
    sigma.beta2.psi ~ dunif(0, 10)
    tau.beta2.psi <- pow(sigma.beta2.psi, -2)

    mu.beta3.psi ~ dnorm(0, 0.01)
    sigma.beta3.psi ~ dunif(0, 10)
    tau.beta3.psi <- pow(sigma.beta3.psi, -2)

    mu.beta4.psi ~ dnorm(0, 0.01)
    sigma.beta4.psi ~ dunif(0, 10)
    tau.beta4.psi <- pow(sigma.beta4.psi, -2)

    mu.beta5.psi ~ dnorm(0, 0.01)
    sigma.beta5.psi ~ dunif(0, 10)
    tau.beta5.psi <- pow(sigma.beta5.psi, -2)

    mu.beta6.psi ~ dnorm(0, 0.01)
    sigma.beta6.psi ~ dunif(0, 10)
    tau.beta6.psi <- pow(sigma.beta6.psi, -2)

    mu.beta1.p ~ dnorm(0, 0.01)
    sigma.beta1.p ~ dunif(0, 10)
    tau.beta1.p <- pow(sigma.beta1.p, -2)

    # Hyper prior for half-Cauchy scale parameter
    xi.tau <- pow(xi.sd, -2)
    xi.sd ~ dunif(0, 10)

# Species-specific parameters drawn as realisations from the community distributions
#============================================================
=
    for(i in 1:n.sp){
        alpha1.psi[i] ~ dnorm(mu.alpha1.psi, tau.alpha1.psi)
        alpha2.psi[i] ~ dnorm(mu.alpha2.psi, tau.alpha2.psi)

        for(h in 1:4){
            alpha.p[h,i] ~ dnorm(mu.alpha.p[h], tau.alpha.p[h])
            }
```

```
    beta1.psi[i] ~ dnorm(mu.beta1.psi, tau.beta1.psi)
    beta2.psi[i] ~ dnorm(mu.beta2.psi, tau.beta2.psi)
    beta3.psi[i] ~ dnorm(mu.beta3.psi, tau.beta3.psi)
    beta4.psi[i] ~ dnorm(mu.beta4.psi, tau.beta4.psi)
    beta5.psi[i] ~ dnorm(mu.beta5.psi, tau.beta5.psi)
    beta6.psi[i] ~ dnorm(mu.beta6.psi, tau.beta6.psi)
    beta1.p[i] ~ dnorm(mu.beta1.p, tau.beta1.p)
    }

# Hyperpriors/priors for temporal random effects
#=================================
for(i in 1:n.sp) {
# Random year effects
    for(year in 1:n.year){
        eps[year, i] ~ dnorm(0, eps.tau[i])
        }
    eps.tau[i] ~ dgamma(0.5, 0.5)
    xi[i] ~ dnorm(0, xi.tau)
    sigma.cauchy[i] <- abs(xi[i]) / sqrt(eps.tau[i])
    }

# Ecological process model for abundance of species i in site j
# Continuous forest sites only
#==========================================
for(i in 1:n.sp){
    for(j in 1:CLF.sites){
        log(lambda[j,i]) <- alpha1.psi[i] + beta1.psi[i]*cov1.psi[j] +
                            beta2.psi[i]*cov2.psi[j] + xi[i]*eps[year.counter[j],i]
        N[j,i] ~ dpois(lambda[j,i])
        psi[j,i] <- step(N[j,i]-1)

        logit(r[j,i]) <- alpha.p[cov1.p[j],i] + beta1.p[i]*cov2.p[j]
        p[j,i] <- 1 - pow(1-r[j,i], N[j,i])
        y[j,i] ~ dbin(p[j,i], n.reps[j])
        }
    }

# Fragmented forest sites only
#====================
for(i in 1:n.sp){
    for(j in (CLF.sites+1):(n.sites)){
        log(lambda[j,i]) <- alpha2.psi[i] + beta1.psi[i]*cov1.psi[j] +
                            beta2.psi[i]*cov2.psi[j] + beta3.psi[i]*cov3.psi[j] +
                            beta4.psi[i]*cov4.psi[j] + beta5.psi[i]*cov5.psi[j] +
                            beta6.psi[i]*cov6.psi[j] + xi[i]*eps[year.counter[j],i]
        N[j,i] ~ dpois(lambda[j,i])
        psi[j,i] <- step(N[j,i]-1)

        logit(r[j,i]) <- alpha.p[cov1.p[j],i] + beta1.p[i]*cov2.p[j]
```

```
      p[j,i] <- 1 - pow(1-r[j,i], N[j,i])
      y[j,i] ~ dbin(p[j,i], n.reps[j])
      }
   }

# Calculate Pearson's chi-squared residuals to assess goodness of fit
# Calculate the observed (chi2.obs) and expected (chi2.exp) residuals
# Add small value to prevent division by zero
#=====================================================
for(i in 1:n.sp){
   for(j in 1:n.sites){
      y.exp[j,i] ~ dbin(p[j,i], n.reps[j])
      chi.obs[j,i] <- (y[j,i] - p[j,i] * n.reps[j]) / sqrt((p[j,i] + 0.0001) * n.reps[j] *
                        abs(1- p[j,i] - 0.0001))
      chi.exp[j,i] <- (y.exp[j,i] - p[j,i] * n.reps[j]) / sqrt((p[j,i] + 0.0001) * n.reps[j]
                        * abs(1- p[j,i] - 0.0001))
      chi2.obs[j,i] <- pow(chi.obs[j,i], 2)
      chi2.exp[j,i] <- pow(chi.exp[j,i], 2)
      }

# Calculate chi-squared discrepency for each species
#========================================
   fit.sp.obs[i] <- sum(chi2.obs[,i])
   fit.sp.exp[i] <- sum(chi2.exp[,i])
   c.hat.sp[i] <- fit.sp.obs[i]/fit.sp.exp[i]
   bpv.sp[i] <- step(fit.sp.exp[i] - fit.sp.obs[i])
   }

