Effective monitoring and conservation prioritisation of threatened mammals in Sumatra

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Author declaration

All chapters in this thesis were written by Ardiantiono, with editorial feedback and statistical guidance by supervisors Matthew J. Struebig, Nicolas J. Deere, and David J.I. Seaman. Chapters 2-5 include collaborations with governmental institutions, universities, and non-governmental organisations.

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Chapter 2. Ardiantiono and Irene M. Pinondang led the writing as joint first authors with input from Matthew J. Struebig. Ardiantiono, Irene M. Pinondang, and Matthew J. Struebig conceived the study conception and design. The first authors conducted literature search, synthesize, and analyse the results. All authors contributed to the revision of the manuscript. Figures were produced by Irene M. Pinondang and Ardiantiono. This chapter was published in the journal *Oryx* journal (https://doi.org/10.1017/S0030605323001539).

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

Abstract

Effective conservation requires accurate assessments of biodiversity and the optimal allocations of conservation efforts. This is especially crucial in tropical regions that are not only rich in biodiversity but also subject to some of the highest anthropogenic pressures, where conservation efforts are often hindered by limited resources and expertise. Based on research in Indonesia, my thesis investigates various approaches to enhancing biodiversity conservation in tropical forests, with two main objectives: 1) improving the effectiveness of biodiversity monitoring, and 2) targeting conservation actions through systematic conservation planning. I begin with a systematic review of research on medium and large mammal populations in Indonesia published between 2000-2020 (Chapter 2). This review identifies key knowledge gaps, including: 1) a disproportionate focus on a few species; 2) geographical bias toward western Indonesia, 3) limited study design and analysis, and 4) a lack of long-term studies. Building on these findings, the remainder of the thesis focuses on improving biodiversity monitoring and exercising conservation prioritisation within the Leuser Ecosystem, the largest tropical forest landscape in Sumatra, Indonesia. Using comprehensive camera trap datasets, in Chapter 3 I evaluate the performance of eight candidate umbrella species in representing broader patterns of mammal biodiversity, including community occupancy, species richness, functional diversity, and phylogenetic diversity. I found that species often overlooked in conservation, such as the sambar deer (*Rusa unicolor*) and clouded leopard (*Neofelis diardi*), consistently ranked among the top umbrella species, while the charismatic Sumatran tiger (*Panthera tigris sumatrae*) and rhinoceros (*Dicerorhinus sumatrensis*) performed poorly. I propose monitoring "umbrella fleets", which involves working with several highly ranked umbrella species to better represent overall mammal biodiversity. Chapter 4 explores the application of data integration approaches to enhance biodiversity monitoring. I combined unstructured data from ranger patrols with systematic data from camera traps and sign transects to inform landscape-wide occupancy analysis of tigers and their principal prey (sambar deer and wild pigs *Sus scrofa*). Data integration improved the precision of species occupancy estimates by

14–42%, expanded the spatial scope of inference to landscape-level, and reduced operational costs by up to 51-fold. The study highlights the underappreciated value of integrating unstructured data, which is often overlooked in species monitoring studies. In Chapter 5, I conducted a spatial prioritisation analysis for tiger conservation in Leuser that incorporated tiger distribution and its key anthropogenic threats, namely forest loss, hunting, and human-tiger conflict. I used two different data sources: primary data collected through field surveys and secondary data from public databases and satellite imagery. The findings reveal significant discrepancies between priority areas identified using primary versus secondary datasets, underscoring the impact of the source data used in conservation prioritisation. Finally, I conclude with a discussion on the contributions of this research to advancing biodiversity monitoring and promoting effective conservation in tropical regions.

Keywords: biodiversity management, conservation priority, cost-effectiveness, hierarchical modelling, mammals, occupancy, Southeast Asia, tropical forests

Abstrak Bahasa Indonesia

Konservasi yang efektif membutuhkan penilaian akurat keanekaragaman hayati dan alokasi upaya konservasi yang optimal. Hal ini terutama penting di kawasan tropis, yang tidak hanya kaya akan keanekaragaman hayati tetapi juga menghadapi tekanan antropogenik tertinggi, dimana upaya konservasi seringkali terhambat oleh keterbatasan sumber daya dan keahlian. Tesis saya menyelidiki berbagai pendekatan untuk memperkuat konservasi keanekaragaman hayati di hutan tropis, dengan dua tujuan utama: 1) meningkatkan efektivitas pemantauan keanekaragaman hayati, dan 2) menargetkan aksi konservasi melalui perencanaan konservasi yang sistematis. Saya memulai dengan tinjauan sistematis terhadap penelitian populasi mamalia ukuran sedang dan besar di Indonesia yang diterbitkan antara tahun 2000-2020 (Bab 2). Tinjauan ini mengidentifikasi kesenjangan pengetahuan utama, termasuk: 1) fokus yang tidak proporsional pada beberapa spesies; 2) bias geografis terhadap Indonesia bagian barat, 3) desain dan analisis penelitian yang terbatas, dan 4) kurangnya studi jangka panjang. Berdasarkan temuan-temuan ini, tesis ini berfokus pada peningkatan pemantauan keanekaragaman hayati dan prioritisasi konservasi di Ekosistem Leuser, lanskap hutan tropis terbesar di Sumatera, Indonesia. Menggunakan dataset kamera jebak yang komprehensif, Bab 3 mengevaluasi kinerja delapan kandidat spesies payung dalam mewakili keanekaragaman mamalia yang lebih luas, termasuk okupansi komunitas, kekayaan spesies, keanekaragaman fungsional, dan keanekaragaman filogenetik. Saya menemukan bahwa spesies yang sering diabaikan dalam konservasi, seperti rusa sambar (*Rusa unicolor*) dan macan dahan (*Neofelis diardi*), secara konsisten berada di peringkat teratas sebagai spesies payung, sementara harimau (*Panthera tigris sumatrae*) dan badak sumatera (*Dicerorhinus sumatrensis*) yang karismatik memiliki performa yang kurang. Saya mengusulkan pemantauan “armada payung”, yang melibatkan beberapa spesies payung peringkat atas untuk lebih baik dalam mewakili keanekaragaman mamalia secara keseluruhan. Bab 4 mengeksplorasi penerapan integrasi data untuk meningkatkan pemantauan keanekaragaman hayati. Saya menggabungkan data tidak terstruktur dari patroli penjagaan hutan dengan data sistematis dari survei kamera jebak dan transek tanda satwa untuk memberikan informasi tentang okupansi harimau dan mangsa utamanya (rusa sambar dan babi hutan *Sus scrofa*). Integrasi data meningkatkan presisi estimasi okupansi spesies sebesar 14-42%, memperluas cakupan spasial prediksi ke tingkat lanskap, dan mengurangi biaya operasional hingga 51 kali lipat. Studi ini menyoroti nilai penting dari integrasi data tidak terstruktur, yang sering diabaikan dalam studi pemantauan spesies. Dalam Bab 5, saya melakukan analisis prioritisasi spasial untuk konservasi harimau yang menggabungkan distribusi harimau dan ancaman antropogenik utama seperti kehilangan tutupan hutan, perburuan, dan konflik manusia-harimau. Saya menggunakan dua sumber data yang berbeda: data primer yang dikumpulkan melalui survei lapangan dan data sekunder dari basis data publik dan citra satelit. Temuan kami mengungkapkan perbedaan signifikan antara area prioritas yang diidentifikasi menggunakan dataset primer versus sekunder, yang menyoroti dampak pemilihan sumber data. Sebagai penutup, saya menyimpulkan tesis ini dengan diskusi tentang kontribusi penelitian ini dalam memajukan pemantauan keanekaragaman hayati dan mendorong konservasi yang efektif di wilayah tropis.

Kata kunci: pengelolaan keanekaragaman hayati, prioritas konservasi, efektivitas biaya, pemodelan hierarkis, mamalia, okupansi, Asia Tenggara, hutan tropis

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Chapter 1 Introduction

Conservation strives to be effective in improving the state of declining biodiversity. To protect biodiversity, decision-makers need accurate assessments of the current status of species, population trends over time, and threats faced (Lindenmayer *et al.*, 2012; Schmeller *et al.*, 2017). However, biodiversity monitoring efforts are often hampered by limited resources and expertise, resulting in unequal spatial, temporal, and taxonomic coverage (Schmeller *et al.*, 2017; Steenweg *et al.*, 2017). Therefore, improving current monitoring approaches is critical to rapidly generate accurate information on biodiversity status while minimizing operational budgets. High quality biodiversity data can thus enhance systematic conservation planning, which aims to allocate scarce conservation resources effectively (Kukkala and Moilanen, 2013).

This introductory chapter will begin by examining the current state of global biodiversity, introducing the concept of "defaunation" and exploring the key drivers behind this phenomenon. The scope of the discussion will be narrowed to tropical forest ecosystems, which support a greater number of threatened species and experience some of the highest pressures on biodiversity across the world (Allan *et al.*, 2019; Raven *et al.*, 2020). Within this context, the chapter will place particular emphasis on mammals, which are not only highly threatened but also frequently serve as flagship species in conservation initiatives (Ripple *et al.*, 2016; Brum *et al.*, 2017; Holmes *et al.*, 2022). The chapter will proceed with an overview of current methodologies used to monitor mammals in tropical forests, highlighting existing challenges and potential strategies for improvement. A specific focus will be placed on Southeast Asia and Indonesia, regions of global significance for biodiversity conservation. Finally, the chapter will conclude by outlining the objectives and structure of this thesis.

1.1 Status of global biodiversity

There is a scientific consensus that global biodiversity is in decline. Approximately a quarter of all living species are threatened (Díaz *et al.*, 2019), and 32% of the world's species have experienced declines in their populations and distributions since 1900 (Ceballos, Ehrlich and Dirzo, 2017). Recently, the Living Planet Index reported an alarming 69% decrease in global vertebrate populations from 1970 to 2018 (WWF, 2022).

Biodiversity loss is particularly severe in tropical ecosystems, which are among the most biodiverse regions on Earth. Tropical forests are home to approximately 62% of the world's terrestrial vertebrate species, harbouring twice as many species as any other terrestrial biome (Pillay *et al.*, 2022). These forests are crucial for mammal conservation, supporting around 3,480 mammal species, which represent 63% of all mammal species, with around 45% of the world's mammals being endemic to tropical forests (Brum *et al.*, 2017; Pillay *et al.*, 2022). However, these regions have experienced significant declines in mammal populations. Terrestrial mammal distributions contracted by up to 41% between 1992 and 2015 (Gallego-Zamorano *et al.*, 2020), and another study reported a 13% decline in mammal abundances between 1980 and 2017 (Benítez-López *et al.*, 2019).

Despite the severity of this biodiversity crisis, the topic often receives less attention than other environmental issues such as climate change and deforestation (Williams *et al.*, 2021; Jaureguiberry *et al.*, 2022). Biodiversity loss is frequently a cryptic phenomenon, which takes time to be detected, as illustrated befittingly by the concept of the "empty forest syndrome" where forest ecosystems appear largely intact but void of large animals (Redford, 1992). The process that leads to empty forest syndrome is known as defaunation, which is defined as global and local species extinction, as well as declines in species abundance and distribution, ecological and evolutionary diversity, and species interactions (Dirzo *et al.*, 2014; Young *et al.*, 2016; Brodie, Williams and Garner, 2021).

Defaunation impacts all biodiversity, but the effects vary across taxa due to differences in species' life histories, ecological traits, and threats they face (Cardillo *et al.*, 2008; Young *et al.*, 2016). Large mammal species, particularly carnivores and herbivores, are among the most threatened as they possess traits that increase their vulnerability: late weaning age, large home ranges, low population density, limited geographical range, and significant overlap with human populations (Cardillo *et al.*, 2008; Benítez-López *et al.*, 2019; Bogoni, Peres and Ferraz, 2020). It remains uncertain whether small mammals are at a higher risk of defaunation. For instance, a study found that some of the world's smallest vertebrate species face a significant extinction risk due to their limited ranges and specialized niches (Ripple *et al.*, 2017). However, this contrasts with other research showing that populations of small species, particularly more resilient species like rodents, actually increase or persist under defaunation pressures (Young *et al.*, 2014; Leung *et al.*, 2020).

Despite these declining trends, conservation actions have proved effective in reversing or halting defaunation, underscoring the importance of such efforts (Langhammer *et al.*, 2024). For example, active protection within protected areas has contributed to the recovery of threatened megafauna like Sumatran tigers (*Panthera tigris sumatrae*; Linkie *et al.*, 2015; Pusparini *et al.*, 2018) and African elephants (*Loxodonta africana* and *Loxodonta cyclotis*; Poole and Granli, 2022). An initiative like the IUCN Green Status of Species was developed to document species recovery and successful conservation actions, with the hope that more recovery stories will emerge and bring optimism to conservation efforts (Grace *et al.*, 2021). Recently, governments have set ambitious biodiversity targets, such as the Kunming-Montreal Global Biodiversity Framework in 2022, to achieve "nature positive" (UNEP, 2022). This international policy commitment provides a direction for future strategies and conservation plans to be implemented by governments at national and international levels.

1.2 Drivers of defaunation

Habitat loss and overexploitation are the primary drivers of defaunation (Dirzo et al. 2014; Young et al. 2016). Land-use changes, particularly the conversion of natural habitats to agricultural and urban landscapes, have led to significant habitat loss and fragmentation, which are predicted to shrink global terrestrial vertebrate ranges by up to 23% by 2100 (Beyer and Manica, 2020). Despite some restoration efforts, the past four decades have witnessed a net loss of 199,000 km^2 of the tropical forest (Song et al. 2018), further threatening a high number of species with extinction.

While land-use change has widespread impacts, hunting poses the greatest immediate threat to many species (Harrison *et al.*, 2016; Tilker *et al.*, 2024). Over half of the world's tropical forests (~14 million km^2) are expected to be partly defaunated due to hunting pressures (Benítez-López *et al.*, 2019). For instance, 95% of neotropical forests have experienced over 20% of mammal loss (Bogoni, Peres and Ferraz, 2020). Hunting, often unsustainable due to weak regulation and easy access to hunting equipment, disproportionately targets large herbivores and carnivores, but also endangers non-target species through indiscriminate methods like snares (Linkie *et al.*, 2015; Harrison *et al.*, 2016).

Other drivers of defaunation include climate change, human-wildlife conflict, invasive species, and diseases (Young *et al.*, 2016). Climate change affects biodiversity by altering precipitation patterns and temperature, creating suboptimal environments that may eliminate species unable to adapt (Habibullah *et al.*, 2022). Human-wildlife conflicts often result in retaliatory killings, particularly when wildlife inflicts economic losses or poses threats to human safety (Sillero-Zubiri *et al.*, 2023). The invasion of alien species, such as non-native predators, can lead to the extinction of local species unable to withstand the competition or avoid predation (Doherty *et al.*, 2016). Additionally, disease outbreaks can have devastating effects, causing mass mortalities that may drive species to local extinction (Luskin *et al.*, 2020).

These drivers are interconnected and often exacerbate each other, creating a compound threat to biodiversity. For example, land clearing and hunting pressures are frequently linked. The expansion of land clearing and road networks increases access to wildlife habitat, therefore facilitating hunting activities (Benítez-López *et al.*, 2019; Ghoddousi *et al.*, 2022). Reduced prey availability and fragmented habitats can escalate human-carnivore conflicts, often resulting in retaliation (Packer *et al.*, 2019; Lubis *et al.*, 2020), while also increasing interactions between wildlife and domestic animals, which can facilitate disease transmission to wildlife populations (Jones *et al.*, 2013).

Additionally, there is growing recognition of the social dimensions influencing defaunation such as demographic, sociocultural, economic, political, and governance

(Díaz *et al.*, 2019). For example, the demand for traditional Chinese medicine, driven by cultural beliefs, contributes to the hunting and illegal trade of wildlife (Cheung *et al.*, 2021). Additionally, community attitudes toward existing regulations, as well as factors like corruption and social norms, can influence their willingness to comply with rules within and around protected areas (Ibbett *et al.*, 2024).

1.3 Methods to monitor mammal biodiversity in tropical forests

Tropical forests are home to at least half of the world's terrestrial biodiversity, but monitoring their wildlife, especially mammals, presents significant challenges. The difficulties in accessing the remote part of the forest and the presence of elusive and cryptic species, often in low density, make it difficult to conduct effective surveys (Mulatu *et al.*, 2017). To overcome these challenges, a variety of methodologies have been employed, ranging from traditional human observation to advanced technological tools.

Human observation has long been a primary method for monitoring biodiversity. Traditional approaches, such as transect-based survey — which relies on direct visual sightings or indirect signs, as well as aural observations — continue to be used to assess species population status e.g. species abundance and occupancy (Sutherland, 2006). This method offers advantages, including lower costs and the ability to cover larger areas (Wibisono *et al.*, 2011). Human observations can be effectively complemented by initiatives like citizen science and ranger patrols, which also rely on human observation (Dobson *et al.*, 2020). However, this method is subject to several biases, such as low detection rates and species misidentification, which can result from limited expertise in wildlife surveying or environmental factors like weather conditions (MacKenzie *et al.*, 2018). Additionally, these methods are often designed to survey a limited number of species, often easily detectable species like arboreal primates or species with distinct signs, making them less effective in monitoring a broader range of species.