# Calculate overall chi-squared discrepency measure
#========================================
fit.obs <- sum(chi2.obs[1:n.sites, 1:n.sp])
fit.exp <- sum(chi2.exp[1:n.sites, 1:n.sp])
c.hat <- fit.obs/fit.exp
bpv <- step(fit.exp - fit.obs)
}
```

Table S4.1: Model fit statistics for individual species and the overall model. We present two test statistics, the "lack of fit" statistic and Bayesian *P* value, values around 1 indicate good model fit for the lack of fit statistic. Values of 0.5 indicate optimal model fit for the Bayesian *P* value while statistics less than 0.05 or greater than 0.95 indicate under- and over-fitting models respectively.

Category	Model Fit Statistic	Species	Value
Species-specific fit	Lack of fit statistic	Asian Elephant	1.00
		Banded Civet	1.12
		Banteng	1.39
		Bearded Pig	1.03
		Binturong	0.95
		Bornean Yellow Muntjac	1.23
		Common Palm Civet	1.05
		Greater Mouse-deer	1.36
		Leopard Cat	1.07
		Lesser Mouse-deer	1.64
		Long-tailed Macaque	1.39
		Long-tailed Porcupine	1.50
		Malay Civet	1.18
		Malay Porcupine	1.22
		Marbled Cat	1.15
		Masked Palm Civet	0.83
		Moon Rat	1.21
		Orangutan	0.99
		Pig-tailed Macaque	1.19
		Red Muntjac	1.22
		Sambar Deer	1.11
		Short-tailed Mongoose	1.21
		Sun Bear	1.26
		Sunda Clouded Leopard	0.91
		Sunda Pangolin	1.16
		Sunda Stink Badger	1.61
		Thick-spined Porcupine	1.59
		Tufted Ground Squirrel	1.04
		Yellow-throated Marten	1.01
	Bayesian P value	Asian Elephant	0.65
		Banded Civet	0.36
		Banteng	0.15
		Bearded Pig	0.50
		Binturong	0.66
		Bornean Yellow Muntjac	0.22
		Common Palm Civet	0.70
		Greater Mouse-deer	0.12
		Leopard Cat	0.49
		Lesser Mouse-deer	0.08

		Long-tailed Macaque	0.25
		Long-tailed Porcupine	0.13
		Malay Civet	0.31
		Malay Porcupine	0.18
		Marbled Cat	0.50
		Masked Palm Civet	0.76
		Moon Rat	0.50
		Orangutan	0.58
		Pig-tailed Macaque	0.18
		Red Muntjac	0.15
		Sambar Deer	0.33
		Short-tailed Mongoose	0.43
		Sun Bear	0.15
		Sunda Clouded Leopard	0.69
		Sunda Pangolin	0.59
		Sunda Stink Badger	0.20
		Thick-spined Porcupine	0.10
		Tufted Ground Squirrel	0.59
		Yellow-throated Marten	0.56
Overall model fit	Lack of fit statistic		1.11
	Bayesian P value		0.38

Table S4.2: Scale optimisation outputs for fragmentation, quality and hunting covariates. We determine optimal spatial-sclaes based on the lowest WAIC value, presented here in bold.

Model	**Scale**	**DIC**	**lppd**	**pD**	**WAIC**
Biomass	50	7067.66	3623.15	92.60	3808.35
	100	6908.52	3620.78	90.98	3802.75
	250	**6882.77**	**3607.24**	**89.40**	**3786.03**
	500	6880.43	3610.47	90.89	3792.25
	1000	6883.94	3621.96	90.74	3803.44
	1500	6952.12	3625.55	91.78	3809.12
	2500	6990.17	3622.11	93.56	3809.24
	5000	6969.65	3640.17	93.49	3827.14
Distance to continuous logged forest	50	3660.60	1643.59	113.09	1869.78
	100	3582.63	1654.20	101.99	1858.18
	250	3607.47	1654.91	102.36	1859.64
	500	**3613.70**	**1653.69**	**100.59**	**1854.86**
	1000	3623.14	1654.41	101.73	1857.86
	1500	3597.17	1655.49	101.02	1857.53
	2500	3540.06	1655.75	101.12	1857.99
	5000	3624.63	1660.39	99.87	1860.14
Distance to roads	50	7062.42	3627.42	94.51	3816.45
	100	7089.48	3628.23	95.13	3818.50
	250	6936.20	3627.38	95.11	3817.60
	500	6920.55	3627.94	94.44	3816.82
	1000	6897.28	3624.28	93.84	3811.97
	1500	6981.96	3627.37	93.33	3814.03
	2500	**6948.43**	**3618.01**	**95.64**	**3809.28**
	5000	6837.97	3630.24	95.13	3820.50
Distance to villages	50	7092.55	3643.14	95.34	3833.81
	100	7078.73	3642.11	94.16	3830.43
	250	7053.11	3643.12	95.92	3834.95
	500	7017.13	3644.02	94.19	3832.40
	1000	6938.98	3641.90	96.07	3834.03
	1500	7019.17	3643.07	95.64	3834.35
	2500	6939.23	3640.92	96.92	3834.77
	5000	**6875.88**	**3636.82**	**95.53**	**3827.87**
Forest cover	50	6934.52	3623.97	95.11	3814.19
	100	7099.05	3602.22	97.87	3797.96
	250	6965.47	3591.65	95.93	3783.51
	500	6901.33	3599.94	91.85	3783.64
	1000	6976.34	3594.76	92.24	3779.25
	1500	**6863.68**	**3588.16**	**94.27**	**3776.70**
	2500	6958.89	3607.13	94.17	3795.47
	5000	6920.69	3638.43	93.11	3824.65
HCS class	50	6958.209	3611.972	99.28788	3810.547
	100	6856.968	3626.993	96.04671	3819.086
	250	7091.005	3618.916	98.69391	3816.304
	500	6885.917	3628.756	93.99001	3816.736
	1000	6947.921	3646.376	90.25862	3826.894

	1500	**6921.314**	**3642.42**	**83.32021**	**3809.06**
	2500	6928.466	3714.251	76.27908	3866.81
	5000	7318.008	3767.166	73.58192	3914.33
Hunting Pressure	50	6826.40	3618.54	94.46	3807.46
	100	6918.47	3619.62	94.84	3809.30
	250	**6952.19**	**3614.49**	**94.08**	**3802.66**
	500	6922.27	3622.08	92.42	3806.91
	1000	7039.11	3619.76	95.35	3810.46
	1500	6867.57	3618.84	94.08	3807.01
	2500	6950.36	3627.85	93.85	3815.55
	5000	6953.00	3636.60	94.17	3824.95
Population density	50	7064.62	3645.59	90.22	3826.02
	100	6979.68	3651.67	90.55	3832.78
	250	6867.11	3646.11	90.65	3827.41
	500	6923.30	3637.30	93.19	3823.68
	1000	**6976.54**	**3626.67**	**93.56**	**3813.79**
	1500	6902.97	3629.71	92.56	3814.84
	2500	6910.16	3631.10	91.47	3814.03
	5000	6988.24	3636.51	91.60	3819.72

Table S4.3: Mammal life-history characteristics and group assignment. Details of group assignment for modelling guild responses to fragmentation, forest quality and hunting pressure. We classify a species as threatened if it has an IUCN red-list status of vulnerable (VU), endangered (EN) or Critically Endangered (CR). Species were considered non-threatened if they were associated with a least concern (LC) or Neat-threatened (NT) status. Ecological specialism was determined by information provided in (Wilson et al., 2010). We define three body classes based on body mass information derived from the PanTHERIA database (Jones et al., 2009): medium- (<5 kg), large- (5-25 kg) and mega-bodied (>25 kg).

Common Name	**IUCN Status**	**Conservation Status**	**Ecological Specialism**	**Body Size**	**Trophic Guild**
Asian elephant *Elephas maximus*	EN	Threatened	Specialist	Large	Herbivore
Banded civet *Hemigalus derbyanus*	VU	Threatened	Specialist	Small	Insectivore
Banteng *Bos javanicus*	EN	Threatened	Specialist	Large	Herbivore
Bearded pig *Sus barbatus*	VU	Threatened	Generalist	Large	Omnivore
Binturong *Arctictis binturong*	VU	Threatened	Specialist	Medium	Frugivore
Bornean yellow muntjac *Muntiacus atherodes*	LC	Non-threatened	Specialist	Medium	Herbivore
Common palm civet *Paradoxurus hermaphroditus*	LC	Non-threatened	Generalist	Small	Frugivore
Greater mouse-deer *Tragulus napu*	LC	Non-threatened	Specialist	Small	Frugivore
Leopard cat *Prionailurus bengalensis*	LC	Non-threatened	Generalist	Small	Carnivore
Lesser mouse-deer *Tragulus kanchil*	LC	Non-threatened	Specialist	Small	Frugivore
Long-tailed macaque *Macaca fascicularis*	LC	Non-threatened	Generalist	Small	Frugivore
Long-tailed porcupine *Trichys fasciculata*	LC	Non-threatened	Generalist	Small	Frugivore
Malay civet *Viverra tangalunga*	LC	Non-threatened	Generalist	Medium	Carnivore
Malay porcupine *Hystrix brachyura*	LC	Non-threatened	Generalist	Medium	Frugivore
Marbled cat *Pardofelis marmorata*	VU	Threatened	Specialist	Small	Carnivore
Masked palm civet *Paguma larvata*	LC	Non-threatened	Generalist	Small	Frugivore
Moon rat *Echinosorex gymnura*	LC	Non-threatened	Specialist	Small	Insectivore
Orangutan *Pongo pygmaeus*	EN	Threatened	Specialist	Large	Frugivore
Pig-tailed macaque *Macaca nemestrina*	VU	Threatened	Generalist	Medium	Frugivore
Red muntjac	LC	Non-threatened	Generalist	Medium	Herbivore

Muntiacus muntjak					
Sambar deer *Rusa unicolor*	VU	Threatened	Specialist	Large	Herbivore
Short-tailed mongoose *Herpestes brachyurus*	LC	Non-threatened	Generalist	Small	Carnivore
Sun bear *Helarctos malayanus*	VU	Threatened	Specialist	Large	Omnivore
Sunda clouded leopard *Neofelis nebulosa*	VU	Threatened	Specialist	Medium	Carnivore
Sunda pangolin *Manis javanica*	CR	Threatened	Generalist	Small	Insectivore
Sunda stink badger *Mydaus javanensis*	LC	Non-threatened	Generalist	Small	Insectivore
Thick-spined porcupine *Hystrix crassispinis*	LC	Non-threatened	Generalist	Small	Frugivore
Tufted ground squirrel *Rheithrosciurus macrotis*	VU	Threatened	Specialist	Small	Frugivore
Yellow-throated marten *Martes flavigula*	LC	Non-threatened	Generalist	Small	Carnivore

Figure S4.2: Species-specific effects of fragmentation, quality and hunting metrics on mammal abundance. This plots provide species-specific compliments to the community-level trends presented in Fig 4.3. Effect sizes are presented as posterior means (points) and 95% Bayesian credible intervals (BCI). Effects were considered substantial if the 95% BCI did not overlap zero (vertical black dashed line). Responsive species are presented in blue.

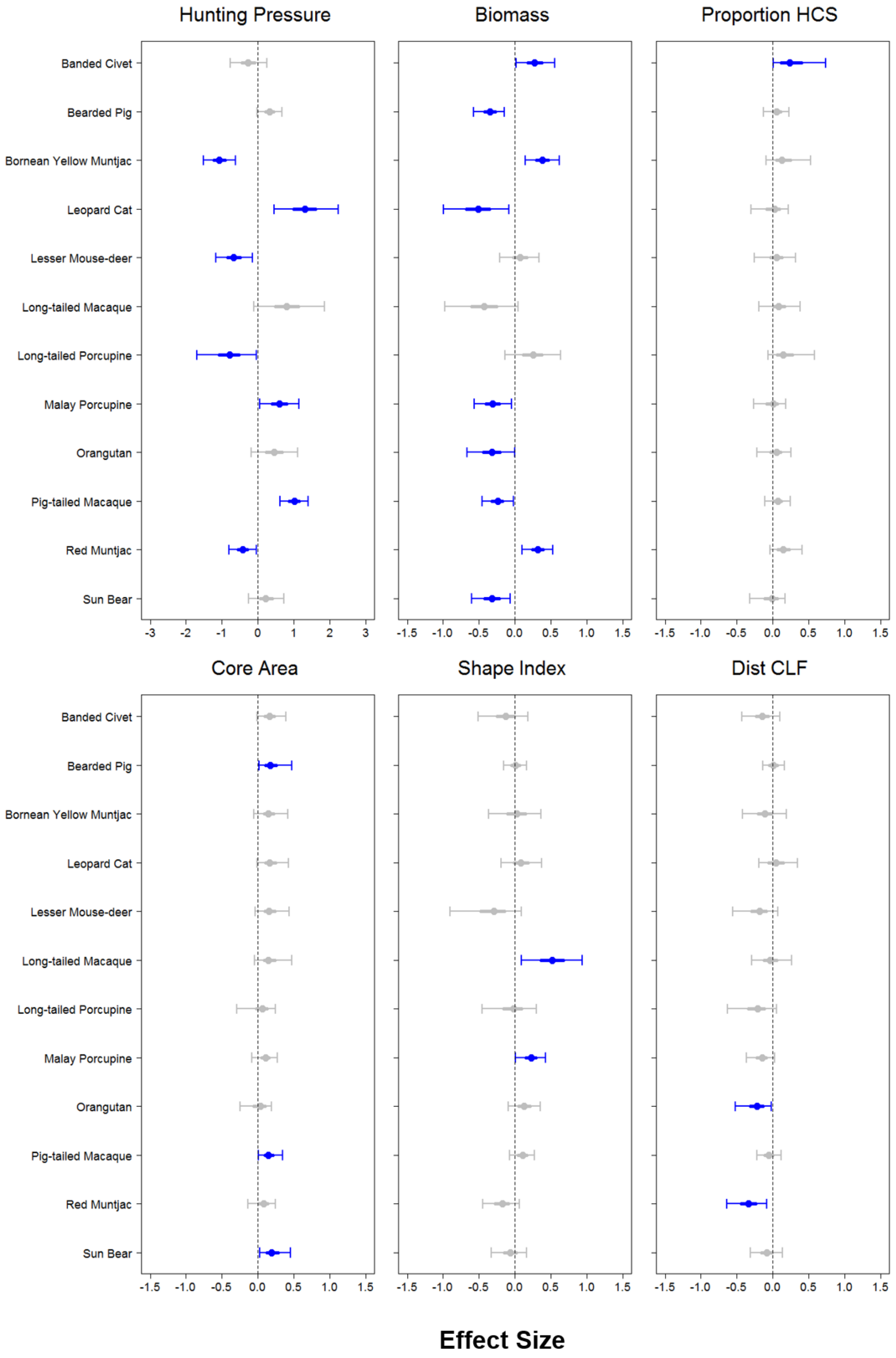
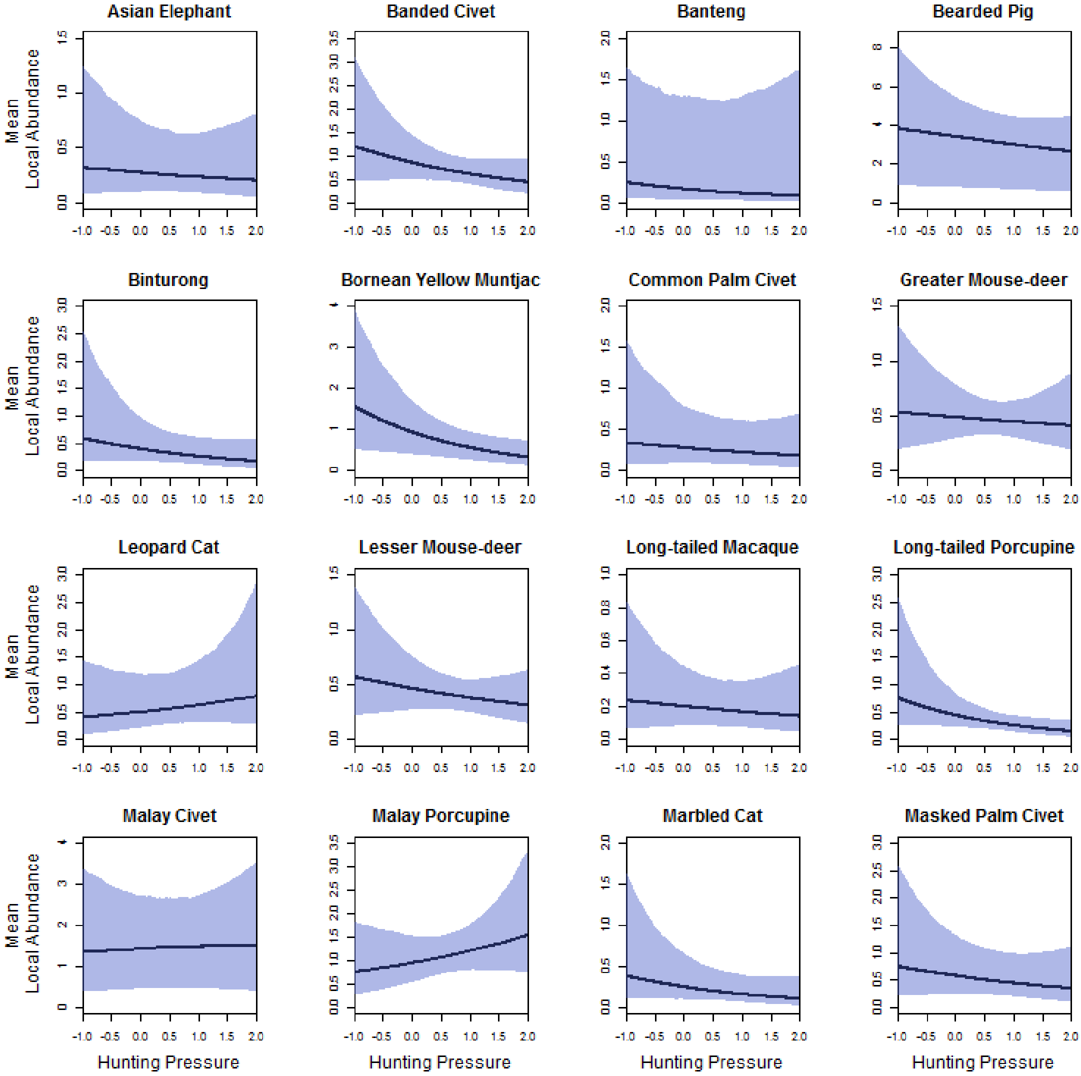

Hunting Pressure
Biomass
Proportion HCS
Core Area
Shape Index
Dist CLF
Banded Civet
Bearded Pig
Bornean Yellow Muntjac
Leopard Cat
Lesser Mouse-deer
Long-tailed Macaque
Long-tailed Porcupine
Malay Porcupine
Orangutan
Pig-tailed Macaque
Red Muntjac
Sun Bear
-3
-2
-1
0
1
2
3
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
Effect Size

Figure S4.3: Numerical response of mammals to hunting pressure. We present outputs for the 29 species of mammal encountered during sampling. Predicted mean posterior distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals, is visualised in light blue.



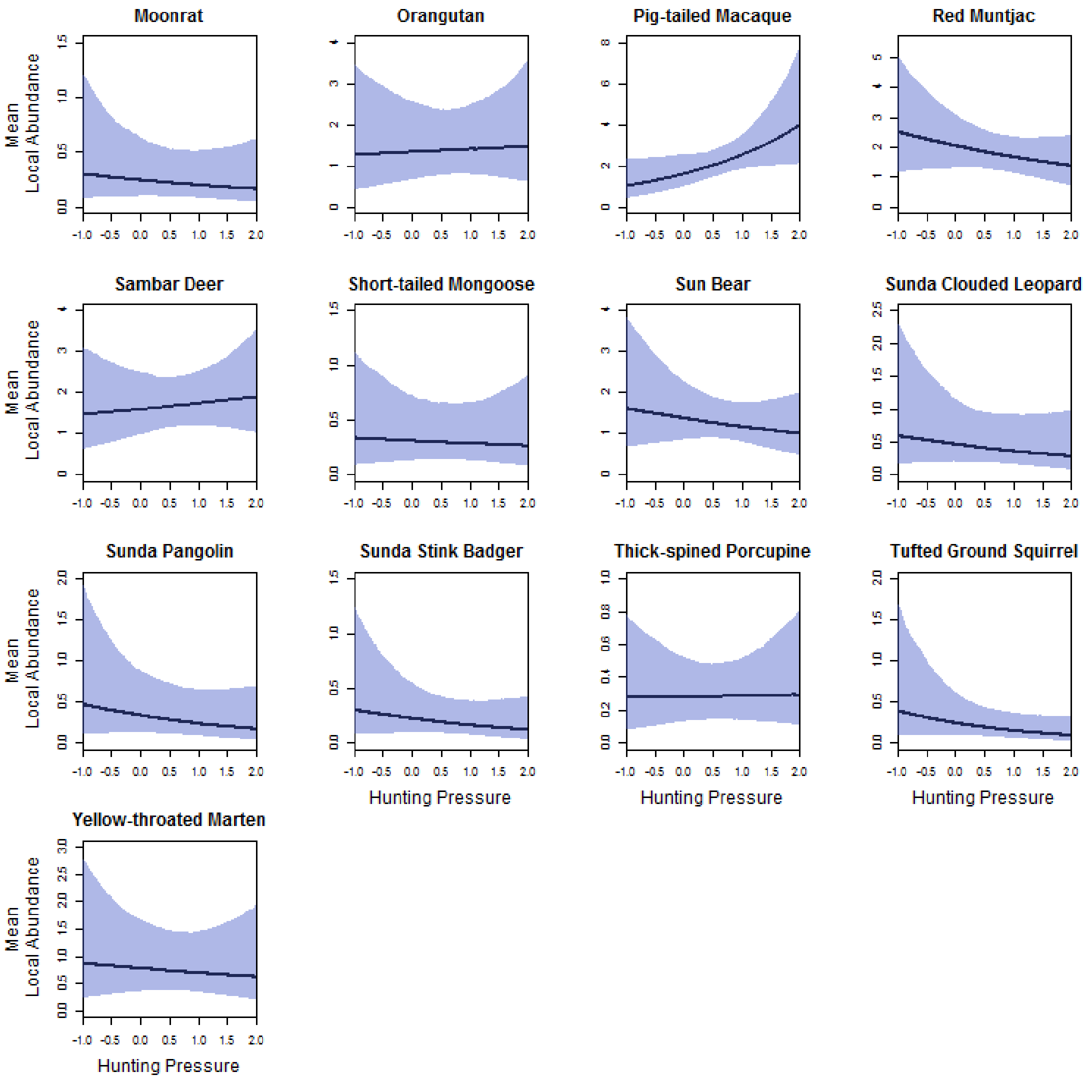
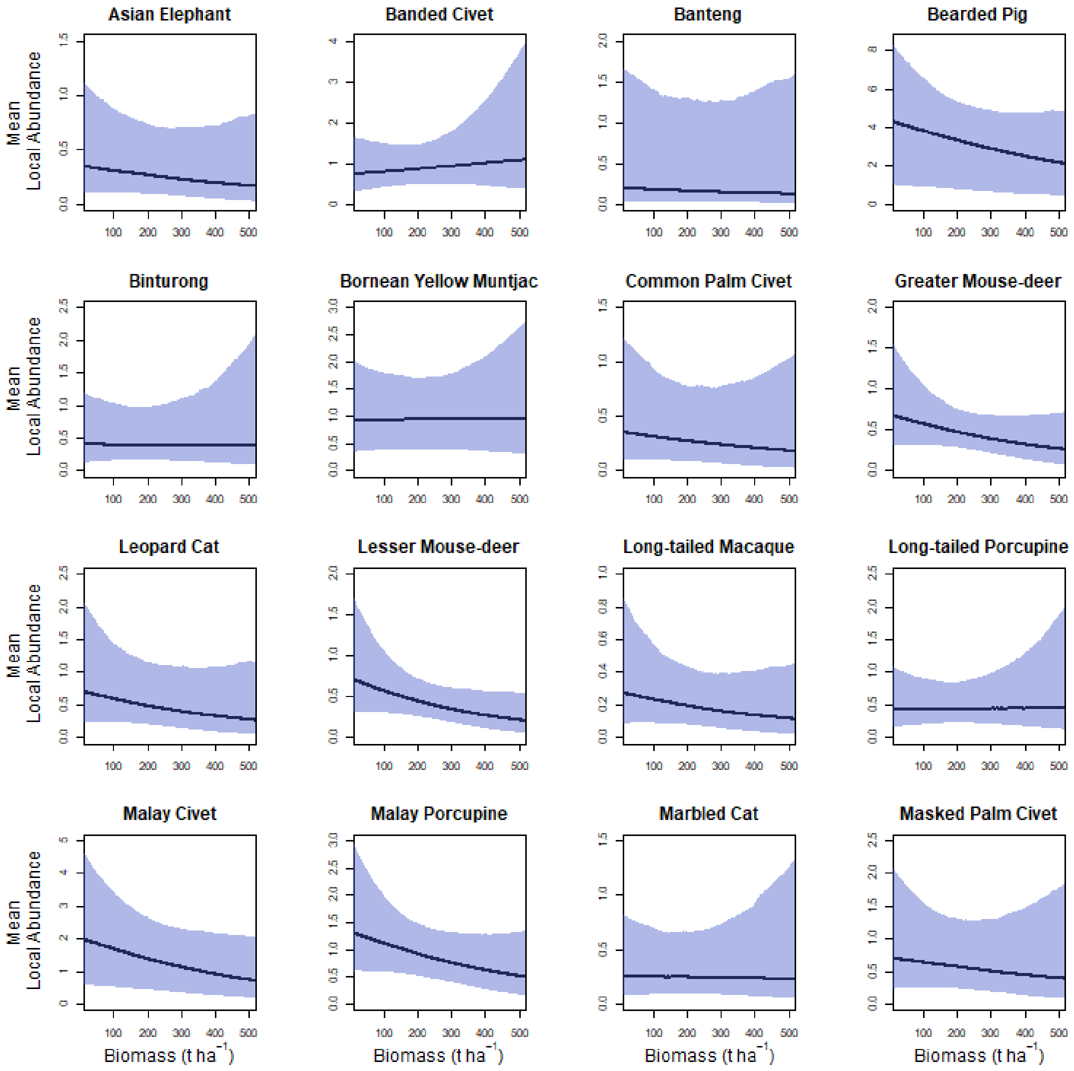

Moonrat
Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Mean
Local Abundance
Hunting Pressure
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
1
2
3
4
5
6
8
0.2
0.4
0.6
0.8