Advances in technology have greatly improved biodiversity monitoring in tropical forests. Camera traps have emerged as a key tool for ecological monitoring, capable of generating vast amounts of data through continuous recording. They can capture a wide range of species, including those that are cryptic and elusive (Wearn and Glover-Kapfer, 2019). Remote sensing techniques, utilizing high-resolution imagery from satellites or unmanned aerial vehicles like drones, further expand the possibilities of rapid surveillance across large areas (Mulatu *et al.*, 2017). While remote sensing is often employed to monitor changes in forests and physical environments, it also shows promise for tracking biodiversity, particularly large-bodied animals (Rahman *et al.*, 2023) and arboreal animals that can be detected from tree canopies (Wich *et al.*, 2015). Additionally, passive acoustic monitoring, which uses sound to track vocal species, offers a cost-effective way of assessing species distribution and community structure (Chhaya *et al.*, 2021). Environmental DNA, which extracts genetic materials from environmental samples, has also become increasingly popular in monitoring efforts. This technique can rapidly detect a broader range of species, including those missed by other methods such as aquatic species, for example, by sampling water from catchment areas without the need to visit every part of the forest (Huerlimann *et al.*, 2020; Mena *et al.*, 2021).

Despite these advantages, the use of technological tools in biodiversity monitoring often comes with high initial costs for the equipment, such as camera traps and drones, or laboratory work, such as DNA processing (Stephenson, 2020). The extensive datasets generated by these technologies can also pose challenges, requiring significant time and technical capacities to process (i.e. identifying camera trap images). However, the integration of Artificial Intelligence can reduce these demands (Green *et al.*, 2020).

Additionally, some data types, such as genetic or acoustic information, are less likely to be adopted by decision-makers because they are more difficult to interpret compared to the clear visual evidence provided by camera traps or drones. This underscores the need to present data in formats that are more accessible (Stephenson, 2020; Lee *et al.*, 2024).

1.4 Challenges in biodiversity research in tropical countries

Research on biodiversity and wildlife populations is often constrained by limitations in data collection and analysis, which include challenges related to: 1) scale and data representation, 2) data sources, 3) lack of time-series data, and 4) data standardization.

1) Scale and data representation

Global-scale studies typically rely on large sampling units, such as grid sizes ranging from 10,000 km^2 to 40,000 km^2 or are conducted on a country scale. These designs can overestimate species distribution ranges by including significant non-habitat areas, potentially leading to inaccurate assumptions about species occurrence (Ceballos, Ehrlich and Dirzo, 2017; Wyborn and Evans, 2021). Additionally, these large-scale studies often struggle with data representation. Biodiversity databases such as the Living Planet Index and PREDICTS collect species abundance and occurrence data worldwide (Hudson *et al.*, 2017; WWF, 2022). However, these databases tend to have more extensive data from the Global North than the Global South, leading to conclusions that may not accurately reflect biodiversity status in these underrepresented regions.

Conversely, while local studies provide more-detailed, fine-scale information, they often suffer from limited spatial coverage. For example, a study on primate population in Bukit Barisan Selatan National Park in Indonesia (365,000 ha), found a drastic population decline of the siamang gibbon (*Symphalangus syndactylus*) in a 900 ha study area (Lappan *et al.*, 2017). However, this localized finding cannot be extrapolated to the entire park. Similarly, the increasing Sumatran tiger population in the central part of the Bukit Barisan Selatan National Park may not reflect the same trends in the other regions of the park (Pusparini *et al.*, 2017).

2) Data sources

While primary data collected from the field is ideal, many studies rely on secondary data from open-access databases or publications. The IUCN Red List, a widely used source for species range and population information is commonly utilized in global biodiversity studies (Ripple *et al.*, 2017; Allan *et al.*, 2019; Belote *et al.*, 2020). However, the information in the IUCN Red List may be outdated or lack sufficient details. For example, the distribution maps of sambar deer (*Rusa unicolor*) and wild pigs (*Sus scrofa*) show their range across the island of Sumatra, Indonesia, while clearly these species won't be found in heavily urbanised areas (IUCN, 2024).

3) Data standardization

Variability in study design, data collection methodologies, and data formatting present additional challenges in big data analysis, which requires standardized data inputs (Miller *et al.*, 2019; Dobson *et al.*, 2020). Different methodologies generate datasets with varying levels of detail, and standardization can either reduce the richness of more informative datasets (e.g. when species identity derived from capture-recapture surveys converted into presence-absence information) or exclude less systematic observations (Dobson *et al.*, 2020). Moreover, comparing data across spatial and temporal scales becomes difficult when population estimates are derived from different study designs. For example, the increasing trend in Sumatran tiger density in the central part of Bukit Barisan Selatan designed in one big cluster (Pusparini *et al.*, 2018) was inferred by comparing it to a previous estimate that assessed 10 smaller clusters of camera traps across the park (O'Brien, Kinnaird and Wibisono, 2003).

4) Lack of time-series data

The scarcity of time-series data limits the ability of studies to track population changes over time, often due to resource constraints that prevent long-term research. Previous studies have used spatial comparisons within a single period, for example, to identify defaunation processes by comparing species communities in intact versus fragmented forests (Gallego-Zamorano *et al.*, 2020; Amir *et al.*, 2022). While spatial comparisons provide valuable insights into the impacts of various pressures on wildlife, integrating temporal comparisons can more effectively elucidate the mechanisms and rates of species population changes over time in response to anthropogenic and environmental disturbances (Harihar *et al.*, 2020; WWF, 2022).

1.5 Enhancing biodiversity monitoring and conservation in tropical forests

Effective conservation strategies must be based on accurate assessments of biodiversity. For instance, integrating threatened species distribution data with maps of potential anthropogenic threats can greatly enhance spatial prioritisation efforts by identifying high-priority areas where species are both prevalent and under significant threat. Without accurate distribution maps, however, prioritisation efforts risk misallocating resources and failing to protect key areas.

While wildlife population research faces significant challenges, particularly in tropical regions, new initiatives are emerging to enhance biodiversity monitoring and address these challenges.

1) Leveraging unstructured or "messy" data

Systematic data collection is often difficult and costly, which forces conservationists to rely on unstructured observational data such as that from citizen science projects or ranger patrols. While these activities are cost-effective and cover large scales, the resulting data is often considered "messy" due to inherent biases, such as observer detection errors and uneven spatial coverage (Dobson *et al.*, 2020). However, the rapid growth of and reliance on these data sources holds great potential for improving biodiversity monitoring.

To address the challenges associated with unstructured data, new initiatives are focusing on developing sampling designs and protocols that guide citizen scientists and rangers in collecting data more systematically, thereby reducing potential biases (Callaghan *et al.*, 2019; Taskforce, 2022). Additionally, advances in analytical frameworks have significantly improved the analysis of such data, enabling their integration with more systematic monitoring datasets (Sun, Hurst and Fuller, 2021) and the development of models that explicitly correct for spatial (Cretois *et al.*, 2021) and detection biases (Louvrier *et al.*, 2018).

2) Collating and standardizing monitoring datasets

Biodiversity monitoring has expanded significantly over time, driven by initiatives such as citizen science, increased funding, and advances in monitoring technologies (Schmeller *et al.*, 2017). Despite these advances, monitoring efforts often remain fragmented across different spatial and temporal scales, utilize varying sampling designs and dataset formats, and tend to focus on specific taxa (Navarro et al., 2017).

Several initiatives have been established to develop standardized protocols for data collection. For instance, the TEAM (Tropical Ecology Assessment and Monitoring) Network has created a protocol for camera trapping surveys aimed at monitoring mammal status and trends in tropical forests (Ahumada, Hurtado and Lizcano, 2013). In Indonesia, the government has developed a national guideline for monitoring Sumatran tiger populations using both camera trap and sign transect methods, aimed at ensuring standardized protocols and datasets for national-scale analysis (Haidir *et al.*, 2017; Chandradewi *et al.*, 2019). Additionally, efforts are underway to create standardized databases accessible to both scientific and public communities. Examples include CamTrapAsia, which compiles data from camera trap studies across tropical Asia (Mendes *et al.*, 2024), the TEAM Network camera trap database (Ahumada, Hurtado and Lizcano, 2013), and the Living Planet Index, which provides insights into global vertebrate species abundance trends (WWF, 2022).

3) Advancing analytical frameworks for biodiversity monitoring

No data is perfect, whether derived from systematic monitoring or unstructured observational surveys. Advancements in analytical frameworks have significantly increased the value of such data, enabling more reliable and accurate biodiversity estimates across broader spatial and temporal scales. For instance, hierarchical models like occupancy frameworks are particularly effective in addressing issues of imperfect detection, which might arise from human observers' varying abilities to detect species or from uneven spatial coverage (e.g. ranger patrols focusing on areas where illegal activities are expected) (MacKenzie *et al.*, 2018; Tilker *et al.*, 2024). These frameworks can also mitigate the risk of potential misidentification, where species are incorrectly recorded as present in the area due to confusion with similar species, leading to false positives.

In addition, recent advancements in data integration offer opportunities to enhance the utility of unstructured data, such as observations from citizen science projects and ranger patrols. Integrated modelling allows the combination of datasets collected through different methodologies within a unified statistical framework, addressing potential biases that arise from varying survey designs and species detections (Isaac *et al.*, 2020). By incorporating more data, integrated models not only improve the precision of species estimates (e.g. occupancy and abundance) but also extend spatial inferences to scales that are more relevant to conservation management (Doser *et al.* 2022).

1.6 Conservation challenges in Southeast Asia and Indonesia

1.6.1 Southeast Asia: a megadiverse region in peril

Southeast Asia is recognized as one of the most critical regions for global biodiversity. This region is home to the highest global average of endemic species per country, with 14-28% of mammal species being unique to the area (Pillay *et al.*, 2022). However, the region's rich biodiversity is under severe threat. Human activities have left a profound impact, with 84% of the Earth's surface heavily impacted by humans, and the highest pressures are found in the tropics, especially tropical Southeast Asia (Allan *et al.*, 2019). Alarmingly, Southeast Asia, along with the Amazon and Central Africa, has been identified as one of the top three regions with the highest number of declining species (Ceballos, Ehrlich and Dirzo, 2017). Under a business-as-usual scenario, it is predicted that 13-85% of the region's biodiversity could be lost by the end of the century (Sodhi *et al.*, 2010).

The threats to Southeast Asia's biodiversity are multifaceted, including land-use change, overexploitation, rapid human population growth, and inadequate conservation management (Sodhi *et al.*, 2010; Duckworth *et al.*, 2012). For instance, the 11 countries that make up the Association of Southeast Asian Nations (ASEAN) lost 32 million hectares of forest cover between 1990 and 2010 — an area equivalent to the size of Vietnam — at an annual loss rate of 1.6 million hectares, surpassing any other region in the world (Stibig *et al.*, 2013).

These pressures are compounded by the fact that many of the region's most biodiversity-important areas are outside the designated protected areas, leaving them vulnerable to further degradation. Adding to these concerns is the potential impact of China's Belt and Road Initiative, the largest infrastructure development project in history, which focuses heavily on Southeast Asia. For instance, the development and improvement of approximately 9,000 km of rail and road networks in the region could affect 142 threatened species and cut 21 protected areas (Ng *et al.*, 2020). Additionally, enhanced trade routes could exacerbate wildlife trafficking, including bushmeat, traditional Chinese medicine, and ornamental species from Southeast Asia to China (Hughes *et al.*, 2020).

1.6.2 Indonesia: challenges in conserving its biodiversity

Indonesia is widely regarded as the most important country for biodiversity among the 11 ASEAN nations (von Rintelen, Arida and Häuser, 2017). Globally, it ranks second for the overall biodiversity value and first for endemic species diversity (Prawiradilaga and Soedjito, 2013; Bappenas, 2024). The country is home to approximately 10% of the world's vertebrate species, including 15% of mammals, 19% of birds, 9% of reptiles, and 6% of amphibians (Bappenas, 2024). Approximately 63% of Indonesia's land area (~120.3 million hectares) is forest, with 18% (22.1 million hectares) designated as conservation areas (MoEF, 2022).

Despite its ecological richness, Indonesia faces imminent threats to its biodiversity. The country has experienced the largest forest cover loss among ASEAN nations (Stibig *et al.*, 2013; Austin *et al.*, 2019), including a loss of 9.79 million hectares (11%) of primary forests between 2001 and 2019 (Gaveau *et al.*, 2022). Massive forest fires, often exacerbated by El Niño events, have further degraded these ecosystems, burning ~9.75 million hectares of forests in 1997-1998 and 4.6 million hectares, predominantly peatlands, in 2015 (Prawiradilaga and Soedjito, 2013; Lohberger *et al.*, 2018). Indonesia's rapid economic growth and dense human population have driven extensive development of large and small-scale oil palm, food crops, and timber plantations, which are among the primary drivers of deforestation and forest fires (Abegão, 2019; Austin *et al.*, 2019; Meijaard *et al.*, 2020). Furthermore, the country has become a significant source and hub for the global illegal wildlife trade, with an estimated annual economic loss of up to USD 600 million, excluding the substantial loss of ecological services provided by trafficked species (Trinirmalaningrum *et al.*, 2016).

Conserving Indonesia's biodiversity presents several significant challenges ranging from the availability of data, law enforcement, and political situations. Below are some of the key challenges in conserving Indonesia's rich biodiversity:

1) Limited scientific data on biodiversity

A significant challenge in conserving Indonesia's biodiversity is the lack of comprehensive scientific data. Information on species population status is often limited to charismatic species like tigers, orangutans, or elephants, with data generally restricted to specific study sites or landscapes (Pusparini *et al.*, 2017; Santika *et al.*, 2017; Lubis *et al.*, 2023). Moreover, varying methodologies used in studies across multiple landscapes, such as the use of DNA surveys versus expert opinions in estimating elephant populations further complicate data analysis and interpretation (Azmi and Gunaryadi, 2011; WCS-IP, 2014; Moßbrucker *et al.*, 2015). The limited analytical capacity also constrains the production of robust biodiversity estimates and the publication of scientific research on Indonesia's biodiversity, creating data gaps in this region.

2. Inadequate conservation efforts in protected areas

There is a pressing need to bolster conservation efforts inside Indonesia's protected areas to curb illegal activities. Research shows that the establishment of protected areas, combined with intensive ranger patrols and law enforcement, could reduce deforestation and hunting within these regions (Linkie *et al.*, 2015; Morgans *et al.*, 2024). However, disparities in resource availability, management quality, and the implementation of conservation programs persist across Indonesia's protected areas. For example, recent evaluations using the Management Effectiveness Tracking Tool revealed that national parks in western Indonesia generally perform better than those in the east, and that national parks are better managed than other types of conservation areas management such as protected forests and wildlife reserves (KSDAE, 2018; Nugraha *et al.*, 2024).

3. Conflicting policy priorities

Conservation-related policies in Indonesia are often outcompeted by social, political, and economic agendas. The recently approved Omnibus Bill, aiming at simplifying business investment regulations, has sparked significant environmental concerns (Sembiring, Fatimah and Widyaningsih, 2020). Key issues include the exclusion of environmental permits as a prerequisite for business permits, a vague definition of which activities require environmental permits, the centralization of authority that undermines local government monitoring, and reduced corporate responsibility for preventing forest fires on their property (Sembiring, Fatimah and Widyaningsih, 2020). These policy shifts could have far-reaching negative impacts on Indonesia's already vulnerable ecosystems and conservation efforts.

1.7 Thesis structure

This thesis aims to optimise the monitoring and conservation prioritisation of threatened mammals in tropical forests. Specifically, my research has two primary objectives: 1) improving the effectiveness of biodiversity monitoring, and 2) targeting conservation actions through systematic conservation planning.

The thesis begins with a literature review to assess the current state of mammal population research in Indonesia, identifying patterns and knowledge gaps (Chapter 2). Subsequently, I evaluate the application of umbrella species as surrogates for mammal biodiversity, utilizing data collected from remote camera traps (Chapter 3). I also test the benefits of integrating data from different activities to enhance the cost-effectiveness of biodiversity monitoring (Chapter 4). Last, I combine species distribution data with multiple anthropogenic threat layers to identify priority areas for conservation (Chapter 5).

Throughout this research, my focus is on terrestrial mammals in the Sumatran rainforest, using the endemic and flagship Sumatran tigers as focal species. This thesis comprises one literature review and three data chapters, each of which is written to stand alone as a research paper. Due to the collaborative nature of these chapters, plural pronouns will be used throughout the thesis.

Chapter 2: Insights from 20 years of mammal population research in Indonesia

Co-led by Irene Margareth Pinondang and Ardiantiono, this chapter reviews 20 years of published research on medium to large mammal populations in Indonesia. We focus on three key population parameters: diversity, distribution, and abundance. By assessing publications in both Bahasa Indonesia and English to ensure language representation, we identify four key knowledge gaps in current research and the challenges faced by local researchers in publishing in international journals. Finally, we provide suggestions to improve future mammal population research, with some recommendations to be implemented in subsequent chapters of this thesis.

Chapter 3: Selecting umbrella species as mammal biodiversity indicators in tropical forest

This chapter evaluates the performance of umbrella species in representing broader mammal communities, accounting for multiple facets of biodiversity: community occupancy, species richness, functional diversity, and phylogenetic diversity. Utilizing comprehensive camera trap datasets, we develop analytical frameworks that explicitly account for imperfect detections to estimate these biodiversity parameters. Our study demonstrates species often overlooked in conservation are better at representing broader biodiversity and that using multiple umbrella species, hence called "umbrella fleets", can improve biodiversity representation across the landscape.

Chapter 4: Improved cost-effectiveness of species monitoring programs through data integration

Focusing on Sumatran tigers and their principal prey, this chapter evaluates how integrating different datasets under hierarchical integrated multispecies occupancy models can improve the monitoring of these species. We combine data from unstructured ranger patrols with datasets from systematic camera traps and sign transects. Our study shows that integrating these datasets enhances occupancy estimate precision and cost-effectiveness of monitoring tigers and prey. Furthermore, the study demonstrates the increased value of unstructured datasets when combined with ecological monitoring data, offering valuable opportunities to advance biodiversity monitoring in the tropics.

Chapter 5: Targeting conservation actions for tigers based on multiple monitoring and anthropogenic threat data

This chapter comprises a prioritisation exercise to identify high-priority areas for Sumatran tiger conservation within their distribution range, focusing on regions with intensive anthropogenic threats including forest loss, hunting, and human-tiger conflict. We test how differences in data sources influence prioritisation by comparing input data from primary datasets, which utilize field-collected data, with secondary datasets, which use expert-derived data and satellite imagery. Our study demonstrates discrepancies between priority regions across data sources, suggesting that the selection of data can lead to different conservation interventions and outcomes.

Chapter 6: Discussion

This final chapter synthesizes insights from the previous chapters and discusses how this thesis contributes to improving biodiversity monitoring and conservation planning in tropical regions, with implications for the existing environmental policies.

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Chapter 2 Insights from 20 years of mammal population research in Indonesia

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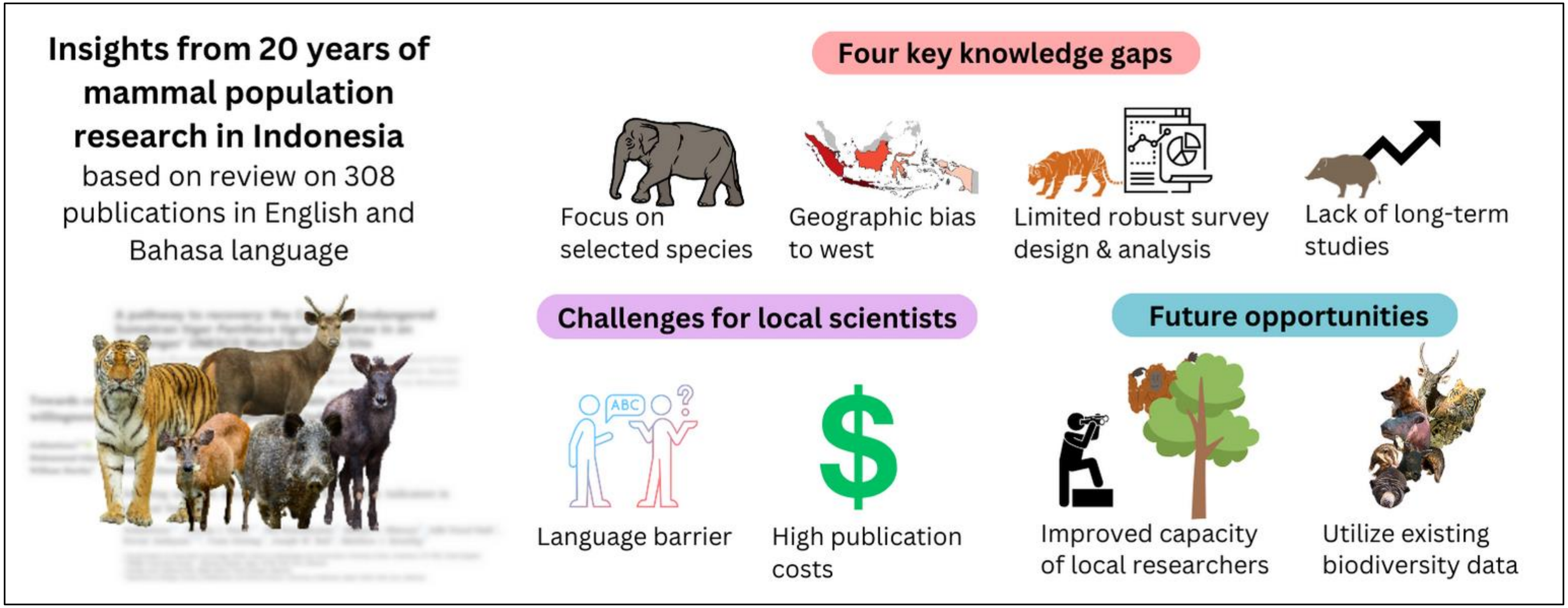
2.1 Abstract

Mammal populations are declining in biodiverse tropical regions. Global analyses have identified Indonesia as a hotspot of vertebrate decline, although relatively few data are available to substantiate these claims. We reviewed research articles published during 2000–2020 on 104 medium-sized to large terrestrial mammal species found in Indonesia to help inform conservation management and future research. We identified 308 peer-reviewed studies published in English or Bahasa Indonesia, with an increase in publication rate (articles published per year) over time. Studies of species distributions dominated the literature, followed by publications on abundance, species diversity and combinations of these topics. Most publications concerned single-species studies conducted at a single location and a single point in time. We identify four key issues that should be addressed by future research and conservation efforts: (1) disproportionate focus on a small number of species; (2) geographical bias towards West Indonesia (Sumatra, Kalimantan and Java–Bali), with few published studies from Central (Sulawesi, Nusa Tenggara and Maluku) and East (Papua) Indonesia; (3) limitations to survey design, sampling effort and data analysis; and (4) lack of long-term wildlife population studies. We also note the challenges local researchers face in publishing their studies in international journals because of language barriers and costs. Greater use of existing biodiversity data and continued capacity building for local researchers, particularly those in central and east Indonesia, are critical to effectively guide future wildlife monitoring and improve the conservation status of Indonesian mammals.

Keywords: Biodiversity loss, capacity building, defaunation, Indonesia, population monitoring, Southeast Asia, species conservation, tropics



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2.2 Introduction

Maintaining biodiversity and ecological functioning is vital to ecosystem health and integrity, but wildlife continues to decline around the world (Ripple et al., 2017). Human activity threatens approximately a quarter of all living species (Díaz et al., 2019), and 32% of the world's monitored species have experienced a decline in population size or distribution since 1900 (Ceballos et al., 2017). This loss of species, also referred to as defaunation, is a global issue, but is currently particularly acute in biodiverse tropical regions, where terrestrial mammal distributions have contracted by >40% since the early 1990s (Gallego-Zamorano et al., 2020), and populations have declined by 13% since 1980 (Benítez-López et al., 2019).

Defaunation disproportionately impacts terrestrial mammals, especially large-bodied species such as carnivores and herbivores, through the combined impacts of habitat loss and overexploitation (Ripple et al., 2016; Benítez-López et al., 2019; Bogoni et al., 2020). Many medium to large-sized mammal species exhibit multiple characteristics that increase their vulnerability to environmental and anthropogenic stressors: they have relatively slow reproductive rates, large home ranges, low population densities, limited geographic distribution, and substantial overlap with human populations (Cardillo et al., 2008).

The loss of mammals in terms of their distribution, abundance and diversity threatens the delivery of regional and global ecosystem services, food security, and human well-being (Dirzo et al., 2014; Young et al., 2016). For example, mammal declines can lead to altered habitat structure, which constrains the regeneration of forests (Gardner et al., 2019) and is also linked to the emergence of zoonotic diseases, disrupted food supplies, and negative interactions between people and wildlife (Singleton et al., 2010; Newbold et al., 2014; Holland et al., 2018).

Global analyses highlight Indonesia and other Southeast Asian countries as defaunation hotspots, but this conclusion is founded on limited data from the region (Ceballos et al., 2017; Allan et al., 2019; Beyer & Manica, 2020). Indonesia harbours 738 terrestrial mammal species, which represents 12% of global mammal diversity

(Maryanto et al., 2019). The country's mammals are among the most threatened taxa in the world, with 79 species (~11%) listed as Endangered or Critically Endangered by the IUCN, 144 (~20%) listed on CITES, and 105 (~14%) formally protected within the country (Maryanto et al., 2019). The increasing stressors acting on mammal populations in Indonesia result from multiple factors. Forest conversion in Indonesia is the most extensive among the Association of Southeast Asian Nations (ASEAN) (Estoque et al., 2019), with 9.79 million hectares (11%) of primary forests lost between 2001 and 2019 (Gaveau et al., 2022). The country has also become a source and hub of global illegal wildlife trade, with estimated financial losses from such trade estimated at USD 600 million per year (Trinirmalaningrum et al., 2016).

Despite this increased scientific attention and global analyses, there is relatively little empirical data available from Indonesia on the topic of biodiversity change or defaunation, implying that the global perception of this problem is underrepresenting – or possibly exaggerating – the true situation in the country. Here we review research articles in the Indonesia-focused literature between 2000 and 2020 in both English and Bahasa Indonesia, considering a broad body of knowledge documenting mammal biodiversity, distributions, or abundance across time and/or locations within the country. We sought to characterize the contents of publications over time, identify the current knowledge gaps, and propose recommendations to the scientific community on how to improve conservation management and future research.

2.3 Materials and methods

2.3.1 Literature search

Defaunation is a relatively new concept, having only been formally introduced in 2014 (Dirzo et al., 2014) Therefore, few publications were likely to explicitly include this term in their title, abstract or keywords. Indeed, even the recent scientific use of defaunation in Indonesia was mainly limited to local agricultural and veterinary studies, absent from ecological studies, and rarely used in popular news coverage (based on Google or Google Scholar search using keywords "DEFAUNATION" OR "DEFAUNASI" - the Bahasa for defaunation, May 2021). Thus, we collated published scientific articles that evaluated the variation in mammal biodiversity, distributions, or abundance, representing different population parameters, over single or multiple spatial scales and temporal periods.

We focused on single or multispecies studies of medium (1-10 kg body mass) to large-bodied (>10 kg) terrestrial mammal species, excluding volant mammals, small mammals (< 1 kg adult body mass), domestic, and introduced animals since these taxa are typically of less concern in the defaunation literature and conservation (See Appendix S2.1 for rationale). Using a national checklist by Maryanto et al. (2019) as the principal reference, we generated a list of 157 medium-large terrestrial mammal taxa, which included arboreal and above-ground species. This amounted to 128 medium-sized species and 29 large species (Appendix S2.2).

Studies were located using a systematic search of peer-reviewed articles published between January 2000 to December 2020. The search, conducted from March to September 2021, used three academic databases: Scopus and Web of Science for English publications, and Indonesia's Garuda (Garba Rujukan Digital) database in which local publications in Bahasa are more prominent. The 21-year study period was used to reflect the growing period of Indonesia's biodiversity publications (Amelia & Rahmaida, 2017) up until the Covid-19 pandemic which impacted scientific activity. We considered studies that utilized both primary and secondary data (e.g. meta-analysis), and excluded literature reviews.

Searching in Scopus and Web of Science databases began via the following keywords with Boolean operators: MAMMAL* AND INDONESIA* AND (BIODIV* OR DIVERS* OR DISTRIBUTION OR POPULATION* OR DENSITY OR ABUNDAN*) NOT MARINE (title, abstract, and keywords). These arguments imply that the keywords must include both mammal and Indonesia keywords, along with a minimum of one of the following keywords (biodiversity, diversity, distribution(s), population(s), density, and abundance), whilst excluding studies from the marine realm. To complement and maximise the findings of the articles, we conducted additional searches using the combinations of two keywords: the common English name of the species and region where the species or mammal distribution is known, e.g. for rhinoceros: RHINO* AND SUMATRA, RHINO* AND JAVA, RHINO* AND KALIMANTAN. The search was replicated for all species in all island groups of Indonesia as appropriate to the taxon (i.e. Sumatra, Kalimantan, Java–Bali, Sulawesi, Nusa Tenggara (Lesser Sunda), Maluku (Mollucas), and Papua), and involved 202 searches.

In the Garuda database, we started the exploration using the terms MAMALIA (Bahasa) or MAMMAL within the title as the database only recognises "AND" Boolean operators. We continued the search by using the species' common English or Indonesian name, for example, RHINOCEROS or BADAK.

2.3.2 Database compilation

Once compiled, the two lead authors (ARD and IMR) read each publication and recorded the following characteristics: population parameter (species diversity, distribution, abundance, or combination of two or three parameters), location (i.e. one of the 34 provinces of Indonesia or regions of West, Central, and East Indonesia), status of study area (protected, non-protected, or both), species group (single or multispecies), first author nationality (Indonesian or non-Indonesian), language used (Bahasa Indonesia or English), and methodology (e.g. study design and data analysis).

Administration boundaries were derived from the Indonesian Geospatial Information Agency (www.big.go.id). The country is divided into three biogeographical regions according to the Wallace and Lydekker lines (Darajati et al., 2016; BPS, 2021): West (Sumatra, Java, Bali, and Kalimantan; 1,160,165 km^2 of land covering 5385 islands), Central (Sulawesi, Nusa Tenggara, and Maluku; 334,750 km^2 covering 6320 islands), and East (Papua; 421,991 km^2 covering 5061 islands). The protected land boundary was confirmed via the Ministry of the Environment and Forestry of Indonesia's protected area database (www.geoportal.menlhk.go.id).

Species group was determined by the number of species studied in the article: single species (e.g. Sumatran orangutan *Pongo abelii*) or multispecies (e.g. primate community) (Maryanto et al., 2019). We assessed the first author locality based on an assessment of author names and affiliations. Publication language was classified based on the principal language of the articles, excluding the abstract. Last, we noted studies that implemented an appropriate scientific design (i.e. reported the study design clearly in the publication or justified the selection of sample size/sites in relation to the research question) and statistical/modelling approach that accounted for imperfect detection.

2.4 Results

Our systematic literature review returned 308 peer-reviewed articles. The publication rate increased over time with an average addition of two publications per year ($R2 = 0.78$, $F1,19 = 67.1$, $p < 0.0001$) (Fig. 2.1). This trend was associated with the increase of publications on distribution (125 publications, 40.6%), abundance (84, 27.3%), diversity (42, 13.6%), and a combination of parameters (57, 18.5%) respectively ($\beta = 0.68, 0.41, 0.33, 0.29$, $p < 0.001$). The highest number of publications was produced in 2019.

Single-species publications dominated our search results (217, 70.5%). The rest focused on multiple species (e.g. herbivores or carnivores) or the mammal community as a whole. Most studies were conducted at a single point in time (277, 89.9%) and in one location (225, 73.1%). The number of articles published in English (155, 50.3%) was similar to that of papers published in Bahasa Indonesia (153, 49.7%). More English-language publications were led by non-Indonesian authors (90, 58.1%) than Indonesian authors (66, 42.6%), and all Bahasa articles were led by Indonesian authors.