Figure S4.4: Numerical response of mammals to biomass (t ha^{-1}). We present outputs for the 29 species of mammal encountered during sampling. Predicted mean posterior distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals, is visualised in light blue.



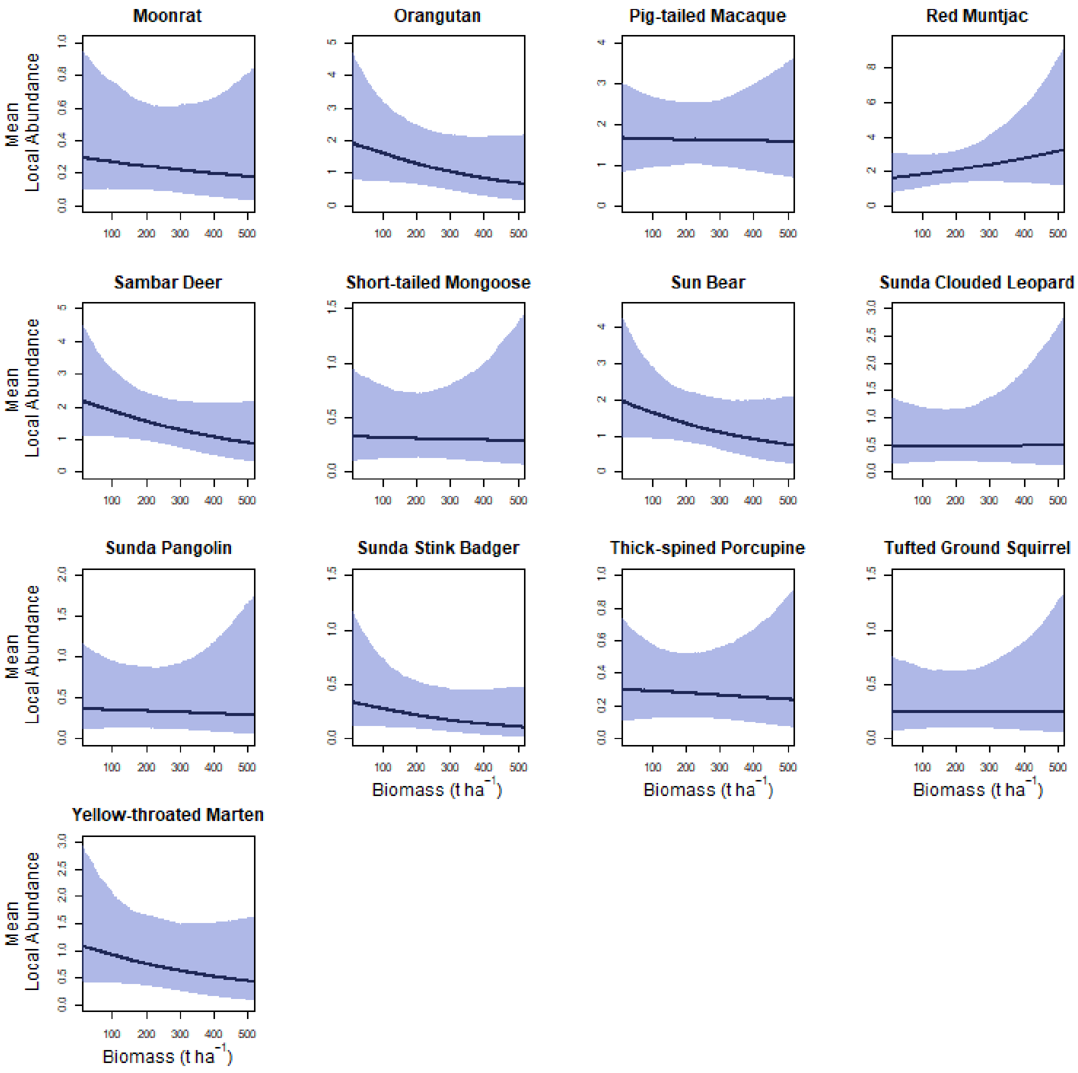
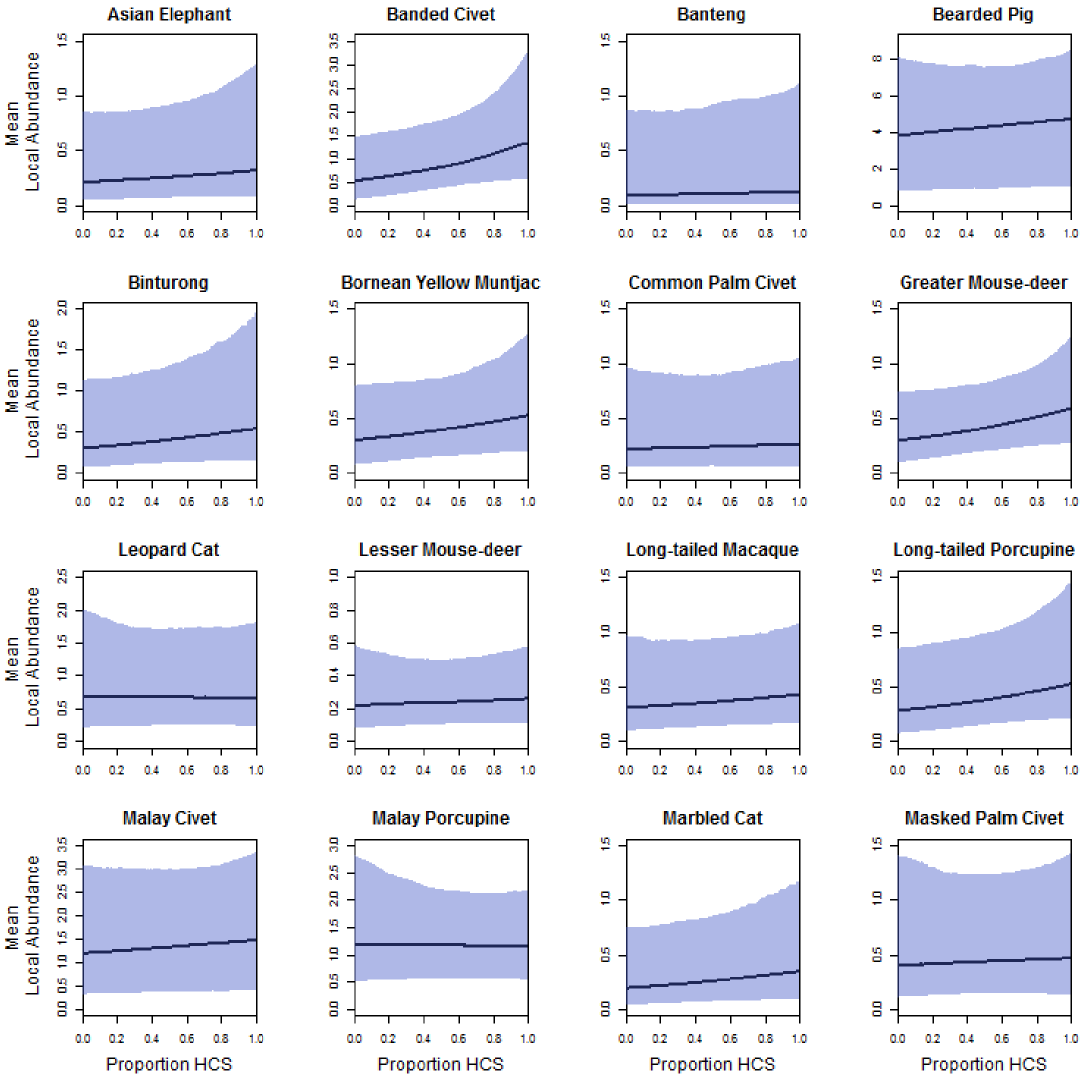

Moonrat
Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Mean
Local Abundance
100 200 300 400 500
Biomass (t ha^{-1})

Figure S4.5: Numerical response of mammals to patch-scale forest quality. We define patch scale forest quality according to HCS methods as the proportion of HCS-delineated forest within a forest fragment. We present outputs for the 29 species of mammal encountered during sampling Predicted mean posterior distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals, is visualised in light blue.



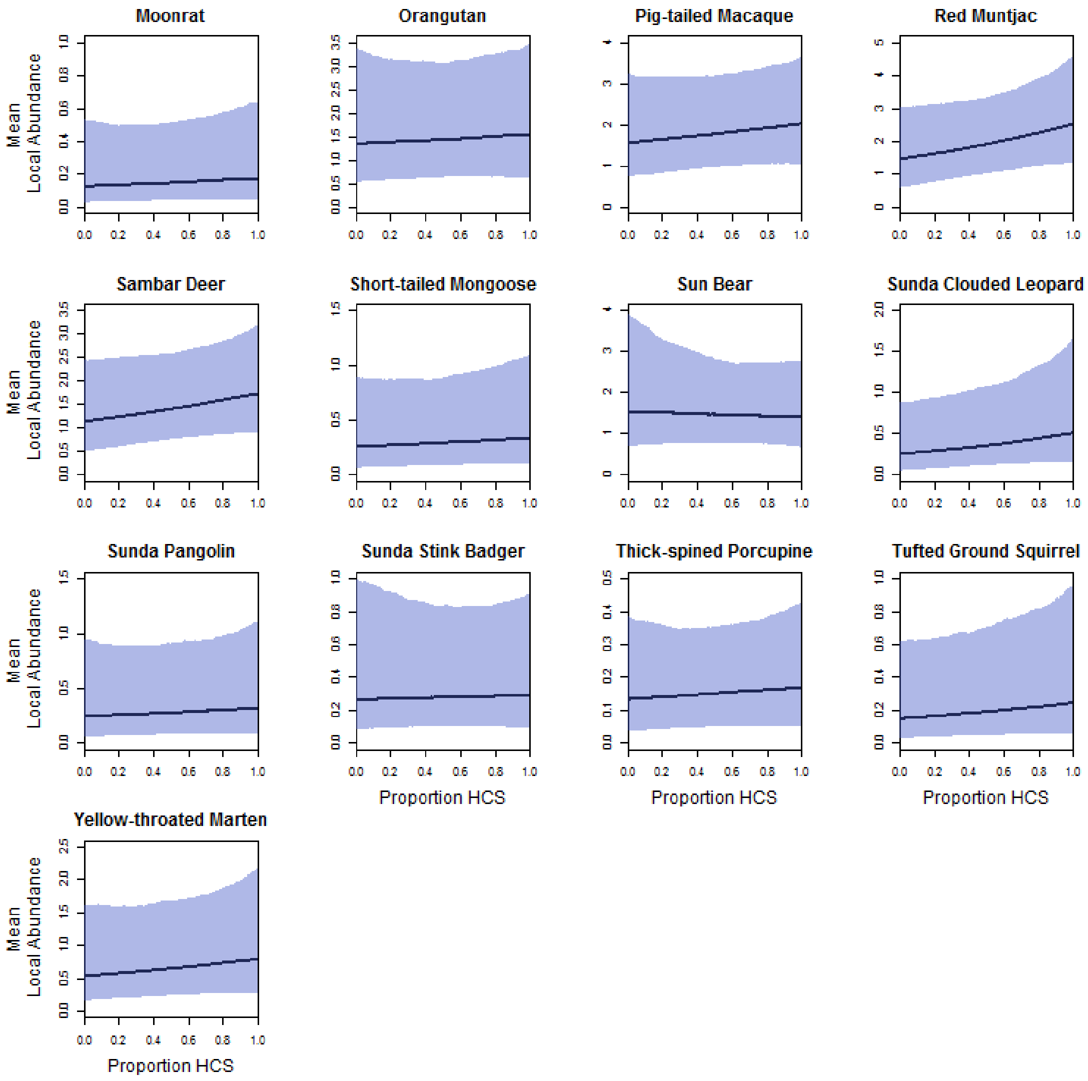
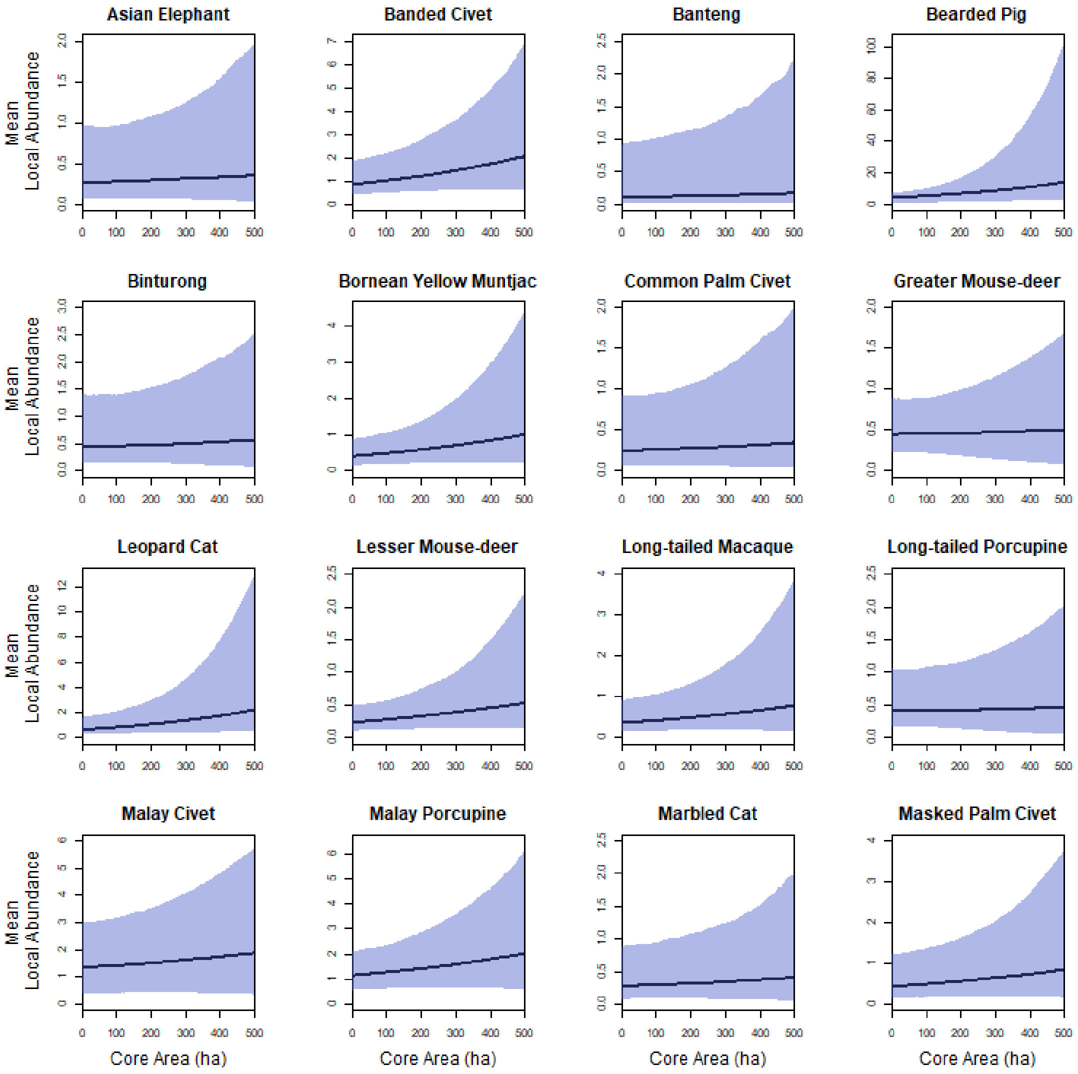

Moonrat
Mean
Local Abundance
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
Orangutan
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
0.0 0.2 0.4 0.6 0.8 1.0
Pig-tailed Macaque
0 1 2 3 4
0.0 0.2 0.4 0.6 0.8 1.0
Red Muntjac
0 1 2 3 4 5
0.0 0.2 0.4 0.6 0.8 1.0
Sambar Deer
Mean
Local Abundance
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
0.0 0.2 0.4 0.6 0.8 1.0
Short-tailed Mongoose
0.0 0.5 1.0 1.5
0.0 0.2 0.4 0.6 0.8 1.0
Sun Bear
0 1 2 3 4
0.0 0.2 0.4 0.6 0.8 1.0
Sunda Clouded Leopard
0.0 0.5 1.0 1.5 2.0
0.0 0.2 0.4 0.6 0.8 1.0
Sunda Pangolin
Mean
Local Abundance
0.0 0.5 1.0 1.5
0.0 0.2 0.4 0.6 0.8 1.0
Sunda Stink Badger
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
Proportion HCS
Thick-spined Porcupine
0.0 0.1 0.2 0.3 0.4 0.5
0.0 0.2 0.4 0.6 0.8 1.0
Proportion HCS
Tufted Ground Squirrel
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
Proportion HCS
Yellow-throated Marten
Mean
Local Abundance
0.0 0.5 1.0 1.5 2.0 2.5
0.0 0.2 0.4 0.6 0.8 1.0
Proportion HCS

Figure S4.6: Numerical response of mammals to fragment core are (ha). We present outputs for the 29 species of mammal encountered during sampling. Predicted mean posterior distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals, is visualised in light blue.



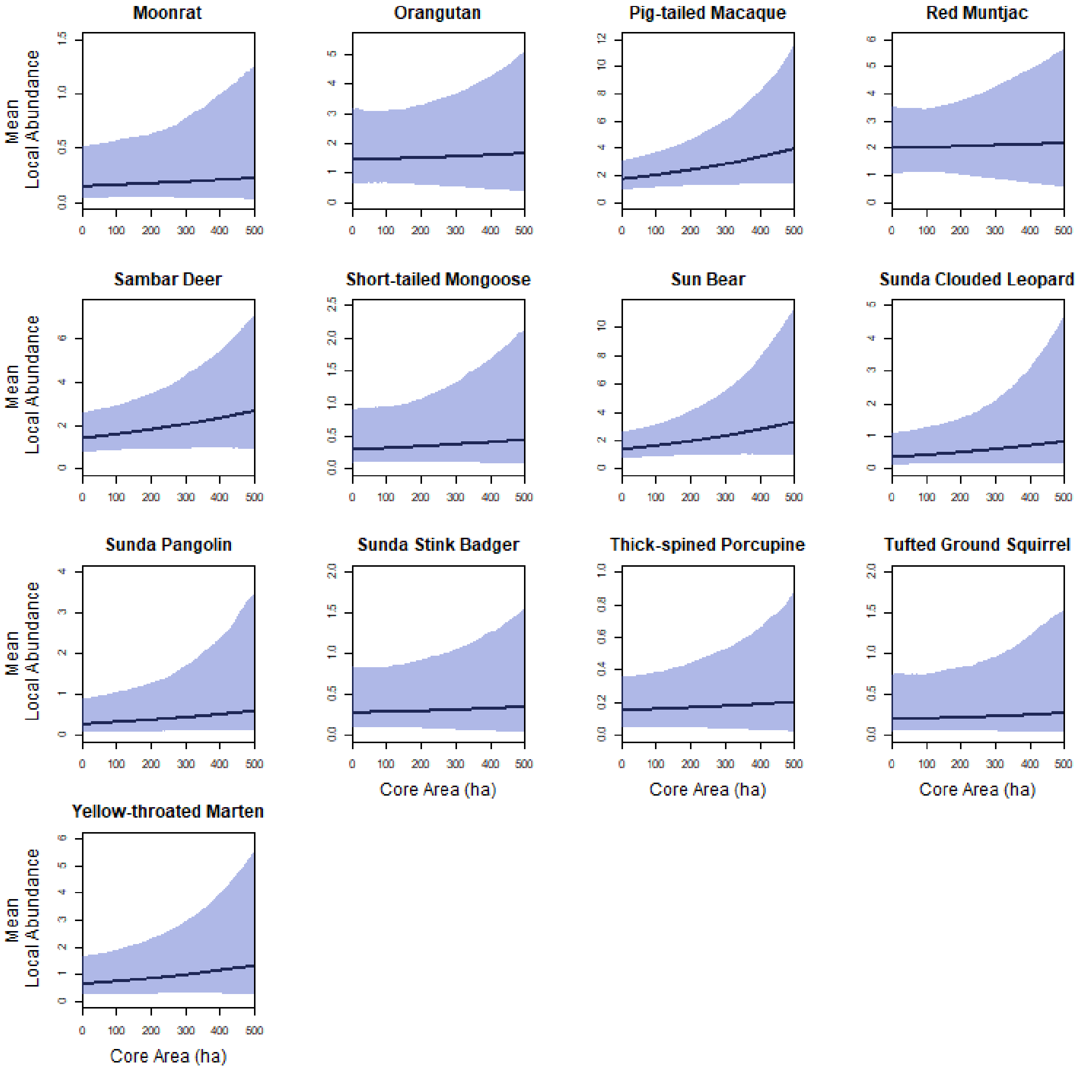
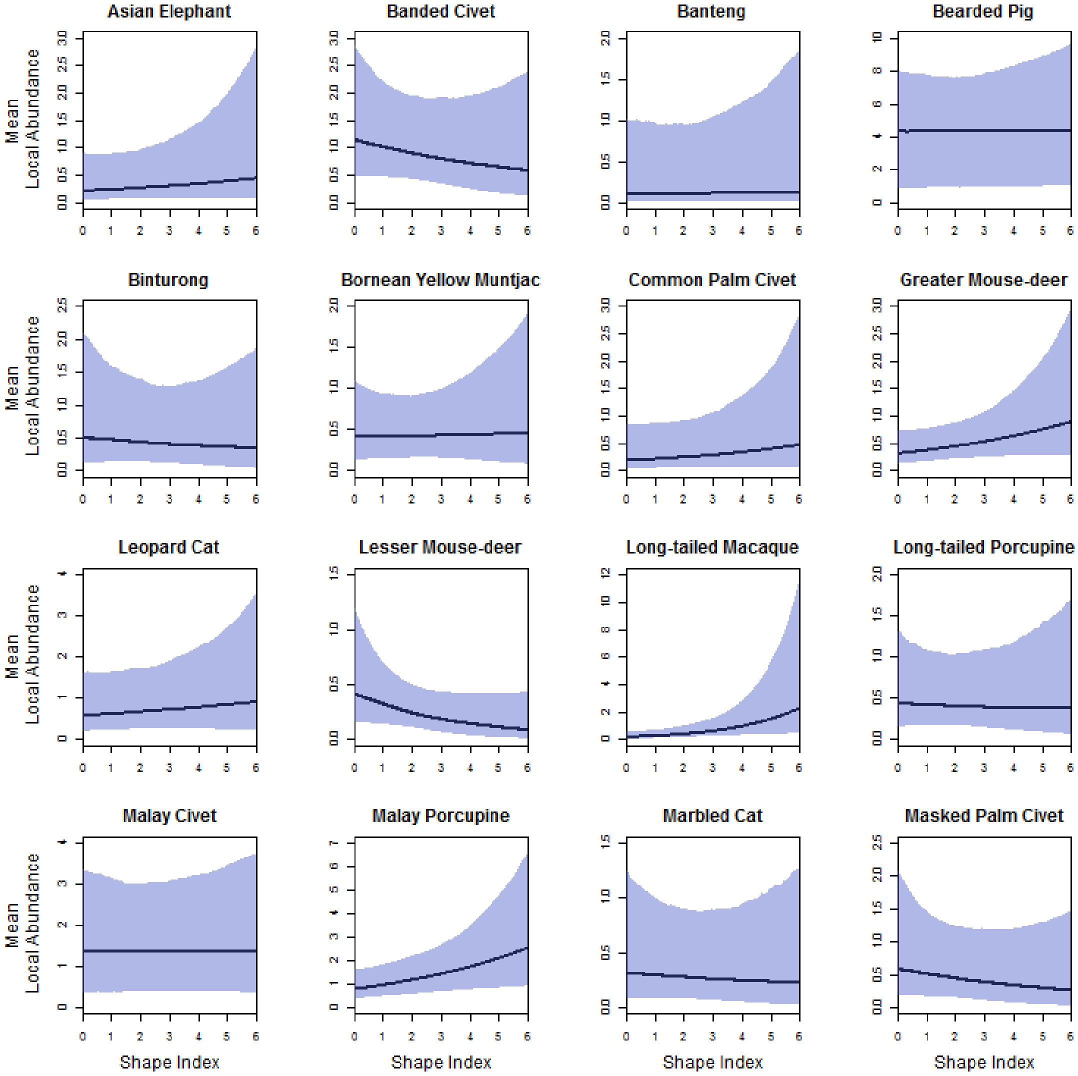

Moonrat
Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Mean
Local Abundance
Core Area (ha)
0
100
200
300
400
500
0.0
0.5
1.0
1.5
2.0
2.5
0
1
2
3
4
5
6
8
10
12
0.2
0.4
0.6
0.8

Figure S4.7: Numerical response of mammals to patch shape. We present outputs for the 29 species of mammal encountered during sampling. Predicted mean posterior distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals, is visualised in light blue.



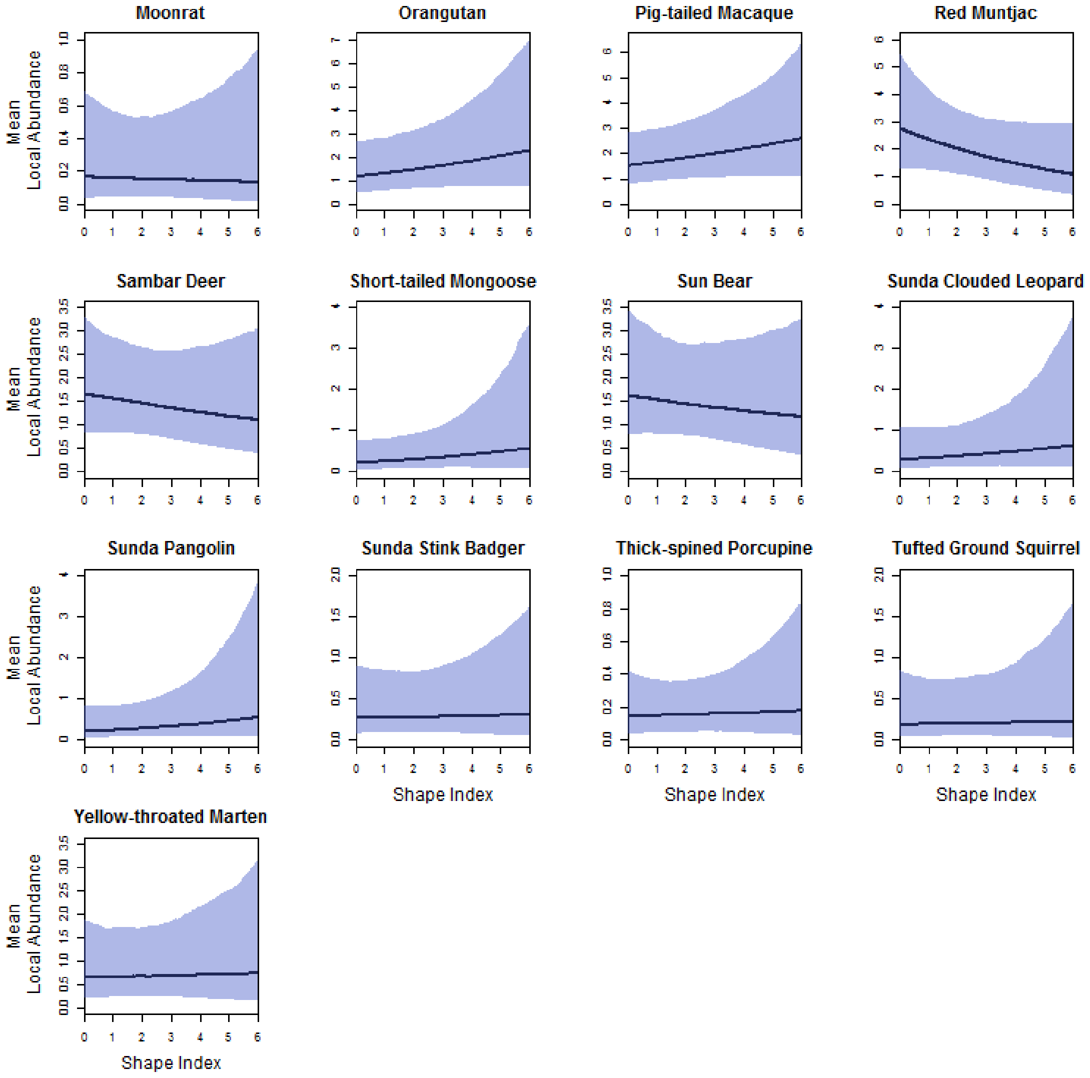
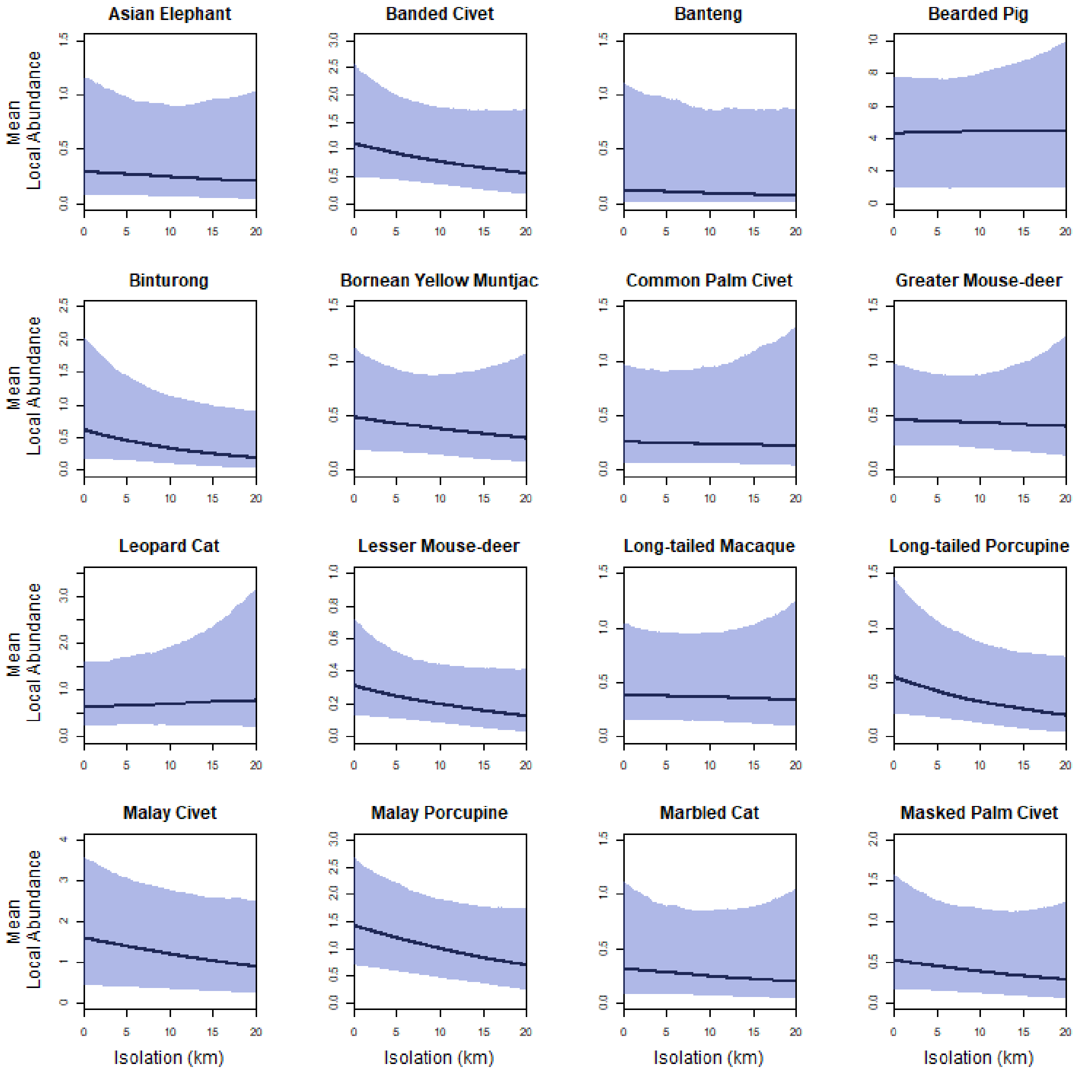

Moonrat
Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Mean
Local Abundance
Shape Index
0 1 2 3 4 5 6
0.0 0.2 0.4 0.6 0.8 1.0
0 1 2 3 4 5 6 7
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
0 1 2 3 4
0.0 0.5 1.0 1.5 2.0

Figure S4.8: Numerical response of mammals to isolation (km). We define isolation as distance in kilometres, from continuous (>50,000 ha). We present outputs for the 29 species of mammal encountered during sampling. Predicted mean posterior distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals, is visualised in light blue.



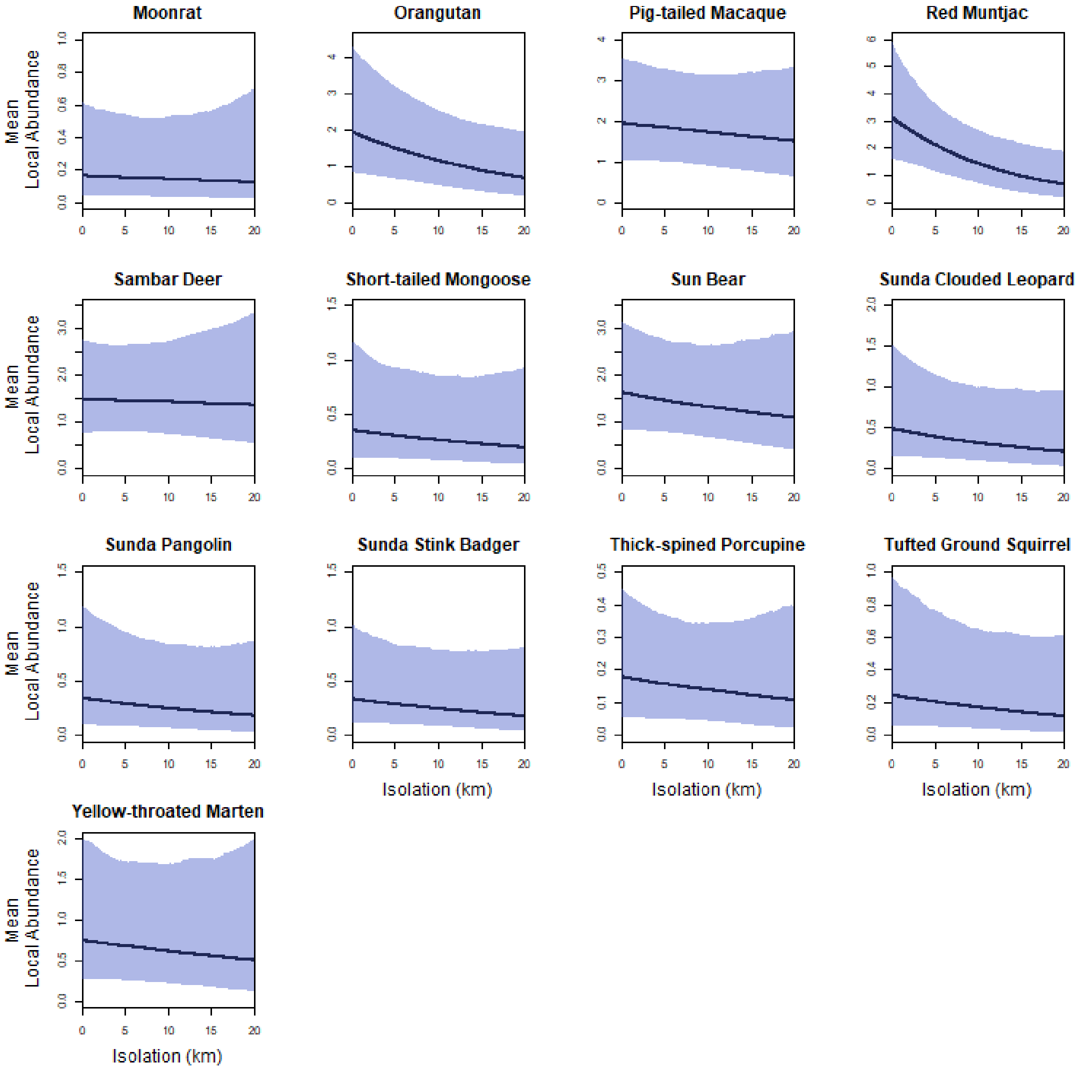
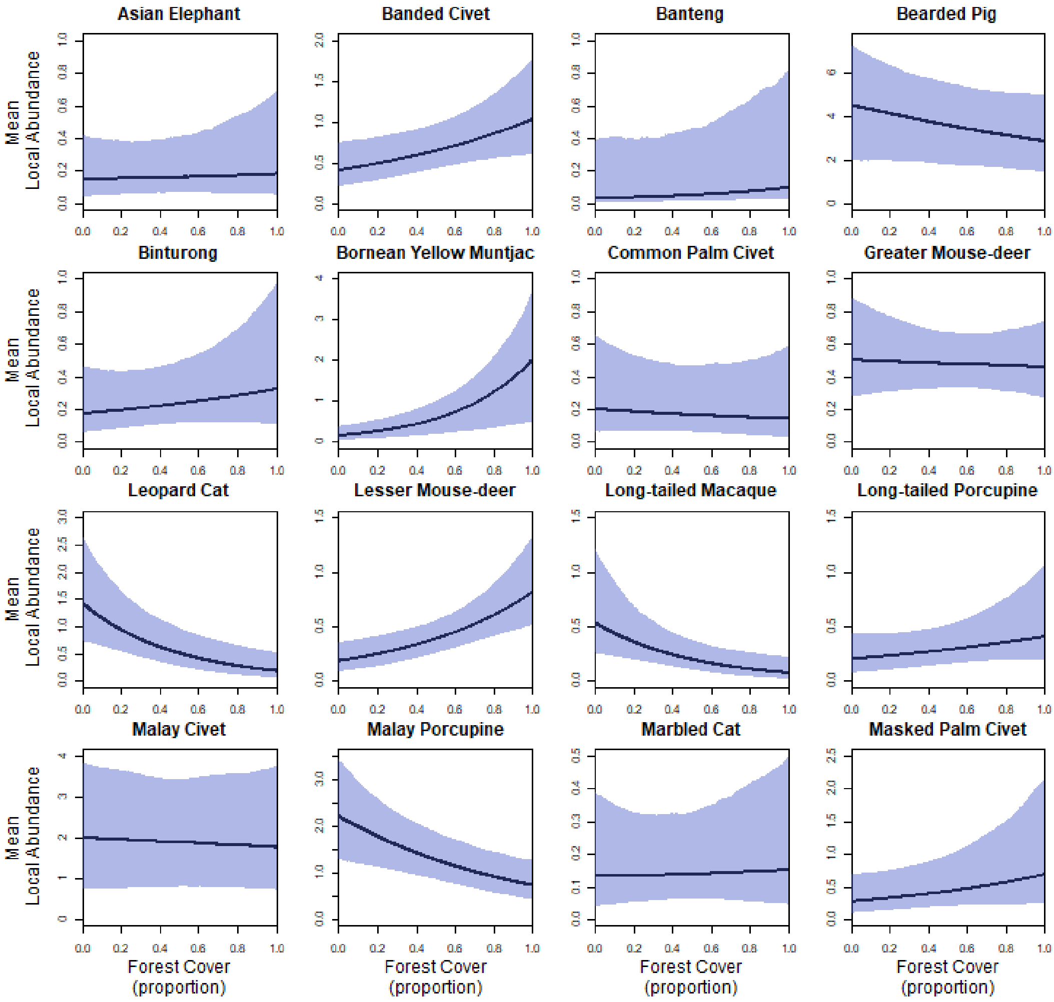

Moonrat
Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Mean
Local Abundance
Isolation (km)
0
5
10
15
20
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
4
5
6
0.0
0.5
1.0
1.5
2.0
3.0
0.1
0.3

Figure S4.9: Numerical response of mammals to the proportion of forest cover. We present outputs for the 29 species of mammal encountered during sampling. Predicted mean posterior distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals, is visualised in light blue.



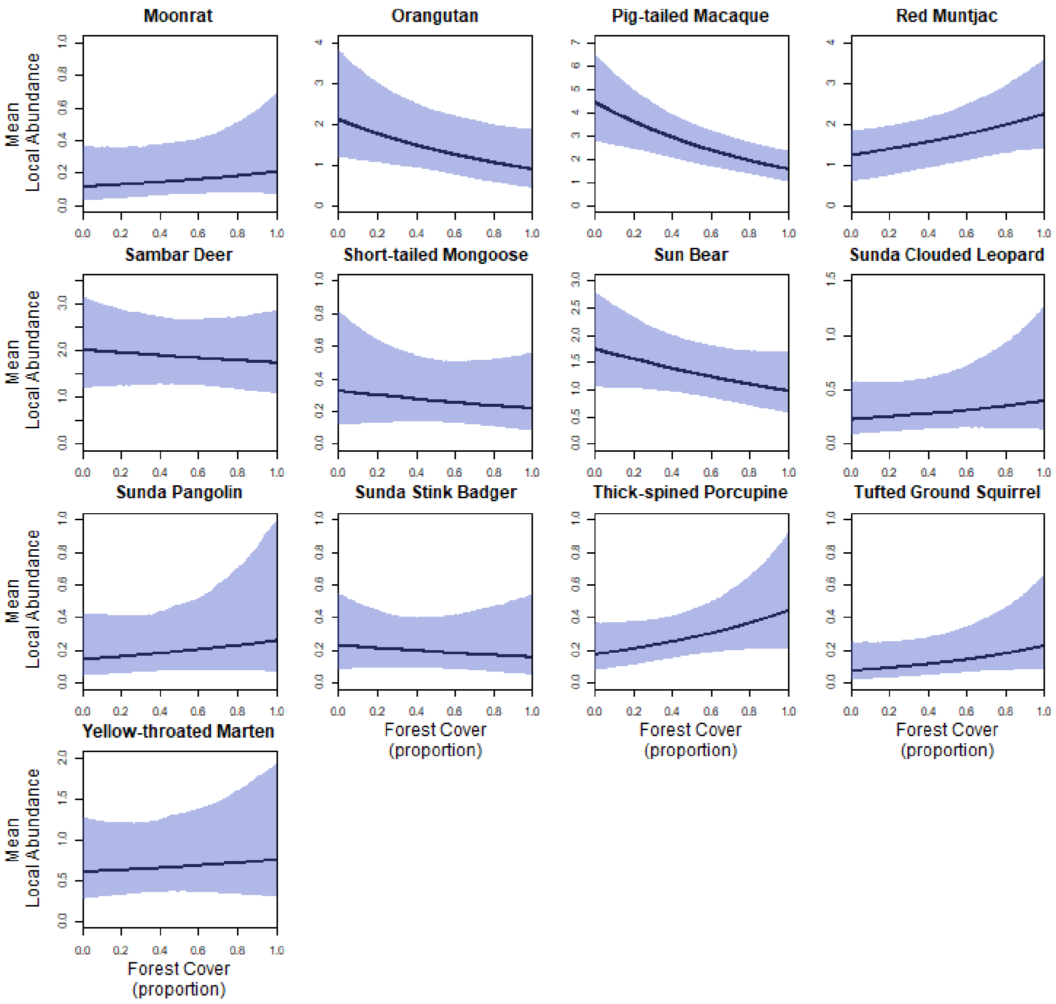
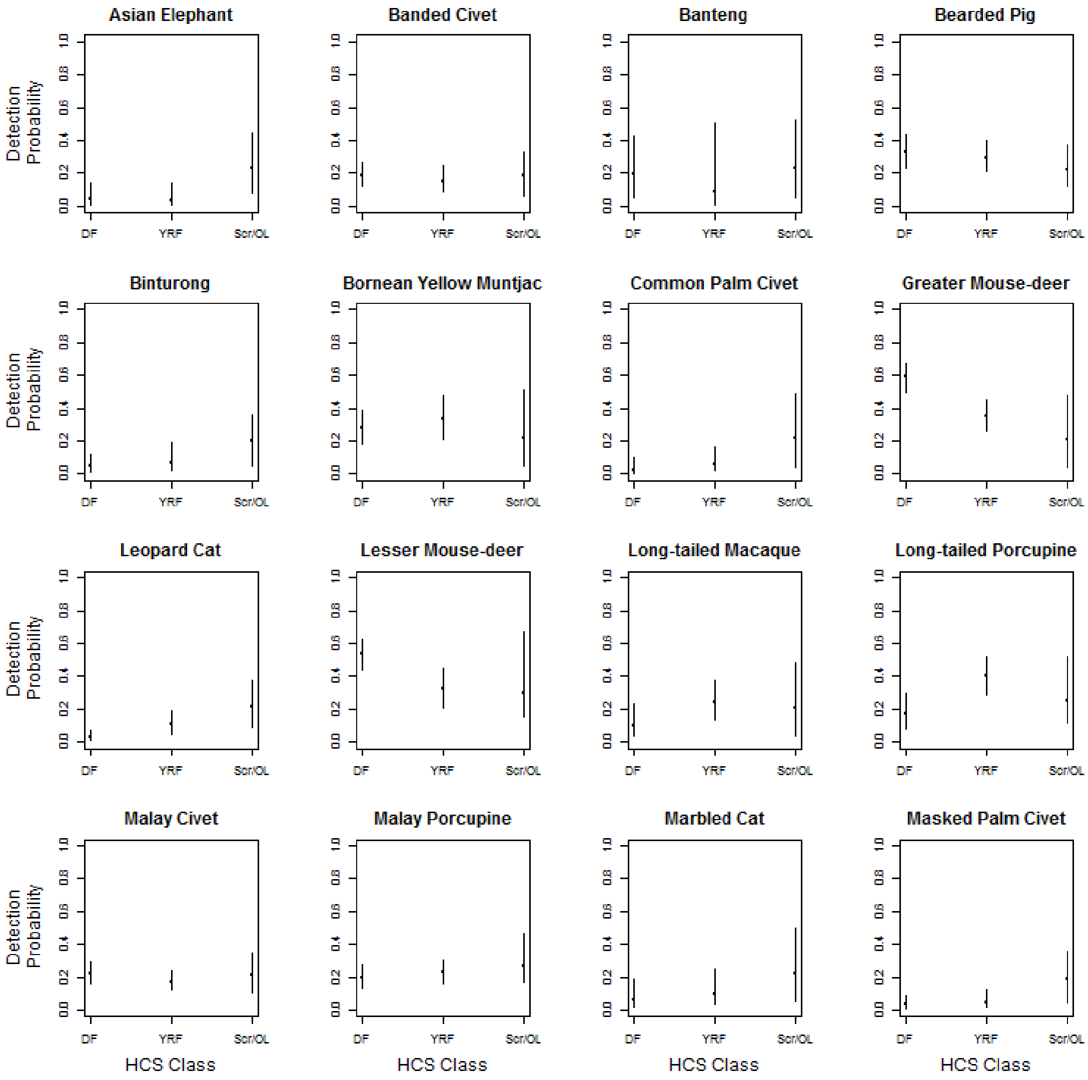

Moonrat
Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Mean
Local Abundance
Forest Cover
(proportion)
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
4
5
6
7
0.5
1.5
2.0
2.5
3.0

Figure S4.10: Influence of habitat type on mammal detectability. We define habitat type as a function of carbon using HCS phase one protocols (dense forest; >75 t C ha-1; young regenerating forest: 35-75 t C ha-1; non-forest habitat: 0-15 t C ha-1; Rosoman, 2017). We present outputs for the 29 species of mammal encountered during sampling.Predicted mean posterior distribution values are presented as points, while uncertainty, as indicated using 95% Bayesian credible intervals, is visualised using vertical lines.



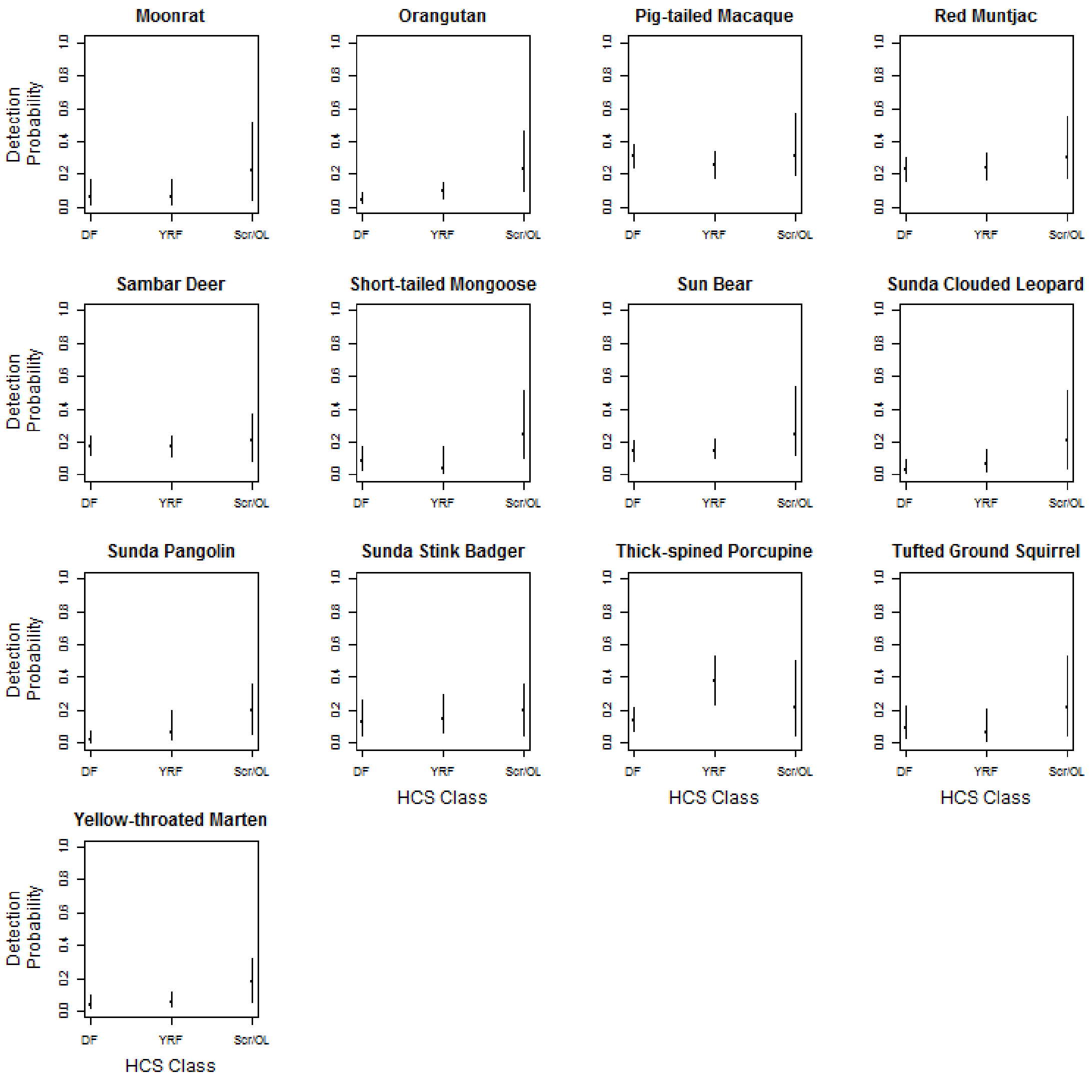
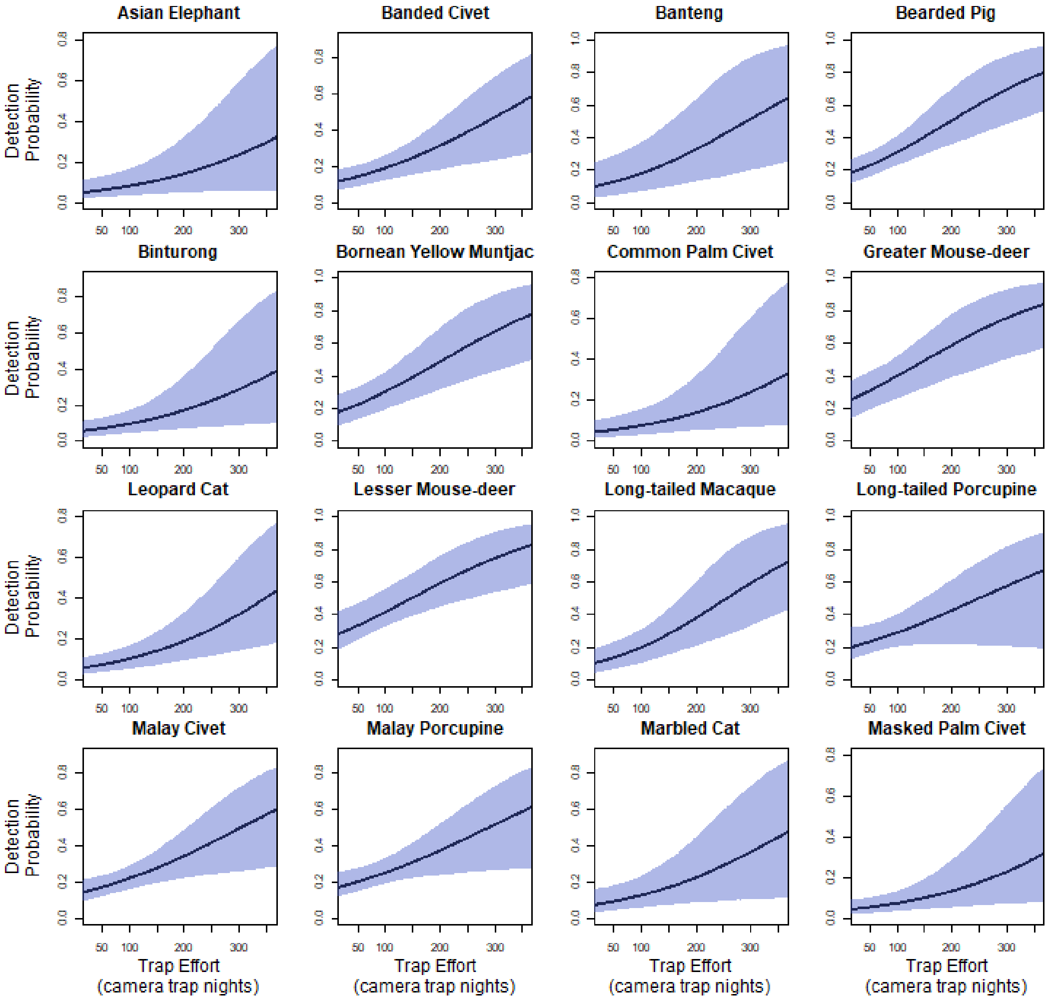
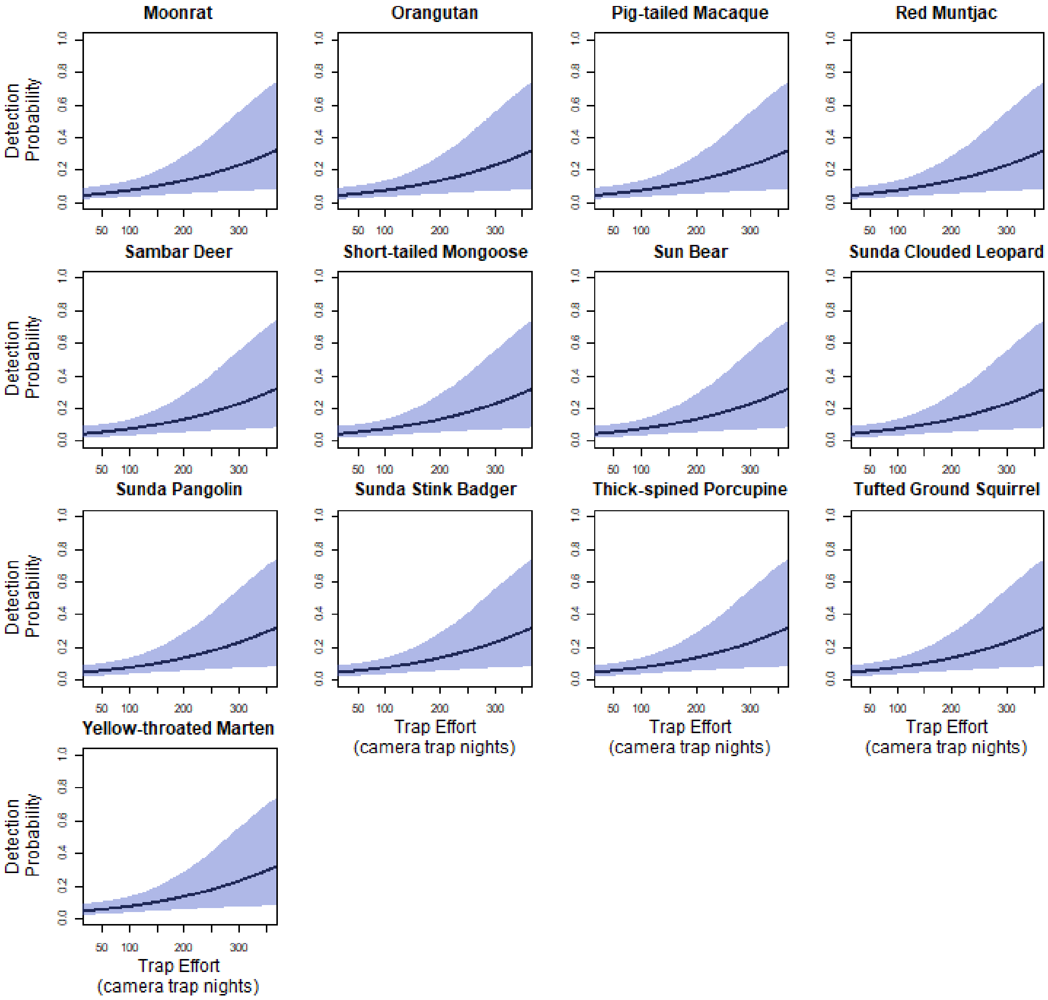

Moonrat
Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Detection Probability
0.0
0.2
0.4
0.6
0.8
1.0
DF
YRF
Scr/OL
HCS Class

Figure S4.11: Influence of survey effort on detection. We define survey effort as the number of camera-trap nights units were operational. We present outputs for the 29 mammal species encountered during sampling Predicted mean posterior distribution values are presented in dark blue, while uncertainty, as indicated using 95% Bayesian credible intervals, is visualised in light blue.




Moonrat
Orangutan
Pig-tailed Macaque
Red Muntjac
Sambar Deer
Short-tailed Mongoose
Sun Bear
Sunda Clouded Leopard
Sunda Pangolin
Sunda Stink Badger
Thick-spined Porcupine
Tufted Ground Squirrel
Yellow-throated Marten
Detection Probability
0.0
0.2
0.4
0.6
0.8
1.0
50
100
200
300
Trap Effort
(camera trap nights)

Chapter 5. Discussion

This thesis explored the ecological consequences of land-use change on medium-large terrestrial mammals in Southeast Asia, a region characterised by unsustainable levels of anthropogenic habitat modification. While providing a valuable evidence-base on the determinants of occurrence, abundance and species richness of little-known tropical mammals, this research demonstrates the efficacy of remote technologies and contemporary statistical innovations to monitor and assess threatened and cryptic species, which would otherwise prove intractable. Collectively, this evidence can be practically applied to inform environmental policies and local management strategies that recognise the value of human-modified landscapes in biodiversity conservation efforts in the tropics.

Mammal ecology in human-modified landscapes

Effective environmental governance in the tropics is frequently compromised by a paucity of biodiversity data due to financial restrictions and logistical constraints (Balmford et al., 2005, Gardner et al., 2008, Lawton et al., 1998). These data deficiencies often necessitate broad geographic extrapolations of biodiversity information based on geographically restricted subsets of focal taxa, which runs the risk of purporting false ecological narratives and misleading conservation paradigms (Gardner et al., 2009). Consequently, primary, locally-specific biodiversity data are essential to develop an understanding of the capacity for modified systems to support viable populations of species and guide management actions that promote biodiversity persistence (Balmford et al., 2005). This is fundamental for many tropical mammal species, which are often poorly represented in protected area networks (Crooks et al., 2017), and have inherent ecological characteristics that make them vulnerable to anthropogenic habitat modification (Hughes, 2017, Keinath et al., 2017, Newbold et al., 2014). This thesis addressed these shortcomings by developing an evidence-base, derived from primary data, of mammalian diversity in a highly threatened tropical region. The results of **Chapters 2-4** indicate that mammal persistence in human-modified landscapes follows an established trajectory of declining occurrence, abundance and species richness when habitat structural complexity is eroded (Barlow et al., 2007, Edwards et al., 2014, Gibson et al., 2011). Mammal diversity declines along a gradient of land-use intensity (Burivalova et al., 2014, Wearn et al., 2017), which could in part be ameliorated by retaining and maintaining natural features that facilitate ecological processes and resource acquisition (Ewers and Didham, 2006).

At the species-level, I identify winners and losers of anthropogenic land-use change, confirming the tendency towards biotic homogenization in human-modified landscapes (Tabarelli et al., 2012). Ecological generalists with broad dietary niches, particularly bearded pigs (*Sus barbatus*) and pig-tailed macaques (*Macaca nemestrina*) (Plumptre and Johns, 2001, Wong et al., 2005), dominated structurally impoverished, disturbed environments (supporting earlier work by Brodie and Giordano, 2013, Brodie et al., 2015a, Granados et al., 2016), often displacing obligate forest species, which were infrequently detected as land-use intensity increased. This response may be mediated by trophic release, which refers to an increase in prey abundance following the extirpation of predators (Terborgh et al., 2001). The apex predator in the system, the Sunda clouded leopard (*Neofelis diardi*), was restricted to infrequent, sporadic encounters in structurally impoverished habitats, indicating a negative correlation with bearded pig and pig-tailed macaque occurrence. Formal testing of co-occurrence patterns to substantiate this claim was beyond the scope of my modelling framework, thus my explanation is merely speculative and in contrast to previous findings (Brodie and Giordano, 2013).