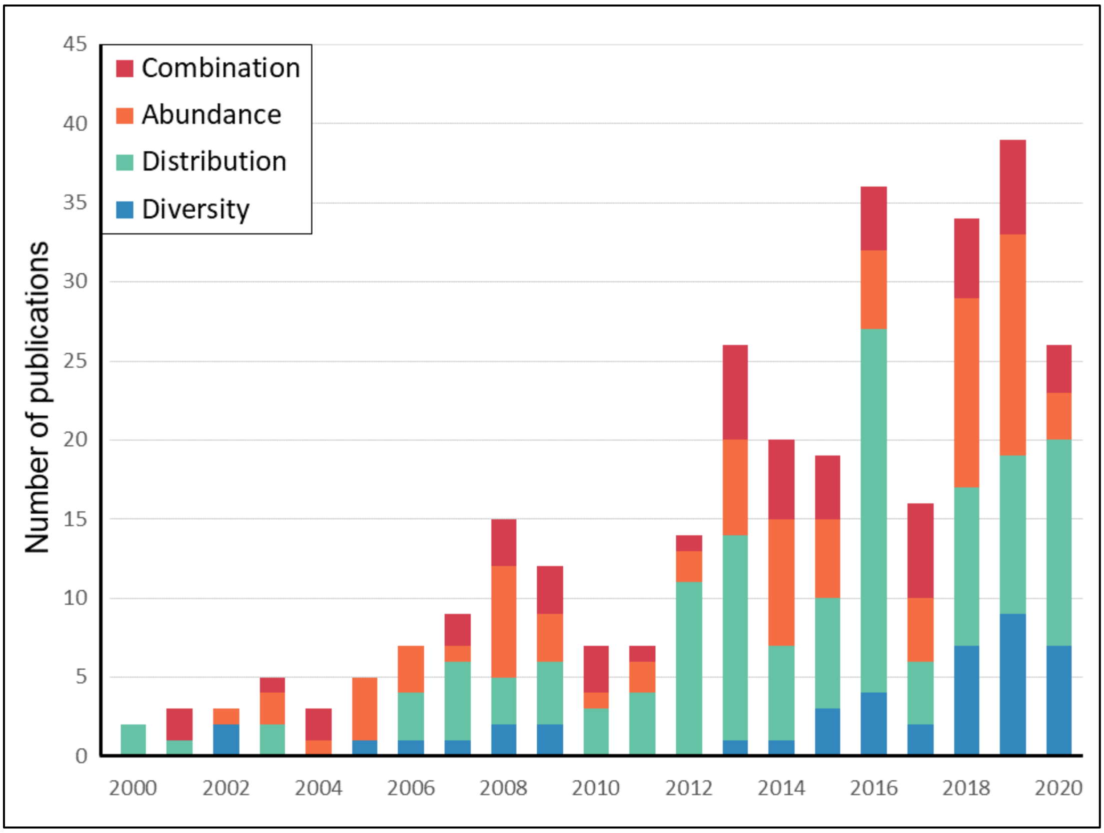

Fig 2.1: Number and type of publications on mammal biodiversity in Indonesia during 2000–2020.

Published studies showed a marked regional/provincial bias (Figs 2.2 & 2.3): most publications were based on research undertaken in West Indonesia (268, 87.0%), with much fewer studies focused on Central (23, 7.4%) and East (9, 2.9%) Indonesia. Even when accounting for variation in species numbers across the archipelago, publication effort (i.e. number of publications per number of species found in the island group) was much higher in western than eastern islands (Fig. 2.2B, Appendix S2.3). For example, 12 times more publications were produced for mammals in Java–Bali than for those in Papua. Only eight publications (2.6%) considered the national scale. The majority of research was based in three provinces in West Indonesia: West Java (37 articles, 12.0%), Central Kalimantan (23, 7.7%) and East Kalimantan (14, 4.5%). Nevertheless, four out of five provinces with no publications were located in West Indonesia: Bangka Belitung, Jakarta Capital Region, the Riau Islands, and the newly established (2012) province of North Kalimantan. There were also no publications from the recently established (2004) West Sulawesi province in Central Indonesia.

Most field studies were undertaken in sites that cover both protected and unprotected areas (193 sites; 41.0%), followed by studies focused solely on either protected areas (181 sites; 39.0%) or unprotected areas (92 sites; 20.0%).

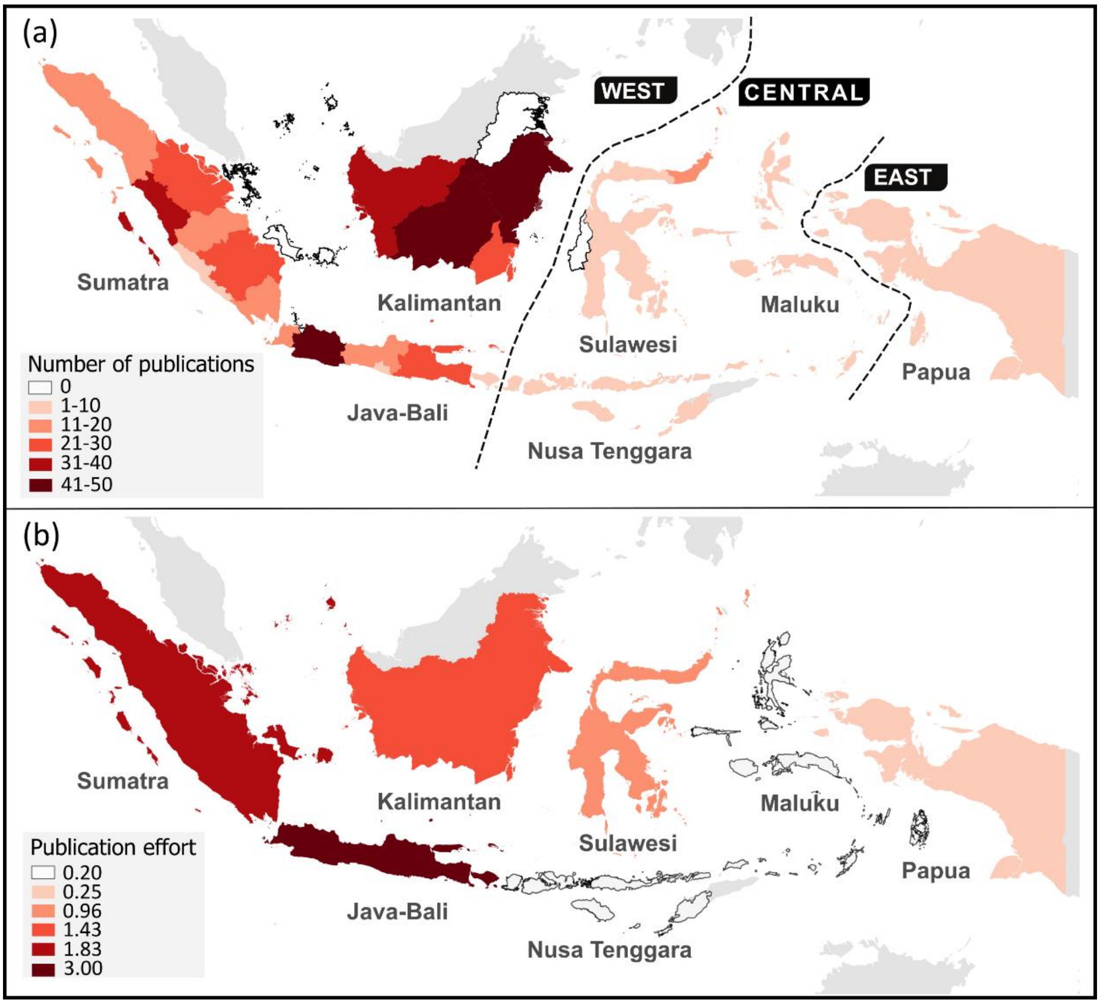

Fig 2.2: (A) Spatial distribution of mammal research effort in Indonesia based on 308 studies published during 2000–2020. The colour of provinces reflects the number of publications focused on the mammals from that province. (B) Spatial distribution of publication effort (number of publications divided by number of species) per island group.

Of the 157 mammal species considered, 104 (66.2%) were studied as either a single focal taxon (64) or within a species group (40). Orangutans *Pongo sp*. (a total of 27 articles), tigers *Panthera tigris* (12), and Asian elephants *Elephas maximus* (11) had more single-species publications than other large mammal taxa (1–15 studies). The long-tailed macaque *Macaca fascicularis*, spangled ebony langur *Trachypithecus* *auratus*, and Javan slow loris *Nycticebus javanicus* dominated publications about medium-sized mammals, with 18, 12, and 10 studies, respectively. Generalist large species such as wild boar *Sus scrofa* (32), southern red muntjac *Muntiacus muntjak* (32), and sun bear *Helarctos malayanus* (25), along with medium-sized species such as the long-tailed macaque (37), leopard cat *Prionailurus bengalensis* (36), and southern pig-tailed macaque *Macaca nemestrina* (28) were often studied in multi-species publications (Appendix S2.2).

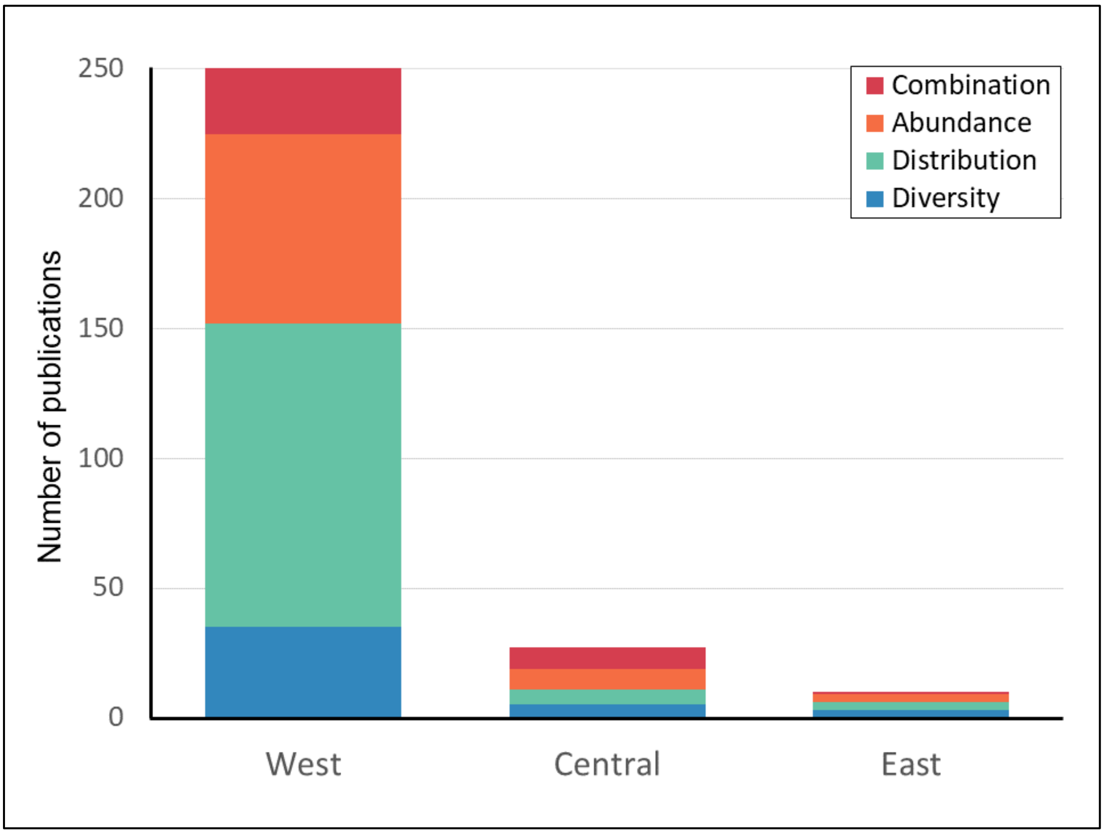

Fig 2.3: Number of studies published during 2000–2020 focusing on the main regions of Indonesia, by study topic.

2.5 Discussion

We found that most publications on Indonesia's mammal populations focused on distributions and abundance of single species and were geographically biased to the west of the country. Nevertheless, useful datasets are being generated as the conservation of medium and large mammals receives increased conservation attention and funding, improving our knowledge on population declines, range contraction, and extirpation dynamics (MacKenzie et al., 2003; Peterman et al., 2013). We outline four major research gaps to be addressed:

1) Disproportionate focus on numbers of species

The taxonomic dominance towards a few well-studied species in the Indonesian literature reflects funding priorities, species conservation status, familiarity with taxa, and research capacity. Wildlife research and conservation measures require long-term financial support, which is often targeted to a narrow subset of high-profile species In Indonesia, the government focusses conservation actions on 25 priority species (MoEF, 2015), 14 of which were included in our review. These species were studied more than any other taxa, in part to support the government's target. Indeed, most research and conservation investments centre on funds raised for tigers, orangutans, rhinoceros *Dicerorhinus sumatrensis*, and elephants (KEHATI, 2019; Santika et al., 2022).

Species familiarity and research accessibility also contribute to species bias. The long-tailed macaque received the greatest publication effort, albeit a commensal primate coexisting with people (Eudey et al., 2021). The species can be easily observed, and most studies were undertaken in accessible human settlements and nearby forests (e.g. Santoso et al., 2019). Publication effort was also reflected by the presence of long-term species conservation projects in west Indonesia (e.g. Kalimantan's orangutans (Knott et al., 2021), Sumatran tigers (Chandradewi et al., 2019), and Javan lorises (Nekaris, 2016). If this trend continues then initiatives established more recently in central and eastern Indonesia might lead to greater research efforts in these regions e.g. Talaud bear cuscus in Sulawesi and long-beaked echidna in Papua (Sheherazade, 2023).

2) Uneven geographical representation

Research efforts focused primarily on Java–Bali, Sumatra and Kalimantan, with relatively little work undertaken in the eastern islands. Ten times more studies were published on mammals from West Indonesia compared to central islands (Sulawesi, Maluku, lesser Sundas), and 20 times more than those in East Indonesia (Papua).

Most Indonesian islands support medium/large mammals, but more species are found in the west, including conservation flagships and commensals that attract research attention. Even when this uneven diversity is accounted for, publication rates per species are still greater for Java–Bali, Sumatra and Kalimantan. In Central Indonesia, small-bodied mammals tend to receive a greater focus, given the interest of the Wallacea region for evolutionary biology and biogeography (Broto & Mortelliti, 2019; Struebig et al., 2022). Taxonomic and molecular studies have also resulted in the splitting of several prominent species (e.g. tarsiers and macaques in Sulawesi; lorises, gibbons and langurs on Kalimantan and Sumatra) into many cryptic taxa, reducing the number of publications per species.

Research capacity is also concentrated in western islands. Of the 219 publications led by Indonesian researchers, 73% were affiliated with universities based in Java–Bali, Sumatra, or Kalimantan. Equally, non-governmental organisations (NGOs) and government ecological and conservation expertise are also disproportionately focused in this region. Research effort thus follows the distribution of threats to a restricted set of species. The two decades of research that we assessed coincided with intensive deforestation in Kalimantan and Sumatra (Margono et al., 2014; Gaveau et al., 2022), however, in recent years, industrial agriculture and mining have expanded eastwards (Supriatna et al., 2020; Voigt et al., 2021). Wildlife exploitation and trade are also prominent in Central and East Indonesia (Pattiselanno et al., 2019; Latinne et al., 2020), which could exacerbate population declines of endemic and forest-dependent species through habitat change. Thus, threats to mammals are shifting and/or expanding across the country, implying that research and monitoring efforts will need to follow suit to be effective.

3) Study limitations

Most articles reported little information on study design, disregarded advances in survey methods, and/or lacked robust statistical analyses. For example, 92% of studies did not account for imperfect detection, and would have benefited from more rigorous analytical approaches such as occupancy modelling, distance sampling, or capture-recapture. Sampling location often appeared based on convenience (i.e. near forest boundaries or accessible terrain), with publications frequently omitting key information on sampling approaches. Some were also prone to replication issues, such as limited sample sizes or highly unequal efforts between habitat types or treatments. The potential for species misidentification (i.e. false positives) was high. For instance, the Javan mouse deer *Tragulus javanicus* was reported beyond the confirmed species distribution in Java in several studies. To rectify these problems, researchers should appropriately consider species ecology (i.e. grid size for camera trapping reflecting species home range) and the minimum sample sizes required to support statistical models (i.e. through power analysis). Accounting for bias (i.e. imperfect detection and false positives) is essential to ensure scientifically robust conclusions can be derived from analyses.

4) Limited long-term population studies

Appropriate study design and data analysis also allow researchers to replicate population studies over time, which can be highly useful for tracking population trends and evaluating conservation impact (Purwandana et al., 2014; Chandradewi et al., 2019). This is the very information that is lacking from global defaunation analyses, especially in Southeast Asia (Dornelas et al., 2018). In Indonesia, most biodiversity studies have been undertaken over short timeframes, often to provide baseline data without adequate planning for future monitoring.

While comparing biodiversity patterns between various habitats or treatments can yield useful information on disturbance, studying population or community changes over time can better explain response mechanisms (Setiawan et al., 2018). Long-term studies can also reveal potential impacts of population changes on the wider community and ecosystem (e.g. removal of tigers can lead to surges of ungulate prey that raid farmland (Thinley et al., 2018)). Yet, we found only a few published examples that span more than one decade (e.g. siamang *Symphalangus syndactylus* densities in Sumatra (Lappan et al., 2017); Javan rhinoceros *Rhinoceros sondaicus* in Java (Setiawan et al., 2018)).