My findings provide novel ecological insights into Southeast Asian mammals that can be used to inform targeted conservation campaigns. For example, much of the limited ecological information on the Sunda clouded leopard has been derived from anecdotal evidence (Rabinowitz et al., 1987), captive specimens, and chance encounters (Hearn et al., 2013, Matsuda et al., 2008). While intensive monitoring efforts are contributing to conservation assessments of this species (Hearn et al., 2016, Hearn et al., 2013, Macdonald et al., 2018, Sollmann et al., 2014, Wilting et al., 2012), documented habitat associations are limited to elevational preferences and a tendency towards areas of high forest cover (Hearn et al., 2018a, Hearn et al., 2018b). My work in **Chapter 2** has extended this body of evidence considerably by identifying the specific structural features of forest cover associated with Sunda clouded leopard occurrence. These insights represent a refined appreciation of habitat preference that can directly inform the designation of conservation priority areas for a wide-ranging, conservation priority species. Moreover, **Chapter 2** provided the first documented habitat associations for the cryptic tufted ground squirrel (*Rheithrosciurus macrotis*) and uncovered valuable ecological associations for a number of cryptic taxa, including the binturong (*Arctictis binturong*) and marbled cat (*Pardofelis marmorata*).

My findings also demonstrate potential complications arising from aggregating indistinguishable ungulate species into a single analytical unit. I document diverging habitat associations for mouse-deer- (*Tragulus* sp.) and, to a lesser extent, muntjac species (*Muntiacus* sp.), which are frequently lumped into genera-level designations as they have been difficult to distinguish in camera images (Brodie and Giordano, 2013, Brodie et al., 2015a, Brodie et al., 2015b). This aggregation masks important differences in habitat selection for the various species, which, without recognition, could result in unintended recommendations for conservation management. Consequently, I advocate stringent taxonomic identification and caution against indiscriminate aggregation.

The extent to which my findings can inform biodiversity provisions in human-modified landscapes at regional, national and pan-tropical scales remains open to question. The sensitivity of biodiversity to habitat modification has been shown to be scale-dependent, idiosyncratic and contextual (de Andrade et al., 2014, Gardner et al., 2009, Lindenmayer and Likens, 2011). Consequently, cross taxonomic congruence represents the exception rather than the rule (de Andrade et al., 2014, Gardner et al., 2008, Yong et al., 2016). For mammals in particular, wide-ranging behaviour and long generation times may give a false impression as to the conservation value of human-modified landscapes due to spill-over effects or extinction debts (Koh, 2008, Wearn et al., 2012). Moreover, considerable structural and taxonomic differences in vegetation within and between tropical biogeographic realms limits the spatial transferability of findings (Deikumah et al., 2014, Lewis et al., 2015, Slik et al., 2018). While this thesis makes a valid contribution to the understanding of mammal ecology across the human-modified landscapes of Southeast Asia, understanding the broader ecological significance of these systems must be built on coordinated regional research to inform global strategies while accounting for biogeographic nuances.

Despite the substantial scientific advances made by this thesis, there remains some uncertainty in our understanding as to how arboreal mammals respond to landscape change. Tropical forests are inherently three-dimensional environments that accommodate greater species diversity through vertical partitioning of niche space (Corlett and Primack, 2011, Oliveira and Scheffers, 2018). Arboreality is an evolutionary adaptation to structural complexity facilitating access to canopy resources and microclimatic conditions (Scheffers et al., 2013, Scheffers et al., 2017). It is estimated that 75% of forest-dwelling vertebrates demonstrate some degree of arboreality (Kays and Allison, 2001), yet multidimensionality is rarely accounted for in conservation assessments of tropical ecosystems due to methodological constraints associated with sampling canopy elements (Whitworth et al., 2016). Throughout this thesis, I excluded exclusively arboreal species from assessment as they cannot be reliably monitored using terrestrial methods. Arboreal camera-trapping has emerged as a reliable method to quantify the arboreal community (Bowler et al., 2017, Malhi et al., 2014, Whitworth et al., 2016), though applications to assess the impact of human modification on vertically-stratified mammal communities are lacking. Given that arboreality is an adaptation to the structural environment and anthropogenic habitat modification directly disrupts canopy elements, arboreal mammals are likely to be disproportionately affected by human disturbance. Assessments that embrace methodological advances to determine prospects for arboreal mammals in human-modified landscapes are a clear research priority in tropical forests.

Technological considerations for biodiversity monitoring

Monitoring of threatened species and ecosystems is still hindered by technological and logistical challenges, resulting in a disparity between the required scale of conservation effort and the accessibility of ecological data (Fraser et al., 2013). This thesis demonstrates how remote technologies can be applied to circumvent sampling issues associated with rare or cryptic species and develop unprecedented insights into biodiversity patterns and processes at scales appropriate to conservation management. This is particularly evident in **Chapter 2** which combined camera-traps and airborne multispectral remote-sensing (LiDAR) to quantify the three-dimensional properties of tropical forests across multiple spatial scales to inform the conservation management of a high conservation priority species. The analytical framework presented in this chapter could have practical applications for Southeast Asian conservation policy. Recent proposals by the Sabah government to increase protected area coverage by 5%, coupled with the state-wide availability of LiDAR data (Asner et al., 2018), provides an unparalleled opportunity to mobilise a collaborative network of camera-trap data and fully integrate biodiversity considerations into the conservation agenda. Moreover, the launch of NASAs Global Ecosystem Dynamics Investigation (GEDI; https://gedi.umd.edu/), promises to increase the scope of LiDAR coverage to global scales. Capitalising on these developments could greatly enhance the limited ecological understanding of mammals across a pantropical gradient of forest modification. At a broader scale, achieving ambitious global conservation objectives through practical application of remote technologies is dependent upon explicit recognition of current limitations.

The use of camera-trap methods to monitor wildlife has grown exponentially over the last decade, with applications doubling across three year intervals (Burton et al., 2015). Conservative estimates suggest that up to 20,000 localities are currently being sampled using camera-traps (Burton et al., 2015, Steenweg et al., 2017), providing the scope and scale necessary to address global conservation challenges. However, such aspirations are hindered by poorly coordinated research effort and a reluctance to collaborate, which results in fragmented data developed from contrasting methodologies that can be challenging to incorporate into a cohesive analytical framework to inform broader management objectives (Meek et al., 2014). To match the extent of data available through remote-sensing, biodiversity monitoring requires a paradigm shift from disparate, localised assessment to up-scaled, integrated global monitoring (Steenweg et al., 2017). The Tropical Ecology and Assessment Monitoring Network (TEAM; Jansen et al., 2014) demonstrates the value of concerted camera-trap efforts to address a range of environmental concerns at scales that can support regional and global conservation targets (Ahumada et al., 2011, Beaudrot et al., 2016b, Rovero and Ahumada, 2017, Rovero et al., 2014). Consequently, camera-trap biodiversity monitoring should strive for globally standardised protocols to facilitate collaborative research between regional and international actors (Steenweg et al., 2017).

The proliferation of remote-sensing has afforded ecologists and conservation practitioners a mechanism to expand their spatio-temporal scope of inference, unveiling patterns and processes that had previously proved elusive (Marvin et al., 2016). However, the expense, and accessibility of remotely-sensed data products limits their widespread application in ecology and management. For example, while this thesis has demonstrated the value of LiDAR, the associated financial costs may prove financially prohibitive, particularly for conservation initiatives that typically operate under budgetary restrictions (Hummel et al., 2011, McCarthy et al., 2012). Associated costs extend much further than data acquisition, logistical requirements for data analysis also represent a significant financial outlay (Pettorelli et al., 2014, Turner et al., 2015). Moreover, data accessibility, referring to the capacity to retrieve and manipulate ecologically-relevant metrics from remote-sensing data, is hindered by limitations in distribution strategy, software availability and the technological proficiency of end users (Turner, 2014). For developing tropical nations with limited capacity, partnerships with existing operators and academic institutions may represent the only feasible option to mobilise remotely-sensed data products, thus sacrificing a degree of autonomy over environmental decision making. To this end, I advocate the availability of free/low-cost, pre-processed data on user-friendly online platforms to prevent the proliferation of technological colonialism creeping into the conservation agenda.

Statistical considerations for evidence-based mammal conservation

Previously, evidence-based conservation has proved challenging for rare and cryptic species due to insufficient records for reliable statistical inference. This thesis demonstrates that hierarchical modelling provides an analytical compliment to remote technologies to increase statistical precision for species most vulnerable to land-use change. However, interpretation of my outputs should be informed by an explicit understanding of the principal caveat of my underlying modelling framework. The aggregation of data at the community-level, shifts species-specific parameter estimates towards the community mean, thus environmental impacts may be understated for species with few detections (Broms et al., 2016). Pacifici et al. (2014) highlighted that species-specific parameter estimates were strongly influenced by how species were grouped within the community-level component of the model; while community aggregation provided the most precise estimates, alternative classifications, based on dietary specialisation or body size, offered unique insights into species responses to ecological covariates. While the precision of parameter estimates was of overarching importance in this thesis, I acknowledge that some species-specific effects may have been overlooked as a result of the grouping criteria adopted.

From a broader perspective, this thesis highlights the value of Bayesian statistical methods for applied ecological assessment, environmental decision making and conservation management. The hierarchical modelling procedures I adopted are analytically intractable within a classical framework (Dorazio et al., 2011), thus Bayesian methods provide an important statistical tool to overcome sampling constraints associated with monitoring tropical mammals. Moreover, Bayesian methods provide an intuitive expression of confidence in derived quantities, allowing conservation practitioners and policy-makers to account for uncertainty in management actions and environmental decisions (Ellison, 2004). Bayesian frameworks also follow the principles of adaptive management by seeking to integrate uncertainty and current knowledge of a system into an iterative process in order to continuously inform, modify and strengthen interventions (Ellison, 1996). In the context of long-term ecological monitoring, the outputs presented throughout this thesis can be incorporated as prior information into future assessments of biodiversity trends in human-modified landscape to reduce uncertainty and develop robust management and policy recommendations.

Policy options for biodiversity in human-modified landscapes

Protected areas are considered integral to global conservation strategies (Gaston et al., 2008, Laurance et al., 2012). However, 90% of the world's terrestrial surface area falls beyond the bounds of formal protected status, with the distributions of 20% of all threatened species demonstrating little spatial overlap with the reserve network (Rodrigues et al., 2004). Throughout **Chapters 2-4** I have demonstrated the sensitivity of tropical mammals to anthropogenic land-use designations, thus persistence will ultimately be determined by the effectiveness of environmental policies in making human-modified landscapes more hospitable to biodiversity. Reflecting on conclusions drawn from this thesis, I elaborate on potential applications of interventions and discuss barriers to implementation.

Capitalising on the conservation value of logged forests

Logged forests comprise a significant proportion of the remaining forest estate, thus mobilising their inherent conservation potential is fundamental to securing biodiversity persistence in the tropics. However, identifying which logged forests to prioritise for conservation is challenging given limited conservation budgets. To optimise conservation spending, interventions must be targeted to where they will have the greatest impact. The results presented in **Chapter 2** emphasize that logged forests that retain structural characteristics of old growth forests could be optimal areas for conservation interventions as they represent preferential habitat for high conservation value species. Across my study site these areas corresponded to lightly logged forests where timber extraction has been less severe, though, at a broader scale, these could encompass sustainably managed forests. It has been proposed that high conservation value forests in logged areas provide a cost-effective option to expand and connect the existing protected area network or delineate new reserves (Fisher et al., 2011b, Giam et al., 2011, Struebig et al., 2015). Complementing the reserve network with a mosaic of protected logged forests increases the capacity of landscapes to support viable populations of mobile, wide-ranging mammal populations (Meijaard and Sheil, 2008, Struebig et al., 2015). Studies suggest that logged forests retain 76% of their carbon stocks and sequester carbon at five times the rate of undisturbed forest (Berry et al., 2010, Putz et al., 2012), indicating that this strategy will also feed into climate change mitigation. Moreover, integrating logged forests within a protectionist strategy is financially self-sustaining, generating income and job opportunities, which would offset some of the economic drivers of land-use change and garner local support for conservation (Gaveau et al., 2013). Given that the conservation value of logged forests is likely to increase as they recover, integrating logged forests into the conservation agenda can be viewed as a long-term investment to maintain populations of obligate forest species (Fisher et al., 2011b, Meijaard and Sheil, 2008).

Averting the agricultural conversion of heavily degraded forests is paramount to enhancing species representation at landscape- and regional scales. Heavily degraded forests retain up to 75% of their biodiversity (Edwards et al., 2011, Struebig et al., 2013), yet reductions in the standing value of timber mean they can be procured at a modest cost (US$2,010 ha-1; Fisher et al., 2011b). In heavily degraded forests subjected to sustained extraction and secondary disturbance impacts, ecological restoration may be required to reinstate biodiversity values, prevent a permanent state shift, and improve human well-being in adjacent lands (Chazdon and Guariguata, 2016, Wilson et al., 2011). It is estimated that 130 million ha of forest may be amenable to rehabilitation in Southeast Asia alone, indicating considerable scope for restoration efforts (Kettle, 2010). Consequently, there is an urgent need to direct restoration to regions with the highest likelihood of success (Chazdon and Guariguata, 2016, Budiharta et al., 2014a). Within **Chapter 2** of this thesis, I delineate priority restoration areas as those with compromised structural integrity exhibiting the highest rate of change in species occurence, indicating that management actions that enhance the structural environment will optimise biodiversity outcomes. Enrichment planting, is considered a cost-effective approach to landscape-level forest restoration that can be achieved at 30% of the price of restoring fully degraded land while providing employment for local people (Chazdon, 2008, Kettle, 2010, Lamb, 1998). However, regional restoration efforts have been hindered by limited technical capacity to propagate dipterocarp trees and impediments posed by their challenging reproductive ecology (Kettle, 2010). Moreover, even low-cost restoration projects may require long-term financial and political support to achieve desired outcomes (Kettle, 2010). Consequently, long-term financial commitments with no guarantee of success may limit the application of forest restoration to enhance biodiversity values in heavily degraded landscapes.

Challenges and opportunities of a coupled carbon and biodiversity approach: implications for REDD+

Carbon sequestration in tropical forest ecosystems is inextricably linked to biodiversity (Poorter et al., 2015), thus effective mitigation must acknowledge their inherent interdependencies. Consequently, policy options that couple climate change mitigation and species conservation have gained traction in recent decades. In **Chapter 3**, I demonstrate a positive relationship between aboveground carbon and the diversity of IUCN threatened species, however, lack of consensus in the scientific literature indicates that these patterns may be influenced by underlying drivers. Tropical forests are subjected to a suite of anthropogenic pressures (Barlow et al., 2016) that, if unmeasured could potentially confound the carbon-biodiversity relationship. For example, mammals are acutely sensitive to hunting (Benitez-Lopez et al., 2017, Ripple et al., 2016), thus distribution patterns in heavily exploited regions may reflect the spatial signature of anthropogenic pressure rather than associations with forest properties. In **Chapter 4**, I identified that forest quality was a stronger determinant of species persistence than hunting pressure, suggesting that win-win conservation outcomes may be possible in areas where habitat factors rather than anthropogenic pressure drives biodiversity patterns. As governments demonstrate greater commitment to climate change mitigation, an understanding of confounding factors in the carbon-biodiversity relationship is essential to advance coupled policy options.