2.5.1 Enhancing Indonesia's biodiversity research capacity

Mainstreaming well-designed wildlife population research is important for biodiversity conservation across the world. From our review of Indonesian literature, only 104 of 156 medium-large mammal species have population information available at local or regional scales, and much of this is patchy. It will be important to further enhance the scientific capacity of local researchers, who are highly capable of collecting data, but often struggle to design or resource ecological studies appropriate for analysis. Access to training and/or literature is often limited, not least because the bulk is in English. This is also a problem for publishing research internationally – only 28% of 156 articles were led by Indonesian authors in English-language journals.

Language is a barrier for many non-English speakers to remain updated with research advances and techniques, as well as writing and publishing in international journals (Amano et al., 2021). Local language publications are thus highly important for informing mammal population assessments, but these studies have limited exposure internationally – particularly to global analyses (Amano et al., 2016). Publication costs are also prohibitive with a typical journal publication fee of $1,300 per article being four times the monthly minimum wage in Jakarta. There are few options available to fund these costs institutionally in Indonesia (Sunol & Saturno, 2008), leaving researchers reliant on fee waivers or open access agreements between publishers and institutions overseas. Thus, substantial data useful for conservation and defaunation research are in the 'grey literature', and remain difficult to access – including for this review.

Nevertheless, English language proficiency is improving, and early-career researchers have greater access to postgraduate training and overseas scholarships than at any time in Indonesia's history. More resources are needed in Bahasa, and universities, NGOs, and local chapters of global professional societies (e.g. Association for Tropical Biology and Conservation; Society for Conservation Biology) have key roles to play. Notable initiatives include Conservation Camps led by the Tambora Muda Conservationist Network, R statistical workshops by R-Ladies Indonesia, and NGO scholarships (e.g. Research Fellowships by the Wildlife Conservation Society-Indonesia Program). This is also an opportunity for local universities to establish more conservation-focused postgraduate programmes outside of Java to ensure capacity reaches eastern regions.

2.5.2 Utilizing existing data

Indonesia's ecological research and conservation programmes produce a significant amount of wildlife data that could inform population monitoring and conservation. For example, tiger researchers pooled occupancy data across Sumatra from 2007 and 2009 (and new data are being collected using the same survey design), producing valuable 'bycatch' data on other non-target species; although only tiger data have been analysed so far (Wibisono et al., 2011). The country also adopted Spatial Monitoring and Reporting Tool (SMART) in protected areas nationwide, thus offering more joined-up data on biodiversity and threats (Kholis et al., 2016). The government's launch of a national biodiversity database is also a promising development that should help track population status and biodiversity trends. Yet, these databases will need significant investment for maintenance, verification and analysis to be of use. Granting access to researchers to query and analyse biodiversity data (i.e. in similar ways to the Global Biodiversity Information Facility/GBIF), will be an important step in achieving this goal.

Many tropical countries face significant challenges monitoring large numbers of species, thereby undermining evidence-based conservation management (Ceballos et al., 2017). Our review of the English and Bahasa-based literature on mammal population research in Indonesia revealed notable knowledge gaps (species bias, geographic disparity, study design and analysis, and limited long-term research) that are also relevant to wildlife monitoring in other countries. Furthering research capacity and making it easier to share and utilize existing data are some of the key ways to enhance the data needed for robust wildlife population monitoring and investigation of possible defaunation trends. Moreover, we advocate a holistic approach by integrating human perspectives to better understand and address the interconnected drivers of biodiversity loss.

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2.8 Supplementary information

Appendix S2.1: Rationale for only including medium-sized to large mammal taxa in the review.

Our review focussed on larger taxa and did not account for small (body mass < 1 kg) and volant mammals. Smaller mammals fulfil multiple ecological roles in tropical forests although their susceptibility to population declines due to human activity is not as widespread over taxa as their larger mammal counterparts. The taxonomy of small mammals and bats remains highly complicated east of the Wallace line where there are few field guides available to researchers, and little consensus among taxonomists owing to the highly complicated biogeographic process that shaped the region (Struebig *et al.*, 2022). This resulted in naming conventions and species lists that have changed considerably over 20 years, making it harder to track research efforts over our study period. We also acknowledge that most research on small and volant mammals is biased towards taxonomy to help resolve these issues, and also behaviour (see Broto & Mortelliti (2019) for a review of literature for Sulawesi), which is beyond the scope of our population research review. Most conservation decision-making in Indonesia is based around highly threatened charismatic mammal species (MoEF, 2015). We therefore focussed on these taxa, though we advocate for more research attention on lesser-known, small and volant mammals.

Appendix S2.2: Number of publications by species. Species highlighted in red had no publication recorded in the review. The total number of publications is higher than the number of studies (308) because some studies covered multiple species.

Body size	Species	Type of publications		Total publications
		Single species	Multi-species	
Medium	*Ailurops melanotis*	1	0	1
Medium	*Ailurops ursinus*	1	3	4
Medium	*Aonyx cinereus*	1	6	7
Medium	*Arctictis binturong*	0	13	13
Medium	*Arctogalidia trivirgata*	1	9	10
Medium	*Arctonyx collaris*	0	1	1
Large	*Axis kuhlii*	0	0	0

Large	*Babyrousa babyrussa*	0	0	0
Large	*Babyrousa bolabatuensis*	0	0	0
Large	*Babyrousa celebensis*	1	0	1
Large	*Babyrousa togeanensis*	0	0	0
Large	*Bos javanicus*	7	3	10
Large	*Bubalus depressicornis*	3	0	3
Large	*Bubalus quarlesi*	0	0	0
Large	*Capricornis sumatraensis*	2	4	6
Medium	*Catopuma badia*	1	2	3
Medium	*Catopuma temminckii*	0	10	10
Medium	*Cercartetus caudatus*	0	0	0
Large	*Cuon alpinus*	1	6	7
Medium	*Cynogale bennettii*	1	3	4
Medium	*Dendrolagus dorianus*	0	0	0
Medium	*Dendrolagus goodfellowi*	0	0	0
Medium	*Dendrolagus inustus*	0	2	2
Medium	*Dendrolagus mbaiso*	1	0	1
Medium	*Dendrolagus stellarum*	0	0	0
Medium	*Dendrolagus ursinus*	0	1	1
Large	*Dicerorhinus sumatrensis*	3	2	5
Medium	*Diplogale hosei*	1	1	2
Medium	*Dorcopsis hageni*	0	0	0
Medium	*Dorcopsis luctuosa*	0	0	0
Medium	*Dorcopsis muelleri*	1	1	2
Medium	*Dorcopsulus vanheurni*	0	0	0
Large	*Elephas maximus*	11	5	16
Large	*Helarctos malayanus*	5	25	30
Medium	*Hemigalus derbyanus*	1	11	12
Medium	*Herpestes brachyurus*	1	6	7
Medium	*Herpestes javanicus*	0	6	6
Medium	*Herpestes semitorquatus*	1	2	3
Medium	*Hylobates abbotti*	0	0	0
Medium	*Hylobates agilis*	1	5	6
Medium	*Hylobates albibarbis*	2	2	4
Medium	*Hylobates funereus*	0	1	1
Medium	*Hylobates klossii*	4	4	8
Medium	*Hylobates lar*	0	1	1
Medium	*Hylobates moloch*	6	4	10
Medium	*Hylobates muelleri*	0	6	6

Medium	*Lutra lutra*	0	1	1
Medium	*Lutra sumatrana*	0	3	3
Medium	*Lutrogale perspicillata*	0	3	3
Medium	*Macaca brunnescens*	0	0	0
Medium	*Macaca fascicularis*	18	37	55
Medium	*Macaca hecki*	0	0	0
Medium	*Macaca maura*	1	0	1
Medium	*Macaca nemestrina*	0	28	28
Medium	*Macaca nigra*	6	1	7
Medium	*Macaca nigrescens*	0	0	0
Medium	*Macaca ochreata*	1	1	2
Medium	*Macaca pagensis*	0	1	1
Medium	*Macaca siberu*	0	3	3
Medium	*Macaca togeanus*	0	0	0
Medium	*Macaca tonkeana*	1	1	2
Medium	*Macrogalidia musschenbroekii*	1	0	1
Medium	*Macropus agilis*	1	0	1
Medium	*Manis javanica*	3	16	19
Medium	*Martes flavigula*	2	14	16
Medium	*Melogale orientalis*	0	3	3
Large	*Muntiacus atherodes*	0	3	3
Large	*Muntiacus montanus*	0	0	0
Large	*Muntiacus muntjak*	0	32	32
Medium	*Mustela lutreolina*	0	0	0
Medium	*Mustela nudipes*	1	1	2
Medium	*Mydaus javanensis*	1	8	9
Medium	*Nasalis larvatus*	7	5	12
Medium	*Neofelis diardi*	6	21	27
Medium	*Nycticebus bancanus*	0	0	0
Medium	*Nycticebus borneanus*	0	2	2
Medium	*Nycticebus coucang*	2	3	5
Medium	*Nycticebus javanicus*	10	5	15
Medium	*Nycticebus kayan*	0	0	0
Medium	*Nycticebus menagensis*	0	0	0
Medium	*Paguma larvata*	0	9	9
Large	*Panthera pardus*	4	10	14
Large	*Panthera tigris*	12	16	28

Medium	*Paradoxurus hermaphroditus*	3	25	28
Medium	*Pardofelis marmorata*	1	15	16
Medium	*Phalanger alexandrae*	0	0	0
Medium	*Phalanger carmelitae*	0	0	0
Medium	*Phalanger gymnotis*	0	0	0
Medium	*Phalanger intercastellanus*	0	0	0
Medium	*Phalanger matabiru*	0	0	0
Medium	*Phalanger mimicus*	0	0	0
Medium	*Phalanger orientalis*	0	3	3
Medium	*Phalanger ornatus*	0	1	1
Medium	*Phalanger rothschildi*	0	1	1
Medium	*Phalanger sericeus*	0	0	0
Medium	*Phalanger vestitus*	0	0	0
Large	*Pongo abelii*	9	4	13
Large	*Pongo pygmaeus*	15	7	22
Large	*Pongo tapanuliensis*	3	0	3
Medium	*Presbytis canicrus*	0	0	0
Medium	*Presbytis carimatae*	0	0	0
Medium	*Presbytis chrysomelas*	0	0	0
Medium	*Presbytis comata*	5	5	10
Medium	*Presbytis femoralis*	0	2	2
Medium	*Presbytis frontata*	0	2	2
Medium	*Presbytis hosei*	1	0	1
Medium	*Presbytis ignita*	0	0	0
Medium	*Presbytis melalophos*	1	9	10
Medium	*Presbytis natunae*	0	0	0
Medium	*Presbytis potenziani*	0	4	4
Medium	*Presbytis rubicunda*	2	8	10
Medium	*Presbytis rubida*	0	0	0
Medium	*Presbytis sabana*	0	0	0
Medium	*Presbytis siberu*	0	1	1
Medium	*Presbytis thomasi*	0	1	1
Medium	*Prionailurus bengalensis*	2	36	38
Medium	*Prionailurus planiceps*	3	6	9
Medium	*Prionailurus viverrinus*	0	0	0
Medium	*Prionodon linsang*	1	12	13
Medium	*Pseudochirops albertisii*	0	0	0

Medium	*Pseudochirops corinnae*	0	0	0
Medium	*Pseudochirops coronatus*	0	0	0
Medium	*Pseudochirops cupreus*	0	0	0
Medium	*Pseudochirulus canescens*	0	0	0
Medium	*Pseudochirulus caroli*	0	0	0
Medium	*Pseudochirulus mayeri*	0	0	0
Medium	*Pseudochirulus schlegeli*	0	0	0
Large	*Rhinoceros sondaicus*	6	1	7
Large	*Rusa timorensis*	3	3	6
Large	*Rusa unicolor*	3	24	27
Medium	*Simias concolor*	0	4	4
Medium	*Spilocuscus maculatus*	2	7	9
Medium	*Spilocuscus papuensis*	0	1	1
Medium	*Spilocuscus rufoniger*	0	1	1
Medium	*Spilocuscus wilsoni*	0	0	0
Medium	*Strigocuscus celebensis*	0	2	2
Medium	*Strigocuscus pelengensis*	0	1	1
Large	*Sus barbatus*	1	14	15
Large	*Sus celebensis*	0	2	2
Large	*Sus scrofa*	0	32	32
Large	*Sus verrucosus*	1	0	1
Medium	*Symphalangus syndactylus*	5	10	15
Medium	*Tachyglossus aculeatus*	0	0	0
Large	*Tapirus indicus*	3	15	18
Medium	*Thylogale browni*	0	0	0
Medium	*Thylogale brunii*	0	0	0
Medium	*Thylogale stigmatica*	0	0	0
Medium	*Trachypithecus auratus*	12	10	22
Medium	*Trachypithecus cristatus*	1	5	6
Medium	*Tragulus javanicus*	0	8	8
Medium	*Tragulus kanchil*	0	6	6
Medium	*Tragulus napu*	0	10	10
Medium	*Viverra tangalunga*	1	12	13
Medium	*Viverricula indica*	0	6	6
Medium	*Zaglossus attenboroughi*	0	0	0
Medium	*Zaglossus bartoni*	0	0	0
Medium	*Zaglossus bruijnii*	0	0	0

Appendix S2.3: Publication effort across seven island groups in Indonesia.

Island groups	Number of species	Number of publications	Publication effort (number of publications/number of species)
Sumatra	63	115	1.83
Kalimantan	54	77	1.43
Java-Bali	30	90	3.00
Nusa Tenggara	10	2	0.20
Sulawesi	25	24	0.96
Maluku	20	4	0.20
Papua	40	10	0.25

Reference for supplementary information

Broto, B. and Mortelliti, A. (2019) 'The status of research on the mammals of Sulawesi, Indonesia', Mammal Review, 49(1), pp. 78–93. doi: 10.1111/mam.12141.

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Chapter 3 Selecting umbrella species as mammal biodiversity indicators in tropical forest

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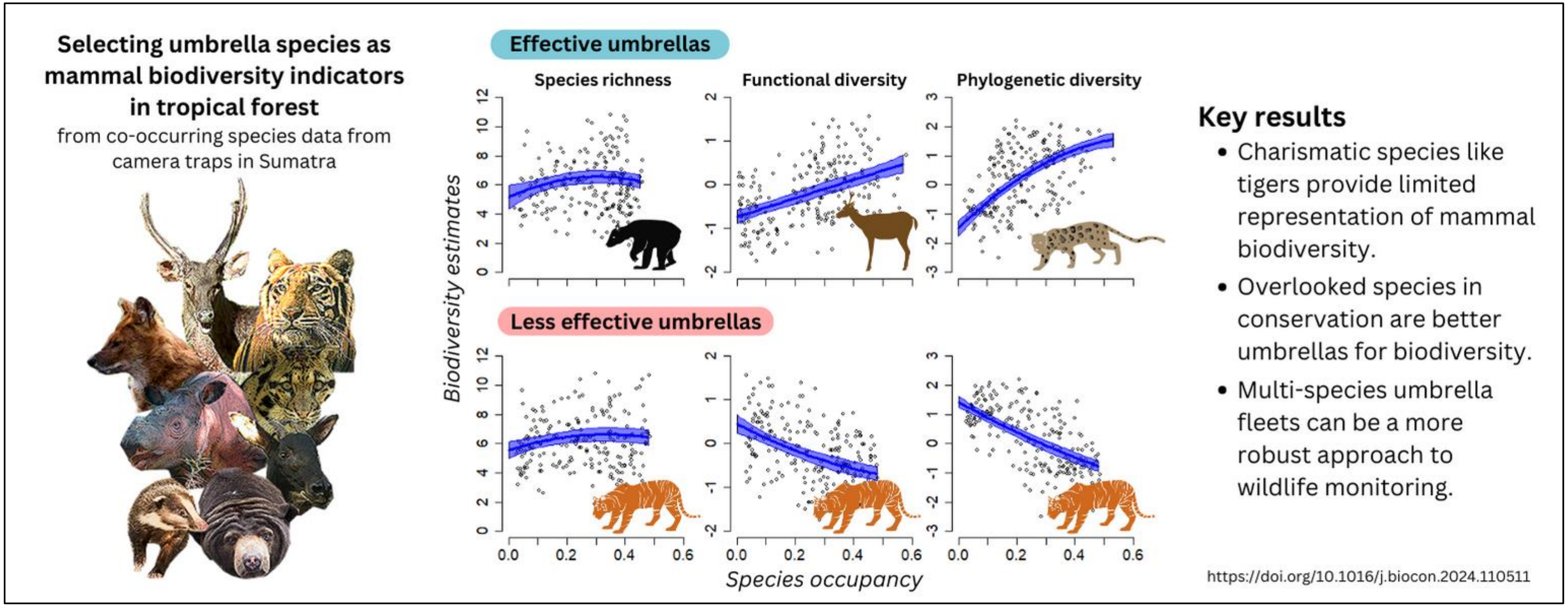
3.1 Abstract

Conservation managers often monitor umbrella species as indicators of broader biodiversity patterns, but this assumption is seldom evaluated due to a lack of survey data and objective umbrella criteria. We evaluated the performance of eight candidate umbrella species in representing broader patterns of mammal biodiversity in Sumatra, Indonesia, using a comprehensive camera trap dataset from the island's largest remaining tropical rainforest. We employed an occupancy modelling framework to quantify the association between species-level occupancy and four community-level biodiversity parameters while accounting for imperfect detection. Sambar deer (*Rusa unicolor*) and clouded leopard (*Neofelis diardi*) were consistently ranked the top umbrellas. Areas where these species were prevalent were associated with higher levels of community occupancy, species richness, functional, and phylogenetic diversity. Sumatran tiger (*Panthera tigris sumatrae*) and rhinoceros (*Dicerorhinus sumatrensis*) were among the lower ranked umbrellas, and inadequately represented other biodiversity parameters despite being the main subjects of monitoring. Our results demonstrate that the occurrence status of charismatic species commonly regarded as umbrellas does not necessarily represent broader patterns of biodiversity. Species that are frequently overlooked by conservation decision-making may better represent overall mammal diversity. We advocate utilizing umbrella fleets with multiple species monitored to better represent biodiversity patterns and encourage broader application of our data-driven framework to assess umbrella species performance.