In light of ongoing uncertainty in the scientific literature, conservation practitioners and policy makers must acknowledge that acting optimally for carbon within a REDD+ framework may induce ecological trade-offs with biodiversity

(Barlow et al., 2018). Acknowledging such trade-offs requires a decision to compromise carbon in favour of biodiversity or vice-versa. While forest carbon is amenable to trade-offs due to its spatial transferability, there are inherent practical and ethical complications concerning ecological compromises to facilitate net gains in biodiversity (Phelps et al., 2011). “Biodiversity blind” implementation of REDD+ has the potential to cause unintentional species loss, by redirecting land-use change towards unprotected, low carbon but highly biodiverse areas (Paoli et al., 2010, Phelps et al., 2012). Moreover, biodiversity is central to ecosystem functioning (Cardinale et al., 2006), thus trade-offs in heterogeneous landscapes have the potential to disrupt community structure and ecological processes with unanticipated consequences for long-term carbon storage capacity (Brodie, 2018). Ferreria et al. (2018) found that minimal compromises in carbon equated to significant biodiversity gains, indicating that biodiversity outcomes could be optimised with little impact on protected carbon. In tropical regions, where the most biodiverse areas do not necessarily correspond with high carbon forests, I advocate explicit recognition of biodiversity values to direct REDD+ applications.

Developing tropical countries typically prioritise economic growth over conservation (Giam, 2017), thus, interventions that incorporate financial incentives are more likely to result in successful outcomes. Previous work has indicated that REDD+ does not provide sufficient recompense to offset foregone revenues from logging or oil palm (Butler et al., 2009, Fisher et al., 2011a). Consequently, averting land-use change and forest modification may not represent a financially optimal implementation strategy. Alternatively, REDD+ will financially reward a number of forest interventions that restore and enhance carbon stocks while simultaneously promoting species conservation, though these are often overlooked (Miles and Dickson, 2010). Thus, biodiversity actors must reconsider their priorities to capitalise on carbon-based mechanisms. Elsewhere in Southeast Asia, 90% of REDD+ projects mobilise financial support to strengthen protected area networks, reforest degraded lands and promote reduced-impact logging (Graham et al., 2016), demonstrating an implicit recognition that avoided deforestation does not represent a profitable application. To ensure that REDD+ has maximum impact on biodiversity conservation and rural livelihoods, greater emphasis needs to be placed on the range of implementation models available to stakeholders.

Supply chain initiatives

The emergence of supply-chain initiatives is an encouraging policy development to integrate sustainability criteria into forestry and agricultural production. However, the long-term success of sectoral standards and corporate pledges is dependent on effective methodologies to identify and protect ecologically valuable tropical forests from conversion and modification. Throughout **Chapters 3 and 4**, I provide the first scientific appraisal of the High Carbon Stock (HCS) Approach, the principal tool to realise zero-deforestation commitments, which has now been formally adopted by the RSPO. In **Chapter 3**, I find that the HCS Approach is an effective tool to delineate tropical forests of high biodiversity value using freely available remote-sensing data. However, I identify some shortcomings in the patch prioritisation algorithm in **Chapter 4**. While HCS-delineated priority patches provided refugia for mammal species that are most vulnerable to land-use change, current core area criteria only sustain 35% of the mammal community, with potentially deleterious ecological consequences. Given the spatial requirements of medium-large mammals it can be argued that conserving patches of sufficient size to support sustainable populations is not economically viable. In recognition of this, I advocate a shift in emphasis towards patch configuration and landscape-level connectivity to ensure that production landscapes maintain a network of forest cover to facilitate the movement of wide-ranging vertebrates between contiguous blocks of forest. This connectivity will be essential to safeguard vulnerable mammals against projected environmental change (Struebig et al., 2015). To this end, riparian reserves, defined as protected forest margins around river habitats (Luke et al., 2018), have an instrumental role to play at the landscape scale, though their capacity to contribute to landscape connectivity is dependent upon corridor width (Yaap et al., 2016) and the maintenance of forest quality (Zimbres et al., 2017, Zimbres et al., 2018). While the value of riparian reserves is recognised in the HCS Approach, I support calls for the adoption of minimum width criteria (Luke et al., 2018).

Recent evaluations of the HCS Approach have been less encouraging. Austin et al. (2017) found that HCS-delineated forest coincided with less than 50% of rare species distributions identified using High Conservation Value (HCV) criteria in Gabon. Recognising such limitations is important to ensure that applications do not result in perverse outcomes. Conservation practitioners should regard HCS and HCV as complimentary tools. Combined applications provide safeguards for vulnerable species that overcome the limitations associated with applying each tool in isolation. This is explicitly acknowledged within the HCS toolkit and integrated within the patch prioritisation decision tree to ensure that rare species are adequately considered during the design of forest mosaics (Rosoman et al., 2012). Moreover the HCS Approach has been criticised as being economically restrictive for developing nations that have retained a high proportion of their primary forest cover, such as Papua New Guinea or Gabon (Senior et al., 2015). However, assessment of a highly-forested nation found that national oil palm targets could be addressed without compromising HCS- or HCV-delineated forests, indicating that compliance with zero-deforestation commitments could be achieved alongside development goals (Austin et al., 2017). Taken as a whole, the HCS Approach is still in its infancy and likely to be refined following scientific appraisal, I recommend that the HCS Approach should be viewed as one of a suite of tools available to land-use planners to realise sustainability commitments.

In the policy arena, supply-chain initiatives face significant implementation barriers due to competing stakeholder values. Low adoption rates and compliance costs restrict the extent to which aspirational goals result in sustainable production (Lambin et al., 2018). While zero-deforestation commitments have received considerable uptake, only 25% of associated companies have developed time-bound action plans to realise sustainability pledges (Bregman et al., 2016). Moreover, RSPO-certified palm oil accounts for only 19% of global production (RSPO, 2015). Ultimately, adoption is dependent on the degree of economic benefit derived from involvement (Giam et al., 2016). Compliance with sustainability standards and avoided deforestation comes at a significant cost to producers, yet commensurate price premiums are rarely realised (Edwards and Laurance, 2012, Lambin et al., 2018). Incentives are further undermined by Indian and Chinese markets which represent two of the top three global palm oil importers (Meijaard et al., 2018), but place greater emphasis on competitive pricing than environmental sustainability (Lyons-White and

Knight, 2018). Smallholders account for 40% of global oil palm production (Azhar et al., 2017) and typically adopt environmentally damaging agricultural practices due to weak economies of scale (Padfield et al., 2016). However, smallholders are particularly disadvantaged by supply-chain initiatives and commonly excluded from market access due to complex enrolment protocols and financially prohibitive compliance procedures (Brandi et al., 2015, Garrett et al., 2013, Glasbergen, 2018).

While voluntary sustainability standards are considered integral to environmental policy in developing nations lacking the governmental capacity to effectively regulate commodity production (Tayleur et al., 2017), there is growing scepticism that supply-chain initiatives can achieve their stated objectives (Curtis et al., 2018, Lyons-White and Knight, 2018). There is a growing body of evidence to suggest that ancillary public governance is an effective mechanism to overcome current shortcomings in private-sector sustainability standards (Lambin et al., 2014, Larsen et al., 2018). Jurisdictional regulations, such as Sabah’s commitment to 100% certified oil palm before 2025 demonstrates how state involvement could expand the scope of supply-chain initiatives and should provide a template for the evolution of hybrid governance structures in agricultural commodity chains.

Mitigating secondary disturbance impacts

The effectiveness of the policy instruments discussed throughout this thesis is contingent on the suppression of secondary disturbance impacts in human-modified landscapes. Illegal encroachment affects biodiversity directly through unsustainable exploitation and indirectly by compromising habitat suitability via illegal timber extraction (Peres et al., 2006). In **Chapter 4**, I found that secondary disturbance impacts are important determinants of mammal abundance, though they are often neglected in conservation policy. Consequently, interventions should be augmented with management actions and state regulations that safeguard forest integrity as well as cover (Barlow et al., 2016). Evidence suggests logging and oil palm concessions provide important refugia for biodiversity when management strategies explicitly consider hunting (Berry et al., 2010, Clark et al., 2009, Laurance et al., 2008). Important management actions at the concession level include site-based enforcement (Harrison, 2011), the implementation of security gates, the destruction of redundant transportation infrastructure and the provision of supplementary protein to workers (Rosin, 2014). Management actions can be strengthened by an explicit recognition of illegal encroachment mitigation measures within sustainability standards. Moreover, actions at the concession-level need to be underwritten by a stronger regulatory framework. Legislation to control the sale and possession of hunting implements and severe judicial penalties are central strategies to deter secondary disturbance impacts in human-modified landscapes (Harrison et al., 2016).

Conclusions: the biological value of human-modified landscapes

Across the world's remaining tropical forests, 76% are considered fragmented or otherwise degraded (Lewis et al., 2015). Such are the threats that face global biodiversity, these modified systems cannot be disregarded from the conservation agenda. This paradigm shift has been opposed by some factions of the scientific community, who suggest that aggressive pursuit of the biological value of human-modified landscapes narrative undermines and destabilizes current conservation efforts (Didham, 2011). There are also concerns that allocating limited financial resources to degraded habitats compromises the preservation of intact primary forests (Betts et al., 2017). Safeguarding primary forests should be regarded as the top priority for conservation practitioners, yet this must also be coupled with explicit recognition that the fate of biodiversity in these ecosystems is inextricably linked to the management of adjacent human-modified lands. In this context, dichotomising the conservation agenda is unlikely to be a worthwhile strategy; rather actors should seek new partnerships with industry, governments and local communities to capitalise on progressive environmental policies.

The work presented in this thesis demonstrates that the biological value of human-modified landscapes is dictated by the intensity of the underlying land-use. Logged forests generally provide favourable habitat for biodiversity, while oil palm plantations are often accompanied by severe ecological costs. Policy and management are essential tools to encourage and enhance the biological values of modified systems. Provided interventions are directed to where they will have the greatest impact, they can be financially self-sustaining and engage local communities to mitigate the social and economic dimensions of land-use change. Based on the findings of this thesis, I provide recommendations for policy implementation across the dominant land-use change trajectories of the tropics. Given the inability of REDD+ to financially compete with selective logging and oil palm, associated revenues will be best placed if they support the expansion of the protected area network to address Aichi Target 11 (increase protected area coverage to 17% of terrestrial and freshwater areas before 2020). Moreover, REDD+ finances can be used to procure logged forest from the permanent timber estate when standing timber stocks make associated costs more agreeable. In the most heavily degraded areas, REDD+ can be used to support ecological restoration efforts. Supply-chain initiatives provide a safety net to the system to ensure that future agricultural expansion is independent of deforestation.

Throughout this discussion I have provided recommendations to strengthen the scope and implementation of these policies to ensure they can have maximum impact. Specifically, I advocate targeted REDD+ projects that embrace applications beyond avoided deforestation, the coupling of privately-led supply-chain initiatives with state regulations and stronger recognition of secondary disturbance impacts in sustainability criteria, underwritten by severe judicial penalties. While the geographic focus of this thesis was on Southeast Asia, the policy insights generated from it are equally as relevant to other parts of the tropics, particularly in regions where commodity production is placing pressure on forest ecosystems and their resident biodiversity.

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Appendix: Co-authored publications

Peer-reviewed journal articles supplementary to the research manuscripts presented within the main thesis, to which I contributed throughout my PhD programme. Each publication is broadly relevant to the main themes presented within this thesis. Here I present the abstracts for reference in reverse chronological order, full text copies are available online.

Research article: Larger gains delivered by improved management over sparing-sharing for tropical forests

Nature Sustainability (in press)

Rebecca K. Runting, Ruslandi, Bronson Griscom, Matthew J. Struebig, Musnanda Satar, Erik Meijaard, Zuzana Burivalova, Susan M. Cheyne, Nicolas J. Deere, Edward T. Game, F.E. Putz, Jessia A. Wells, Andreas Wilting, Marc Ancrenaz, Peter Ellis, Faisal A.A. Khan, Sara M. Leavitt, Andrew J. Marshall, Hugh P. Possingham, James E.M. Watson, Oscar Venter.

Abstract: Tropical forests are globally significant for both biodiversity conservation and the production of economically valuable wood products. Two contrasting approaches have been suggested to simultaneously produce timber and conserve biodiversity; one partitions forests to deliver these objectives separately (sparing), the other integrates both objectives in the same location (sharing). To date, the ‘sparing or sharing’ debate has focused on agricultural landscapes, with scant attention paid to forest management. Here we explored the sparing-to-sharing continuum through spatial optimisations with set economic returns for the forests of East Kalimantan, Indonesia – a global biodiversity hotspot. We found that neither sparing nor sharing extremes are optimal, although the greatest conservation value was attained towards the sparing end of the continuum. Critically, improved management strategies, such as reduced-impact logging, accounted for larger conservation gains than altering the balance between sparing and sharing, particularly for endangered species. Ultimately, debating sparing versus sharing has limited value while large gains remain from improving forest management.

Research article: Addressing human-tiger conflict using socio-ecological information on tolerance and risk

Nature Communications: August 2018

Volume: 9; Article Number: 3455; DOI: 10.1038/s41467-018-05983-y

Matthew J. Struebig, Matthew Linkie, Nicolas J. Deere, Deborah J. Martyr, Betty Millyanawati, Sally C. Faulkner, Steven C. Le Comber, Fachruddin M. Mangunjaya, Nigel Leader-Williams, Jeanne E. McKay, Freya A.V. St John.

Abstract: Tigers are critically endangered due to deforestation and persecution. Yet in places, Sumatran tigers (*Panthera tigris sumatrae*) continue to coexist with people, offering insights for managing wildlife elsewhere. Here, we couple spatial models of encounter risk with information on tolerance from 2386 Sumatrans to reveal drivers of human-tiger conflict. Risk of encountering tigers was greater around populated villages that neighboured forest or rivers connecting tiger habitat; geographic profiles refined these predictions to three core areas. People's tolerance for tigers was related to underlying attitudes, emotions, norms and spiritual beliefs. Combining this information into socio-ecological models yielded predictions of tolerance that were 32 times better than models based on social predictors alone. Preemptive intervention based on these socio-ecological predictions could have averted up to 51% of attacks on livestock and people, saving 15 tigers. Our work provides further evidence of the benefits of interdisciplinary research on conservation conflicts.

Research paper: Estimating above-ground carbon density and its uncertainty in Borneo’s structurally complex tropical forests using airborne laser scanning

Biogeosciences: June 2018

Volume: 15; Issue 12; Pages: 3811-3830; DOI: 10.5194/bg-15-3811-2018

Tommaso Jucker, Gregory P. Asner, Michele Dalphonte, Philip G. Broderick, Christopher D. Philipson, Nicholas R. Vaughn, Yit Arn The, Craig Brelsford, David F.R.P. Burslem, Nicolas J. Deere, Robert M. Ewers, Jakub Kvasnica, Simon L. Lewis, Yadvinder Malhi, Sol Milne, Reuben Nilus, Marion Pfeifer, Oliver L. Phillips, Lan Qie, Nathan Renneboog, Glen Reynolds, Terhi Riutta, Matthew J. Struebig, Martin Svatek, Edgar C. Turner, David A. Coomes.