Keywords: Biodiversity surrogate, functional diversity, occupancy modelling, phylogenetic diversity, protected areas, Southeast Asia, species richness, umbrella fleet



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3.2 Introduction

Safeguarding biodiversity is an overarching conservation goal, but in reality, limited resources place constraints on the scale and extent of species protection (Allan et al., 2019; Sitas et al., 2009). Threats to biodiversity are especially profound in tropical regions where human activities have led to a contraction of terrestrial mammal distributions by >40% since the 1990s (Gallego-Zamorano et al., 2020). To overcome this issue, conservation managers often focus on umbrella species, assuming that prioritizing, protecting, and monitoring a single (e.g. Drever et al., 2019; Thornton et al., 2016) or a small number of species (e.g. Maslo et al., 2016; Steenweg et al., 2023) will benefit other co-occurring taxa. In monitoring programs, umbrella species are often used as proxies for broader patterns of biodiversity without the need to acquire and analyze data for the entire community (Caro, 2010). The use of umbrella species in this way, if proven representative, should lead to efficiencies and cost savings in ecological monitoring and conservation programs.

The umbrella concept assumes the presence of certain species – usually wide-ranging ones with large area requirements – is co-distributed with other taxa (Caro, 2010). Despite being a fundamental tool in wildlife monitoring, the reliability of the umbrella species approach is uncertain since there is limited quantitative evaluation of species performance to reflect overall patterns of biodiversity (Steenweg et al., 2023; Thornton et al., 2016). For example, large-bodied charismatic species (generally mammals) are typically selected as umbrellas based on public interest or their capacity to generate conservation funding, rather than an underlying correlation between their distributions and those of other taxa (Caro, 2010; Di Minin and Moilanen, 2014; McGowan et al., 2020). Moreover, umbrella species assessment is often hampered by insufficient data due to the high cost of monitoring programs in terms of data acquisition and analysis, as well as difficulties in evaluating the status of cryptic and elusive species (Wearn and Glover-Kapfer, 2019). This is exacerbated by approaches that generate data for single or selected species, while ignoring the broader wildlife community (Chaudhary et al., 2022; Lindenmayer and Likens, 2011).

An additional constraint to identifying umbrella species is that most assessments focus on a single biodiversity parameter such as species richness – i.e. the number of species in the community (Drever et al., 2019; Thornton et al., 2016). However, richness can be a misleading biodiversity parameter because it does not account for species identity or distinguish between native and non-native species. Other important biodiversity parameters, such as functional and phylogenetic diversity, are often overlooked (Jarzyna and Jetz, 2016). Functional diversity (FD) informs wildlife community functional uniqueness and trait distribution patterns (Laliberte and Legendre, 2010), while phylogenetic diversity (PD) accounts for community evolutionary history and relationship patterns (Winter et al., 2013). These parameters have important roles in the biological community e.g. the loss of species with important ecological roles can trigger cascading ecological impacts and the extinction of evolutionarily-distinct species extirpates millions of years of evolutionary information (Brum et al., 2017). Measures of functional or phylogenetic diversity are increasingly used to account for the community's resilience towards environmental change and anthropogenic disturbances (Gorczynski et al., 2021; Penjor et al., 2022) and to inform conservation priorities (Brum et al., 2017; Rapacciuolo et al., 2019). Yet they are rarely considered in conservation decision-making at a local level.

Few umbrella evaluations have explicitly accounted for imperfect detection (e.g. Mortelliti et al., 2022; Steenweg et al., 2023), which can cause substantial bias in biodiversity parameter estimates (Laliberte and Legendre, 2010; Si et al., 2018). Advances in monitoring and statistical methods can overcome some of the detectability limitations associated with identifying appropriate umbrella species. For example, remotely-operated technologies such as camera traps can generate data on multiple species, including elusive and cryptic species that inhabit tropical forest ecosystems (Wearn and Glover-Kapfer, 2019).

The proliferation of hierarchical multi-species models provides a robust analytical framework to characterize the occupancy status of individual species and entire communities while accounting for detection bias (Dorazio and Royle, 2005; MacKenzie et al., 2018). Species occupancy is more useful for conservation management than presence/absence or distribution range as it can inform where individuals occur in suboptimal environments on the edge of their fundamental niche (i.e. the environmental conditions in which a species is able to survive and reproduce) (MacKenzie et al., 2018). These models also produce improved precision of species-specific effects for rare or elusive species, effectively allowing more explicit consideration of underrepresented taxa in conservation management (Dorazio and Royle, 2005; Pacifici et al., 2014).

We assessed the performance of eight candidate umbrella species to represent multiple facets of biodiversity (community occupancy, species richness, functional diversity, and phylogenetic diversity) in a tropical rainforest mammal community while accounting for imperfect detection. In particular, we were interested in whether the occupancy of commonly used umbrella species e.g. charismatic megafauna like the Sumatran tiger (*Panthera tigris sumatrae*) and rhinoceros (*Dicerorhinus sumatrensis*) followed the broad patterns of mammal biodiversity, or whether they are better represented by other taxa. To answer this objective, first, we applied an occupancy modelling framework to inform species and community-level occurrence and species richness. Second, we calculated detection-corrected estimates of functional and phylogenetic diversity. Finally, we tested the strengths and patterns of association between umbrella species occupancy and four community-level biodiversity parameters. Our case-study is based on an extensive camera trapping campaign undertaken in an extensive tropical forest in Sumatra, Indonesia, with focus on mammals since they are frequently promoted as umbrellas and the target of conservation programs.

3.3 Materials and methods

3.3.1 Study system

We undertook our evaluation in the Leuser Ecosystem, a 25,000 km^2 tract of contiguous tropical forest in northern Sumatra (Fig. 3.1). The area comprises a mosaic of peat swamp, lowland, hill, sub-montane, and montane forest. While 75% of the landscape (18,673 km^2) is designated for conservation – including the Gunung Leuser

National Park (8282 km^2), a UNESCO World Heritage Site – the remaining forest experiences some encroachment from agricultural expansion, road development, and human settlements (Sloan et al., 2018).

3.3.2 Biodiversity monitoring

To obtain detection/non-detection data for the mammal community, we conducted two systematic camera trap surveys: one in the West of Leuser (multiple clusters; 132 sites; May 2016 – August 2017) and another survey in the East Leuser (a single cluster; 84 sites; June 2017 – March 2018). Four camera trap models were utilized: Panthera V4 and V5, Reconyx HC500, and Bushnell NatureView 119440. After removing malfunctioned cameras from the dataset, we retrieved information from 212 camera trap sites (west = 128; east = 84), stratified across the four dominant forest types of the region: montane (>1800 m; 41 locations), sub-montane (1000-1800 m; 63 sites), hill (300-1000 m; 58 sites), and lowland forest (0-300 m; 50 sites). Camera sites were distributed across an elevational range of 19-2754 m asl (mean = 1008 m asl) and separated by a mean distance of 2 km (range: 0.9-5.3 km). At each site, a pair of cameras were deployed in parallel on forest trails or clearings approximately 0.5 m off the ground. On average, cameras were deployed for 85 consecutive trap nights per site (range: 10-230 nights), yielding a total survey effort of 18,102 nights.

3.3.3 Analytical framework

We calculated four biodiversity parameters derived from an occupancy modelling framework to explicitly account for detection bias: community occupancy and species richness derived from the occupancy model, along with the detection-corrected measures of functional and phylogenetic diversity.

1) Occupancy modelling

We employed Bayesian hierarchical multi-species occupancy models with data augmentation (Dorazio et al., 2006; Kery and Royle, 2016) to estimate community-level occupancy (i.e. the weighted average of all species occupancy estimates based on number of species detections), species-specific occupancy, and species richness. We combined detection data from West and East Leuser study areas and collapsed species-specific detection histories into sampling occasions of five camera trap nights to reduce over-dispersion and increase independence between temporal occasions (MacKenzie et al., 2018). To fulfil the assumption of demographic closure, we limited the data period to 90 days, resulting in a maximum of 18 sampling occasions per site (range: 3-18 occasions). We excluded species that could not be reliably detected using our survey methods (i.e. highly arboreal species like Sumatran orangutan *Pongo abelii*, Thomas' langur *Presbytis thomasi*, and black giant squirrel *Ratufa bicolor*; N = 3) and domestic taxa (i.e. domestic dog *Canis lupus familiaris*). Small-bodied mammals (<1 kg body mass; e.g. rats and squirrels) were also excluded as most were difficult to reliably identify to species level. We considered only mammal species that were detected in at least five sampling occasions due to difficulties differentiating between ecological and observational processes when species detections are very low. This selection process resulted in a community of 23 medium-large mammals (Appendix S3.1).

To identify the environmental factors underpinning mammal occurrence, we extracted six spatial covariates (30 m resolution) in each camera trap site based on their reported influence on medium-large mammal occupancy elsewhere in Southeast Asia (Deere et al., 2020; detail of covariate selection in Appendix S3.2). We characterized the topographic complexity of our study area using elevation and elevation-derived Terrain Ruggedness Index (TRI) data obtained from the Shuttle Radar Topographic Mission (SRTM) (Rabus et al., 2003). To account for the extent and quality of forest habitat we quantified proportional forest cover (MoEF, 2018) and aboveground biomass (t ha-1; Santoro & Cartus 2021) respectively. To assess proximity to key environmental resources we calculated Euclidean distance to the nearest water body (meter; BIG RI 2021). To explore sensitivity to human pressure, we calculated accessibility (i.e. travel time from human settlements in seconds) derived from a travel time cost surface model that accounts for the influence of roads, rivers, land cover, and elevation (Deere et al., 2020; Frakes et al., 2015).

We built a hierarchical multi-species occupancy model with the selected covariates with the following form (Appendix S3.3 for detailed model):

$$\text{logit}(\psi_{i,j}) = \alpha_{0i} + \alpha_{1i}TRI_j + \alpha_{2i}TRI^2_j + \alpha_{3i}Elevation_j + \alpha_{4i}Elevation^2_j + \alpha_{5i}Forest\_Cover_j + \alpha_{6i}Biomass_j + \alpha_{7i}Distance\_to\_Water_j + \alpha_{8i}Accesibility_j + \alpha_{9i}Accesibility^2_j + \varepsilon_i Survey\_Block_j$$

$$\text{logit}(p_{i,j,k}) = \beta_{0i} + \beta_{1i}Camera\_Type_j + \beta_{2i}Elevation_j + \beta_{3i}Trap\_Effort_j$$

We modelled the occupancy ($\psi_{i,j}$) and detection probabilities ($p_{i,j,k}$) of species i at site j across temporal replicates k on the logit scale with species-specific random intercepts (α_0, β_0) and slopes ($\alpha_{1\text{-}9}$, $\beta_{1\text{-}2}$). Species-specific responses were drawn as random effects from community-level distributions in both occupancy and detection models with estimable hyper-parameters that represent community trends. We modelled the influence of TRI, elevation, and accessibility on species occurrence using quadratic terms to account for non-linear responses. The occupancy model also incorporated a spatial random effect term (ε) to account for clustered sampling due to the blocked survey areas (East and West Leuser). Detection probability accounted for the influence of the camera trap model, elevation representing associated changes in forest type, and trapping effort (total trap-nights) in each site.

Occupancy models were specified within a Bayesian framework using JAGS (Just Another Gibbs Sampler) via R package jagsUI (v1.5.1; Kellner 2019). We ran three parallel Markov chains with 100,000 iterations where we removed 50,000 iterations as burn-in, and the remaining iterations were thinned by 50. Model performance was evaluated using Gelman-Rubin statistics and Bayesian p-values (Gelman et al., 1996) which showed a good fit (Appendix S3.4). Estimates of species-specific occupancy of candidate umbrella species along with community occupancy and species richness in each camera trap site were extracted from model output.

2) Functional and phylogenetic diversity

To account for imperfect detection when quantifying functional and phylogenetic diversity we incorporated the detection-corrected occurrence matrix following the approach of Penjor et al. (2022). Throughout, we express diversity estimates at the camera trap site-level.

Functional diversity (FD) was expressed using the functional dispersal (FDis) metric, which represents the distribution of species in multidimensional trait space weighted by their true site-level occurrence (z-value) (Gorczynski et al., 2021). Functional dispersal calculates the average distance to a community centroid in trait space with distance to common species contributing more to the metric than rare species (Laliberte and Legendre, 2010). We collated trait data for conservation priority mammal species from the PanTHERIA database (Jones et al., 2009). Species were classified based on six traits: activity patterns (cathemeral, diurnal, nocturnal), diet (herbivore, carnivore, omnivore), habitat breadth (number of habitats where species lives), body mass (kg), litter size, and life span (maximum adult age; year).

For phylogenetic diversity (PD) we calculated the Mean Pairwise Distance (MPD) that represents phylogenetic distance among all pairs of species in the community (Kembel et al., 2010). We integrated species' true occurrence estimates and based the calculations on phylogenetic profiles from the mammalian phylogenetic super tree. As trait and phylogenetic data for Sumatran hog badger *Arctonyx hoevenii* (e.g. habitat breadth, body mass, litter size, life span) were not available, we used data from its closely related greater hog badger *Arctonyx collaris*.

We accounted for the influence of species richness on FDis and MPD metrics by comparing the observed mammal community in each site with 1000 null communities generated from the pool of all species in the study system using the "tip shuffling" null model approach (Penjor et al., 2022). Abundance-weighted standardized effect sizes or *ses* ($\frac{\mu\text{observed}- \mu\text{expected}}{\sigma\text{expected}}$) were computed using "richness" algorithm that randomizes community data matrix abundances while maintains species richness within samples (Kembel et al., 2010) for both metrics. Positive values of the Standardized Effect Size Functional Dispersal (sesFDis) indicate functional overdispersion (i.e. co-occurring species inhabit different trait niches) and positive Standardized Effect Size Mean Pairwise Distance (sesMPD) suggests phylogenetic overdispersion (i.e. larger phylogenetic distance between co-occurring species), while negative values indicates functional or phylogenetic clustering relative to null communities (Kembel et al., 2010; Penjor et al., 2022). All calculations were performed in the “FD” R package (v.1.0-12; Laliberté et al. 2014) and “Picante” R package (v.1.8.2; Kembel et al., 2010).

3.3.4 Umbrella species performance evaluation

We evaluated umbrella performance in a community of 23 medium-large mammals. Of the species in this community, only two (Sumatran tiger and rhinoceros) are monitored in the park. We selected a further six taxa from the community as candidate umbrellas based on five criteria by Seddon and Leech (2008): 1) well-known natural history and ecology, 2) large home range size, 3) management needs benefit other species in the study system, 4) moderate sensitivity to human disturbance, and 5) easily sampled or observed (detailed criteria see Appendix S3.5). All 23 species were evaluated against each criterion relative to other species in the community using a score of 1-3 (e.g. 3 = large home range (beyond 67th percentile), 2 = medium, 1 = small (below 33rd percentile), with the maximum score across the five criteria being 15). Eight species received a total score ≥ 10, and were selected as candidate umbrella species: Sumatran hog badger, mountain serow (*Capricornis sumatraensis*), dhole (*Cuon alpinus*), Sumatran rhinoceros, sun bear (*Helarctos malayanus*), Sunda clouded leopard (*Neofelis diardi*), Sumatran tiger, and sambar deer (*Rusa unicolor*).

To evaluate how well umbrella species occupancy were associated with biodiversity parameters, we calculated the dependence between these two variables using Bayesian linear regression in JAGS via R package jagsUI with model code adapted from Joseph (2013) and Kery and Royle (2016). This approach accounts for estimation uncertainty in both response and predictor variables to propagate error associated with model-derived biodiversity estimates (Joseph, 2013). Throughout, uncertainty was expressed using site-level standard deviations (SD) of the posterior distribution associated with species occupancy and biodiversity parameters derived from the occupancy framework.

We fitted a regression model with linear and quadratic terms for umbrella candidate occupancy to predict biodiversity parameters with the following form:

$$Biodiversity_i = \beta_{0i} + \beta_1 SpeciesOccupancy_i + \beta_2 SpeciesOccupancy^2_i + eps.site_i$$

where $Biodiversity_i$ is the mammal biodiversity parameter estimates at camera site i, β_0 is the intercept parameter, and $\beta_{1\text{-}2}$ are the species occupancy predictor effects influencing mammal biodiversity across sites. We added a site-level random effect (*eps.site*) to account for spatial autocorrelation in biodiversity parameter estimates (Moran's I observed mean = 1.03; expected mean = -0.005; p-value = <0.00; Appendix S3.6).

We ran three parallel Markov chains with 50,000 iterations where we removed the first 25,000 iterations as burn-in, and the remaining iterations were thinned by 25. We tested model performance using the Gelman-Rubin convergence diagnostic (Gelman et al., 1996), which indicated good convergence. The strength and directionality of the relationships between species occupancy values and the other biodiversity parameters were determined from the β_1 coefficient (linear predictor), and the shape of the relationship (e.g. linear or quadratic) was inferred from the β_2 coefficient (quadratic term) and visual inspection of regression plots. We then ranked species based on their umbrella performance for each biodiversity parameter according to the β_1 coefficient values.

3.4 Results

3.4.1 Biodiversity and umbrella occupancy patterns

Overall mammal community occupancy (mean 0.19; range 0.04-0.34) was highest at low to medium elevation areas (Fig. 3.1A). To a lesser extent, mammal occurrence tended to be higher in moderately rugged forest areas with larger tree biomass that were close to water sources and relatively easy to access, particularly in lowland habitats (Appendix S3.7-S3.8). Species richness (average of six species per site; range 2-11) was distributed evenly across elevations (Fig. 3.1B).

Functional diversity across the study area indicated overall trait clustering relative to null communities (mean sesFDis –0.20; range –1.75-1.55). Functional clustering occurred in 130 camera sites and was mostly found at higher elevations, while the majority of functional overdispersion (82 sites) was distributed in lowland areas (Fig. 3.1C). Phylogenetic diversity indicated a more phylogenetic overdispersion than expected by chance (mean sesMPD 0.16; range –2.50-2.20). Similar to FD, PD distribution showed strong elevational gradients with net clustering (98 sites) at high elevation and overdispersion (114 sites) at low elevation (Fig. 3.1D).

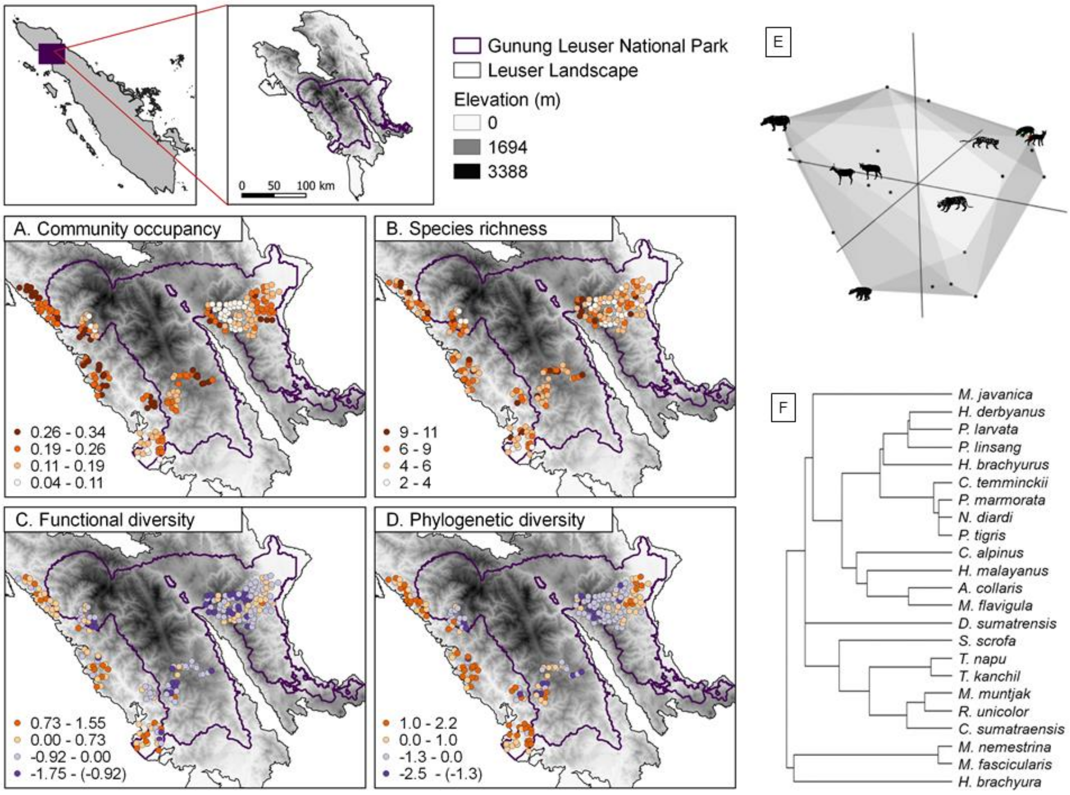


Fig 3.1: (A-D) Distribution of mammal biodiversity parameter values across 212 camera sites in Leuser Ecosystem, Sumatra. Values in legends are divided into four categories based on their quartiles. The upper quartile represents the top 25% values. Negative values of FD and PD (light-deep purple) indicate functional and phylogenetic clustering. (E) Trait space occupied by mammal species in Leuser. Grey areas represent the first three axes used to calculate the functional diversity metric. Species positions are represented by black points while umbrella species are illustrated by icons. (F) Phylogenetic tree (unweighted by detection-corrected matrix) informing the relationship between species in the community.

Species-specific occupancy estimates were influenced by different combinations of predictors, in particular elevational gradients, depending on species ecology (Appendix S3.9). The occupancy of the eight umbrella candidate species varied across the landscape with some species restricted to high-elevation areas (e.g. hog badger), and lowland (e.g. sambar deer), while others were more widespread (Appendix S3.10).

3.4.2 Umbrella species performance

Among the eight candidate species, sambar deer exhibited strong potential as an umbrella species, showing the strongest association with two of the four biodiversity parameters (Fig. 3.2, Appendix S3.11). Clouded leopard best represented phylogenetic diversity and was identified as the second highest ranking umbrella species for other biodiversity parameters. Only sambar deer and clouded leopard had a significant positive association with community phylogenetic diversity.

Sun bear was identified as the best umbrella for species richness although its association strength was similar with other species from the 2^{nd} to 6^{th} rank. Mountain serow and dhole both ranked third as umbrella species for functional and phylogenetic diversity, but their associations were weak and showed negative trends (Fig. 3.3).

Some species occupancy and biodiversity parameter relationships were non-linear (Fig. 3.3), implying that there was a limit to which higher occupancy could reliably predict higher values of biodiversity parameters. Nevertheless, visual inspection of these relationships showed that the top two umbrella species (sambar deer and clouded leopard) exhibited notable positive associations with biodiversity.

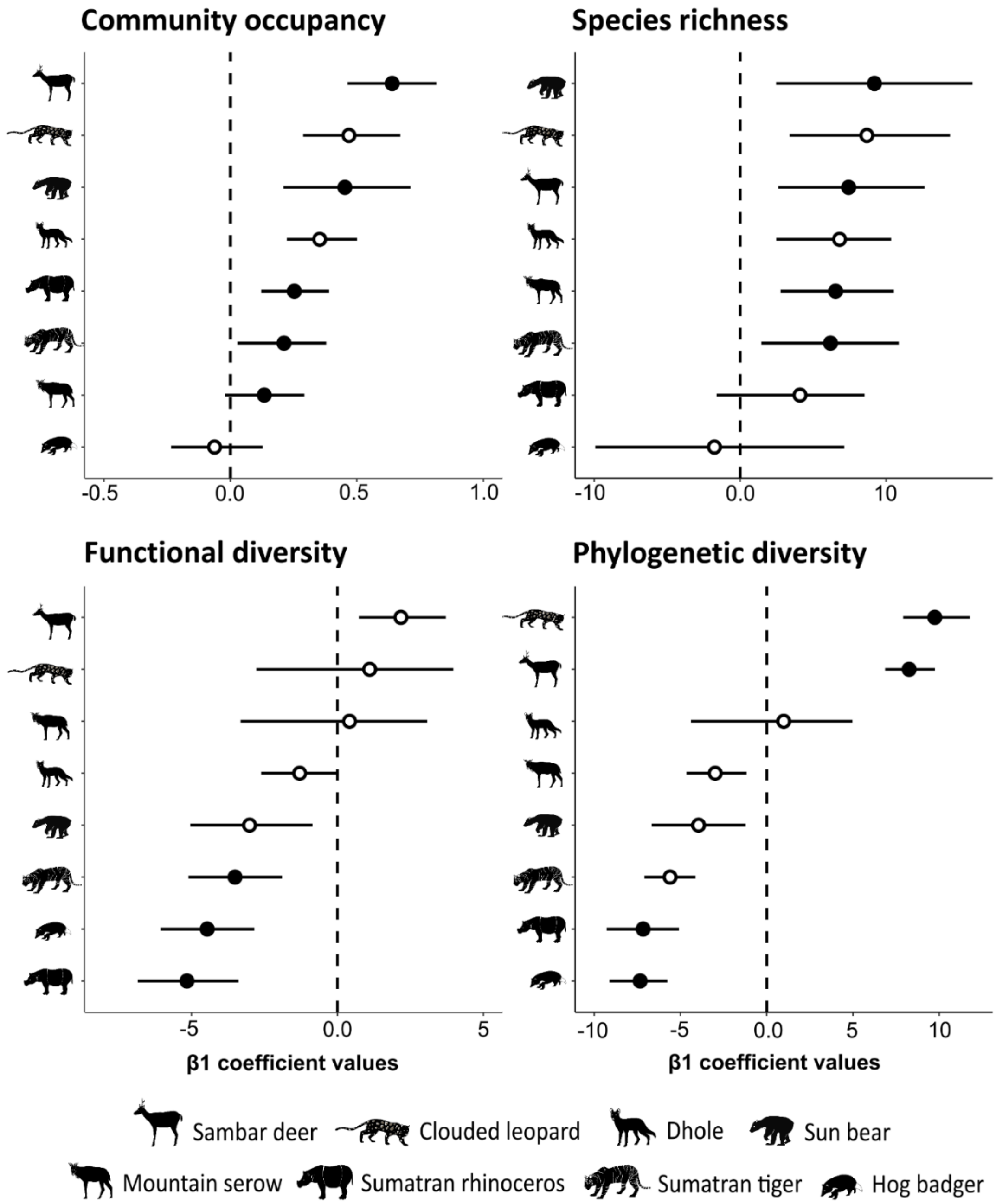


Fig 3.2: Umbrella species performance ranking across four biodiversity parameters in medium-large mammal community. Closed circle points represent the beta coefficient value of linear predictor (β1). White circle points indicate a significant quadratic relationship. Error bars represent 95% Bayesian credible intervals of the coefficient estimates.

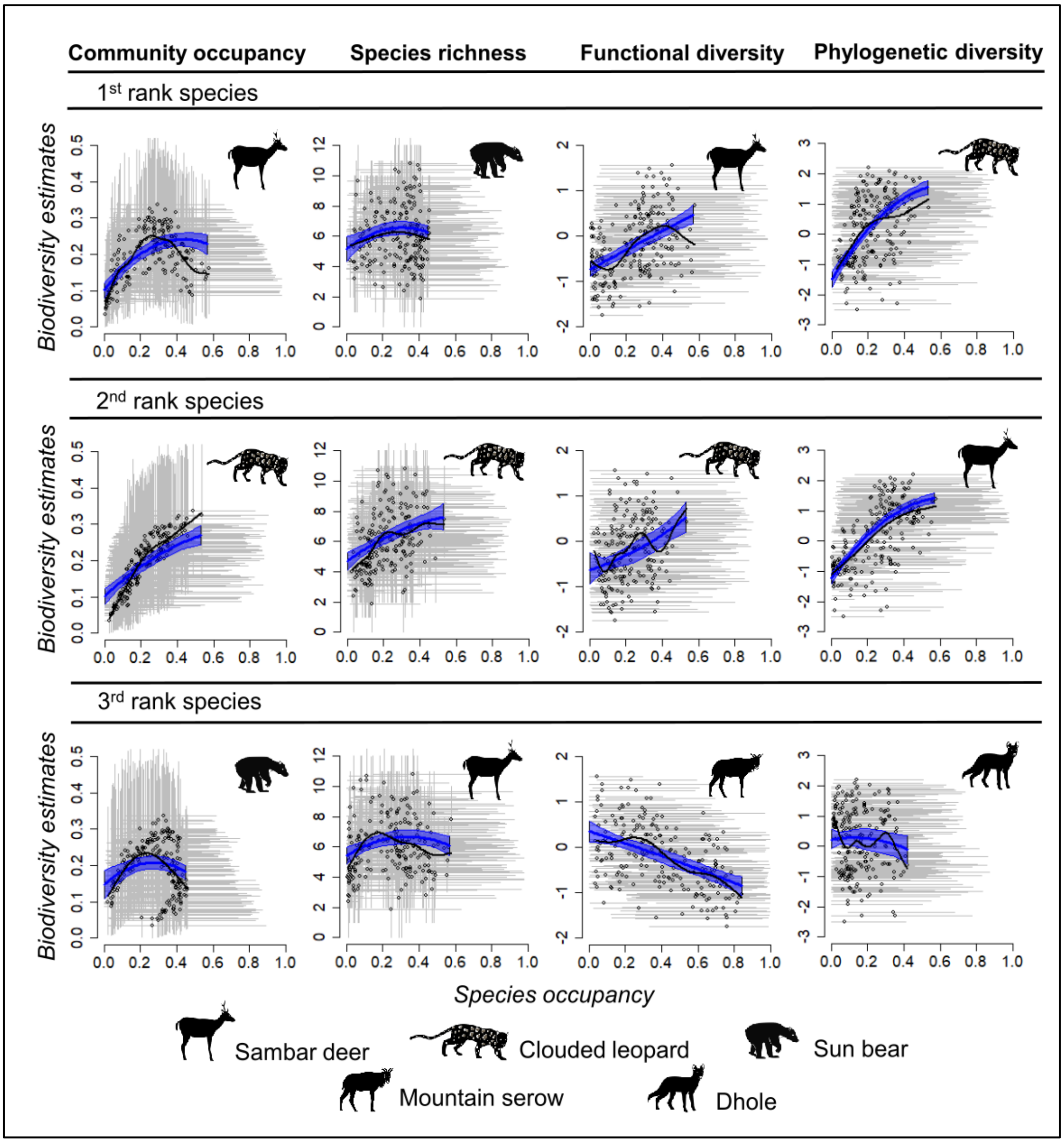
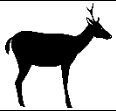


Fig 3.3: Relationships between occupancy of the top three umbrella species with four biodiversity parameters. Points and thin grey lines inform point estimates of relationship with 95% Bayesian credible intervals (BCIs) of response (vertical lines; for biodiversity parameters with uncertainty estimates) and predictor (horizontal lines) variables. Black line represents a spline smooth regression line. Blue line indicates the quadratic regression line that accounts for uncertainty in both response and predictor variables with 95% BCI of the predictions represented by blue area.

Table 3.1: Top umbrella performers based on this study evaluation and their qualification for meeting umbrella species criteria as proposed by Seddon and Leech (2008). Sumatran serow and dhole were excluded as they showed negative association with functional and phylogenetic diversity.

Umbrella criteria			
Natural history & ecology well known (number of scientific publications in Indonesia; relative to other species in community)	Well-studied species (3 articles)	Well-studied species (6 articles)	Well-studied species (5 articles)
Large home range size (relative to other species in community)	Large (15 km^2)	Large (51 km^2)	Large (20.6 km^2)
Management needs benefit other species (in Gunung Leuser National Park)	Management concern (tiger prey)	Management concern (large carnivore)	Management concern (large carnivore)
Moderate sensitivity to human disturbance (forest specialist)	Moderate	Moderate	High
Easily sampled or observed (reliable species signs or easily identified in camera trap photographs)	Easy (reliable signs; easily identified in photographs)	Moderate (signs hard to detect; easily identified in photographs)	Easy (reliable signs; easily identified in photographs)
Co-occurrence with biodiversity parameters (evaluated in this study)	**Community occupancy** **Species richness** **Functional diversity** **Phylogenetic diversity**	**Community occupancy** **Species richness** **Functional diversity** **Phylogenetic diversity**	**Community occupancy** **Species richness**

3.5 Discussion

Conservation managers often monitor umbrella species expecting them to represent broader patterns of biodiversity, but this underlying assumption has rarely been evaluated (Sibarani et al., 2019; Steenweg et al., 2023). Camera trap surveys provide detection data for multiple species simultaneously, but valuable information on species occupancy status, community-level biodiversity patterns, and the interconnecting relationships between them are often unavailable in the Global South due to funding priorities placed on single species and limited capacity to analyze biodiversity data (Chaudhary et al., 2022). Using a comprehensive camera trap dataset to quantitatively assess umbrella species performance, we demonstrate that charismatic species typically selected as conservation umbrellas (e.g. Sumatran tiger and rhinoceros) are in fact poor representatives of community-level patterns of biological diversity. Our results highlight that taxa frequently overlooked by conservation decision-making may better represent overall diversity.