Abstract: Borneo contains some of the world's most biodiverse and carbon-dense tropical forest, but this 750 000 km^2 island has lost 62% of its old-growth forests within the last 40 years. Efforts to protect and restore the remaining forests of Borneo hinge on recognizing the ecosystem services they provide, including their ability to store and sequester carbon. Airborne laser scanning (ALS) is a remote-sensing technology that allows forest structural properties to be captured in great detail across vast geographic areas. In recent years ALS has been integrated into statewide assessments of forest carbon in Neotropical and African regions, but not yet in Asia. For this to happen new regional models need to be developed for estimating carbon stocks from ALS in tropical Asia, as the forests of this region are structurally and composition-ally distinct from those found elsewhere in the tropics. By combining ALS imagery with data from 173 permanent forest plots spanning the lowland rainforests of Sabah on the island of Borneo, we develop a simple yet general model for estimating forest carbon stocks using ALS-derived canopy height and canopy cover as input metrics. An advanced feature of this new model is the propagation of uncertainty in both ALS- and ground-based data, allowing uncertainty in hectare-scale estimates of carbon stocks to be quantified robustly. We show that the model effectively captures variation in aboveground carbon stocks across extreme disturbance gradients spanning tall dipterocarp forests and heavily logged regions and clearly outperforms existing ALS-based models calibrated for the tropics, as well as currently available satellite-derived products. Our model provides a simple, generalised and effective approach for mapping forest carbon stocks in Borneo and underpins ongoing efforts to safeguard and facilitate the restoration of its unique tropical forests.

Review article: Drivers and trajectories of land cover change in East Africa: Human and environmental interactions from 6000 years ago to present

Earth-Science Reviews: March 2018

Volume: 178; Pages: 322-378; DOI: 10.10164/j.earscirev.2017.12.010

Rob Marchant, Suzi Richer, Oliver Boles, Claudia Capitani, Colin J. Courtney-Mustaphi, Paul Lane, Mary E. Prendergast, Daryl Stump, Gijs De Cort, Jed O. Kaplan, Leanne Phelps, Andrea Kay, Dan Olago, Nik Petek, Philip J. Platts, Paramita Punwong, Mats Widgren, Stephanie Wynne-Jones, Cruz Ferro-Vazquez, Jacquiline Benard, Nicole Boivin, Alison Crowther, Aida Cuni-Sanchez, Nicolas J. Deere, Anneli Ekblom, Jennifer Farmer, Jemma Finch, Dorian Fuller, Marie-Jose Gaillard-Lemdahl, Lindsey Gillson, Esther Githumbi, Tabitha Kabora, Rebecca Kariuki, Rahab Kinyanjui, Elizabeth Kyazike, Carol Lang, Julius Lejju, Kathleen D. Morrison, Veronica Muiruri, Cassian Mumbi, Rebecca Muthoni, Alfred Muzuka, Emmanuel Ndiema, Chantal K. Nzabandora, Isaya Onjala, Annemiek Pas Schrijver, Stephen Rucina, Anna Shoemaker, Senne Thornton-Barnett, Geert van der Plas, Elizabeth E. Watson, David Williamson, David Wright.

Abstract: East African landscapes today are the result of the cumulative effects of climate and land-use change over millennial timescales. In this review, we compile archaeological and palaeoenvironmental data from East Africa to document land-cover change, and environmental, subsistence and land-use transitions, over the past 6000 years. Throughout East Africa there have been a series of relatively rapid and high-magnitude environmental shifts characterised by changing hydrological budgets during the mid- to late Holocene. For example, pronounced environmental shifts that manifested as a marked change in the rainfall amount or seasonality and subsequent hydrological budget throughout East Africa occurred around 4000, 800 and 300 radiocarbon years before present (yr BP). The past 6000 years have also seen numerous shifts in human interactions with East African ecologies. From the mid-Holocene, land use has both diversified and increased exponentially, this has been associated with the arrival of new subsistence systems, crops, migrants and technologies, all giving rise to a sequence of significant phases of land-cover change. The first large-scale human influences began to occur around 4000 yr BP, associated with the introduction of domesticated livestock and the expansion of pastoral communities. The first widespread and intensive forest clearances were associated with the arrival of iron-using early farming communities around 2500 yr BP, particularly in productive and easily-cleared mid-altitudinal areas. Extensive and pervasive land-cover change has been associated with population growth, immigration and movement of people. The expansion of trading routes between the interior and the coast, starting around 1300 years ago and intensifying in the eighteenth and nineteenth centuries CE, was one such process. These caravan routes possibly acted as conduits for spreading New World crops such as maize (Zea mays), tobacco (Nicotiana spp.) and tomatoes (Solanum lycopersicum), although the processes and timings of their introductions remains poorly documented. The introduction of southeast Asian

domesticates, especially banana (Musa spp.), rice (*Oryza* spp.), taro (*Colocasia esculenta*), and chicken (*Gallus gallus*), via transoceanic biological transfers around and across the Indian Ocean, from at least around 1300 yr BP, and potentially significantly earlier, also had profound social and ecological consequences across the region.

Through an interdisciplinary synthesis of information and metadatasets, we explore the different drivers and directions of changes in land-cover, and the associated environmental histories and interactions with various cultures, technologies, and subsistence strategies through time and across space in East Africa. This review suggests topics for targeted future research that focus on areas and/or time periods where our understanding of the interactions between people, the environment and land-cover change are most contentious and/or poorly resolved. The review also offers a perspective on how knowledge of regional land-use change can be used to inform and provide perspectives on contemporary issues such as climate and ecosystem change models, conservation strategies, and the achievement of nature-based solutions for development purposes.

Research article: Tropical forest canopies and their relationships with climate and disturbance: results from a global dataset of consistent field-based measurements

Forest Ecosystems: January 2018

Volume: 5; Article: 7; DOI: 10.1186/s40663-017-0118-7

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Background: Canopy structure, defined by leaf area index (LAI), fractional vegetation cover (FCover) and fraction of absorbed photosynthetically active radiation (faPAR), regulates a wide range of forest functions and ecosystem services. Spatially consistent field-measurements of canopy structure are however lacking, particularly for the tropics.

Methods: Here, we introduce the Global LAI database: a global dataset of field-based canopy structure measurements spanning tropical forests in four continents (Africa, Asia, Australia and the Americas). We use these measurements to testfor climate dependencies within and across continents, and to test for the potential of anthropogenic disturbance and forest protection to modulate those dependencies.

Results: Using data collected from 887 tropical forest plots, we show that maximum water defecit, defined across the most arid months of the year, is an important predictor of canopy structure, with all three canopy attributes declining significantly with increasing water defecit. Canopy attributes also increase with minimum temperature, and with the protection of forests according to both active (within protected areas) and passive measures (through topography). Once protectionand continent effects are accounted for, other anthropogenic measures (e.g. human population) do not improve the model.

Conclusions: We conclude that canopy structure in the tropics is primarily a consequence of forest adaptation to the maximum water defecits historically experienced within a given region. Climate change, and in particular changes in drought regimes may thus affect forest structure and function, but forest protection may offer some resilience against this effect.

Article: A new species in the tree genus Polyceratocarpus (Annonaceae) from the Udzungwa Mountains of Tanzania

PhytoKeys: April 2016

Volume: 63; Pages: 63-76; DOI: 10.3897/phytokeys.63.6262

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Abstract: *Polyceratocarpus askhambryan-iringae*, an endemic tree species of *Annonaceae* from the Udzungwa Mountains of Tanzania, is described and illustrated. The new species is identified as a member of the genus *Polyceratocarpus* by the combination of staminate and bisexual flowers, axillary inflorescences, subequal outer and inner petals, and multi-seeded monocarps with pitted seeds. From *Polyceratocarpus scheffleri*, with which it has previously been confused, it differs in the longer pedicels, smaller and thinner petals, shorter bracts, and by generally smaller, less curved monocarps that have a clear stipe and usually have fewer seeds. Because *Polyceratocarpus askhambryan-iringae* has a restricted extent of occurrence, area of occupancy, and ongoing degradation of its forest habitat, we recommend classification of it as Endangered (EN) on the IUCN Red List.