Three of the eight candidate species stood out as high-performing umbrellas for mammal biodiversity: sambar deer, clouded leopard, and sun bear. While sun bear performed best as umbrella for species richness, other species (2nd to 6th ranks) also demonstrated similar performances indicating several potential umbrellas for richness. Sambar and clouded leopard were consistently highly ranked across all four biodiversity parameters. Their habitat preference in forest lowlands aligns with areas where higher biodiversity occurs as evidenced by their umbrella performance. Furthermore, those three umbrellas fulfilled most of the five umbrella species criteria by Seddon and Leech (2008) i.e. they have a large home range (>10 km^2) relative to other species in the community, are sensitive to human disturbance, and can be reliably detected through camera traps or sign identifications (Table 3.1). They also received considerable conservation attention as large carnivore and herbivore taxa, albeit less than their sympatric megafauna species.

3.5.1 *Limited umbrella performance of Sumatran charismatic*

High conservation value species such as Sumatran tiger and rhinoceros poorly represented broader mammal community, despite scoring well as umbrella candidates (Appendix S5). We acknowledge that both species are highly threatened and there is a possibility that their occurrence did not coincide with mammal biodiversity because they have been actively hunted throughout their range, which is particularly the case for the Sumatran rhinoceros (Pusparini et al., 2015; Putra, 2014). The pressure could shape the localized distribution (e.g. relatively few occurrences in lowland forest; Appendix S10) and lower detection for these species, although the current hunting pressure is lower due to the active protection in Leuser. It is worth noting that hunting also impacts other species indiscriminately especially snare hunting, although the scale might be in a lesser extent (Harrison et al., 2016).

An island-wide assessment by Sibarani et al. (2019) reported tigers as the top umbrella for mammal biodiversity among four charismatic Sumatran species: orangutan, rhinoceros, and elephant using expert-driven habitat-suitability models from a global study (Rondinini et al., 2011). This discrepancy in umbrella performance with our more localized study in Leuser highlights the potential limitations of global biodiversity datasets and expert opinion to inform finer-scale species distribution patterns (Merow et al., 2017; Rondinini et al., 2011; Sibarani et al., 2019). Our appraisal, based on primary biodiversity data, shows that tigers occupy medium to high-elevation habitats (e.g. hill and sub-mountain forests). Regardless of its large home range, these areas do not overlap with forest lowlands that tend to harbour a higher diversity of other mammal taxa. Thus, we recommend caution in outlining monitoring priorities based on secondary data sources (e.g. IUCN red list species range) if primary data is available, as evidenced here in the case of tigers.

While our study implies tiger and rhinoceros did not perform well as umbrella species, species-based conservation programs in Sumatra disproportionately focus on these taxa. Between 2017 and 2019 an estimated USD 4.5 million was invested in the conservation of four charismatic megafauna (Sumatran rhinoceros, tiger, elephant, and orangutan) through Debt-for-Nature swaps, surpassing the total investment for landscape-based conservation programs (USD ~3.3 million) across the island (KEHATI, 2019). Focusing conservation actions on single-species, and in particular the charismatic ones, inevitably leads to management decisions solely based on focal species ecology and threats (Chaudhary et al., 2022; Lindenmayer and Likens, 2011).

3.5.2 Integrating umbrella species into wildlife monitoring

Cost-effective monitoring programs that cover a wide range of species are needed to support managers in their efforts to evaluate the impact of anthropogenic disturbances and conservation interventions (Caro, 2010; Mortelliti et al., 2022). Surveying entire ecological communities (mammals or cross-taxa) offers a more holistic picture of biodiversity patterns, but it demands significant amounts of time, expertise, and resources, which are typically in scarce supply in tropical countries. While camera traps are a powerful tool for capturing multi-species data, implementing surveys at scales appropriate to conservation management (e.g. across the whole landscape) can be logistically challenging, thus limiting our capacity to make reliable inferences about rare or threatened species due to insufficient data (Wearn and Glover-Kapfer, 2019; Zipkin and Saunders, 2018). Our study evaluated the robustness of umbrella species performance and provided an alternative to community studies when there are limited resources by focusing the scope of assessment on a few representative species.

While no single species can represent all facets of biological diversity, identifying species with habitat preferences that reflect important areas for other wildlife is imperative for protected area managers so they can optimize monitoring under restricted budgets. As some species are more representative of particular aspects of biodiversity than others, we advocate the adoption of an 'umbrella fleet', which integrates multiple top umbrella species to benefit the overarching purpose of conserving biodiversity and the ecosystem (Lambeck, 1997). The fleet approach ensures the protection of crucial aspects of biological diversity that might be overlooked by prioritizing the needs of single taxa and can be integrated into current species-based programs. For example, sambar deer and clouded leopard are highly complementary umbrella species owing to their different ecological niches (i.e. herbivore vs carnivore; semi-arboreal vs terrestrial). A coupled monitoring approach based on these species would likely be more representative of a greater breadth of species than one focused on other taxa. This strategy also supports the inclusion of multiple facets of biodiversity as strategies focusing on species distribution and richness are not sufficient to ensure the protection of ecological functions and evolutionary history in an ecosystem (Sattler et al., 2014; Sibarani et al., 2019). As shown by our result, the sun bear performed well as umbrella for species richness and community occupancy but did not capture functional or phylogenetic diversity at all. Thus, prioritizing monitoring or management based on sun bear alone could compromise these facets of biodiversity.

In the context of tropical forest management in Sumatra, the presence of charismatic tiger and rhinoceros gathers much-needed public support and funding for biodiversity monitoring and protection. Concurrently, implementing an umbrella fleet approach in the existing monitoring programs can assist in the identification of priority high biodiversity areas. Documenting the detection of umbrella species through current species monitoring programs and other activities such as ranger protection patrols enables efficient documentation of real-time information on their occurrence and anthropogenic pressures. For example, camera trapping and sign surveys targeting Sumatran tiger can inform the occurrence of its prey sambar deer and sympatric carnivores like sun bear (Allen et al., 2020; Widodo et al., 2022). Although not spatially overlapping with tigers, the relatively elusive clouded leopard is often detected by camera traps (Widodo et al., 2022). Combined with multispecies occupancy modelling, the generated occupancy estimates of these umbrella species can serve as indicative of the broader patterns of mammal biodiversity.

3.5.3 Future directions

We note some opportunities to improve future evaluation of umbrella species. First, evaluation of umbrella performance in different habitat types (e.g. disturbed forests, forest edge, or plantations) is needed to assess whether the occupancy of monitored species is indicative of biodiversity across a broader range of habitats. Second is the need to validate umbrella species performance for other taxonomic groups, should these data become available. Third, the opportunity to combine datasets from different surveys (i.e. camera traps and protection patrols) to inform species occupancy and biodiversity at a larger spatiotemporal scale (Miller et al., 2019). The integrated framework then can be incorporated with our analytical framework to extract the occupancy status for each taxon, calculate the overall cross-taxon biodiversity association, and evaluate the umbrella performance amongst individual taxa.

Our appraisal highlights the extent to which mammal species used in wildlife monitoring programs in conservation areas effectively represent the integrity of the overall community present. As the application of the umbrella species concept is context-specific – it depends on landscape, species community, and management goals (Lindenmayer and Likens, 2011; Seddon and Leech, 2008) – we encourage the adoption of our data-driven framework for broader applications. Finally, we advocate the integration of umbrella species with current conservation management practices to ensure the integrated and effective protection of biodiversity and ecosystems.

3.6 Acknowledgements

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3.7 Data availability

Example dataset and model codes associated with this manuscript can be accessed at https://github.com/Ardiantiono/Umbrella-species-assessment-Biological-Conservation.git.

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3.9 Supplementary information

Appendix S3.1. List of 28 medium-large mammal species ordered by their number of detections. Species detected fewer than five times were excluded from the analysis.

Species	Name	Total Detection
Muntiacus muntjak	Muntjak deer	687
Macaca nemestrina	Pig-tailed macaque	520
Hystrix brachyura	Malayan porcupine	194
Sus scrofa	Wild pig	144
Paguma larvata	Masked palm civet	88
Helarctos malayanus	Sun bear	83
Catopuma temminckii	Golden cat	64
Capricornis sumatraensis	Mountain serrow	63
Martes flavigula	Yellow-throated marten	61
Rusa unicolor	Sambar deer	56
Panthera tigris	Sumatran tiger	50
Tragulus kanchil	Lesser mouse-deer	46
Hemigalus derbyanus	Banded palm civet	27
Neofelis diardi	Sumatran clouded leopard	27
Arctonyx hoevenii	Sumatran hog badger	25
Tragulus napu	Greater mouse-deer	24
Prionodon linsang	Banded linsang	22
Pardofelis marmorata	Marbled cat	20
Dicerorhinus sumatrensis	Sumatran rhino	18
Macaca fascicularis	Long-tailed macaque	15
Manis javanica	Sunda pangolin	11
Cuon alpinus	Dhole	10
Herpestes sp.	Mongooses *sp*	8
Arctictis binturong	Binturong	2
Echinosorex gymnurus	Moonrat	2
Elephas maximus	Sumatran elephant	1
Mustela lutreolina	Indonesian mountain weasel	1
Prionailurus bengalensis	Leopard cat	1

Appendix S3.2: Covariate selection.

For each camera trap site, we extracted nine spatial covariates, all in 30 m resolution, based on their reported influence on medium-large mammal occupancy elsewhere in Southeast Asia (Deere et al., 2020; Linkie et al., 2013). We characterized the topographic complexity of our study area using elevation and elevation-derived Terrain Ruggedness Index (TRI) data obtained from the Shuttle Radar Topographic Mission (SRTM) (Rabus et al., 2003). To account for the extent and quality of forest habitat we quantified the proportion of forest (MoEF, 2018) and aboveground biomass (t ha^{-1}; Santoro & Cartus 2021) respectively. To assess proximity to key environmental resources we calculated Euclidean distance to the nearest water body (meter; BIG RI 2021). To explore sensitivity to human pressure, we used four disturbance-related covariates: Euclidean distance to the nearest village, road, and forest edge (meter; MoEF 2018; BIG RI 2021) and accessibility derived from a travel time cost surface model (travel time in second; Deere et al., 2020; Frakes et al., 2015).

All covariates were centred and scaled to one-unit standard deviation to place them on a comparable scale and tested for collinearity using Pearson's correlation coefficient ($|r| \geq 0.7$ indicating serious intercorrelation) resulting in six final covariates: elevation, TRI, forest cover, biomass, distance to water, and accessibility.

Appendix S3.3: Hierarchical multi-species occupancy model detail

We built a hierarchical multi-species occupancy model with the following form:

$$\text{logit}(\psi_{i,j}) = \alpha_{0i} + \alpha_{1i}TRI_j + \alpha_{2i}TRI^2_j + \alpha_{3i}Elevation_j + \alpha_{4i}Elevation^2_j + \alpha_{5i}Forest\_Cover_j + \alpha_{6i}Biomass_j + \alpha_{7i}Distance\_to\_Water_j + \alpha_{8i}Accesibility_j + \alpha_{9i}Accesibility^2_j + \varepsilon_i Survey\_Block_j$$

$$\text{logit}(p_{i,j,k}) = \beta_{0i} + \beta_{1i}Camera\_Type_j + \beta_{2i}Elevation_j + \beta_{3i}Trap\_Effort_j$$

We modelled the occupancy ($\psi_{i,j}$) and detection probabilities ($p_{i,j,k}$) of species i at site j across temporal replicates k on the logit scale with species-specific random intercepts (α_0, β_0) and slopes (α_{1-9}, β_{1-2}). Species-specific responses in both occupancy and detection models were drawn as random effects from community-level distributions described by estimable hyper-parameters representing community trends.

We used the selected covariates (elevation, TRI, and accessibility using both linear and quadratic terms; and proportion of forest cover, biomass, and distance to water using the linear term) as predictors of occurrence. The occupancy model incorporated a spatial random effect (ε) to account for clustered sampling due to the blocked survey design (East and West Leuser). Detection probability accounted for the influence of the camera trap model, elevation representing associated changes in habitat type (e.g. lowland, hill, sub-montane, montane), and trapping effort (total trap-nights) in each site.

To identify the optimal spatial extent of each predictor, we performed scale-optimization for all covariates except proximity-based measures. Single covariate hierarchical multi-species occupancy models were constructed to compare the performance of models containing covariates aggregated across different buffer radii (50, 100, 250, 500, 1000, and 1500 m). Optimal scales for each covariate were determined based on two criteria, 1) the best-ranked model according to WAIC (Watanabe–Akaike Information Criterion; Watanabe 2010) and, 2) the number of species demonstrating a substantial statistical response to the scale (95% and 50% Bayesian credible interval did not overlap zero).

To estimate species-specific occupancy probability, we back-transformed occupancy estimates on the logit scale using the equation:

$$(\psi_{i,j}) = \exp(\text{logit}(\psi_{i,j}) / (1+\exp(\text{logit}(\psi_{i,j}))$$

The same approach was used to estimate community occupancy probability where we used *mu.α* or the community slopes (average of $\alpha_{1\text{-}9}$) at site *j*.

To estimate species richness at each site, we summed the latent binary presence-absence indicators (*z*) from the model output.

Appendix S3.4. Bayesian p-value to assess the occupancy model fitness. A p-value near 0.5 indicates better agreement between observed and simulated data.

Species	**Name**	**Bayesian p-value**
Mammal community		0.444
Arctonyx hoevenii	Sumatran hog badger	0.429
Capricornis sumatraensis	Mountain serrow	0.498
Catopuma temminckii	Golden cat	0.500
Cuon alpinus	Dhole	0.656
Dicerorhinus sumatrensis	Sumatran rhino	0.482
Helarctos malayanus	Sun bear	0.408
Hemigalus derbyanus	Banded palm civet	0.529
Herpestes sp.	Mongooses *sp.*	0.537
Hystrix brachyura	Malayan porcupine	0.369
Macaca fascicularis	Long-tailed macaque	0.519
Macaca nemestrina	Pig-tailed macaque	0.392
Manis javanica	Sunda pangolin	0.677
Martes flavigula	Yellow-throated marten	0.572
Muntiacus muntjak	Muntjak deer	0.341
Neofelis diardi	Sumatran clouded leopard	0.559
Paguma larvata	Masked palm civet	0.420
Panthera tigris	Sumatran tiger	0.500
Pardofelis marmorata	Marbled cat	0.501
Prionodon linsang	Banded linsang	0.558
Rusa unicolor	Sambar deer	0.528
Sus scrofa	Wild pig	0.483
Tragulus kanchil	Lesser mouse-deer	0.541
Tragulus napu	Greater mouse-deer	0.450

Appendix S3.5. (Top table) Evaluation criteria used to assign criteria scores to each species. (Bottom table) Species qualifications to meet umbrella species five out of seven criteria proposed by Seddon & Leech (2008). Bold species were selected as umbrella candidates (total score beyond the 67th percentile). We did not use the other two criteria: 1) High probability of population persistence because of the lack of landscape species population data and 2) co-occurrence with other species as they will be tested in this study.

Criteria	Scoring detail
Natural history & ecology well known	Based on the number of single-species publications in Indonesia relative to other species (Chapter 2) (3) Well studied = number of publications > 2 (beyond 67th percentile) (2) Moderately studied = number of publications (1-2) (1) Less studied = no publication
Large home range size (km^2)	Based on estimated maximum home range size relative to other species (Broekman et al., 2023; Chatterjee et al., 2014; Grassman et al., 2005; Pinsky & McCauley, 2019) (3) Large ≥ 12 km^2 (beyond 67th percentile) (2) Medium ≥ 2 km^2 (between 33rd and 67th percentile) (1) Small < 2 km^2 (below 33rd percentile)
Management needs benefit other species	Based on conservation management in Gunung Leuser National Park (BBTNGL, 2021), the core conservation area of Leuser Landscape. (3) Priority species (2) Management concern (1) Limited attention
Moderate sensitivity to human disturbance	Based on forest specialist species categorization by Wilson et al. (2010). (3) Moderate sensitivity to disturbance (2) High sensitivity to disturbance (1) Low sensitivity to disturbance

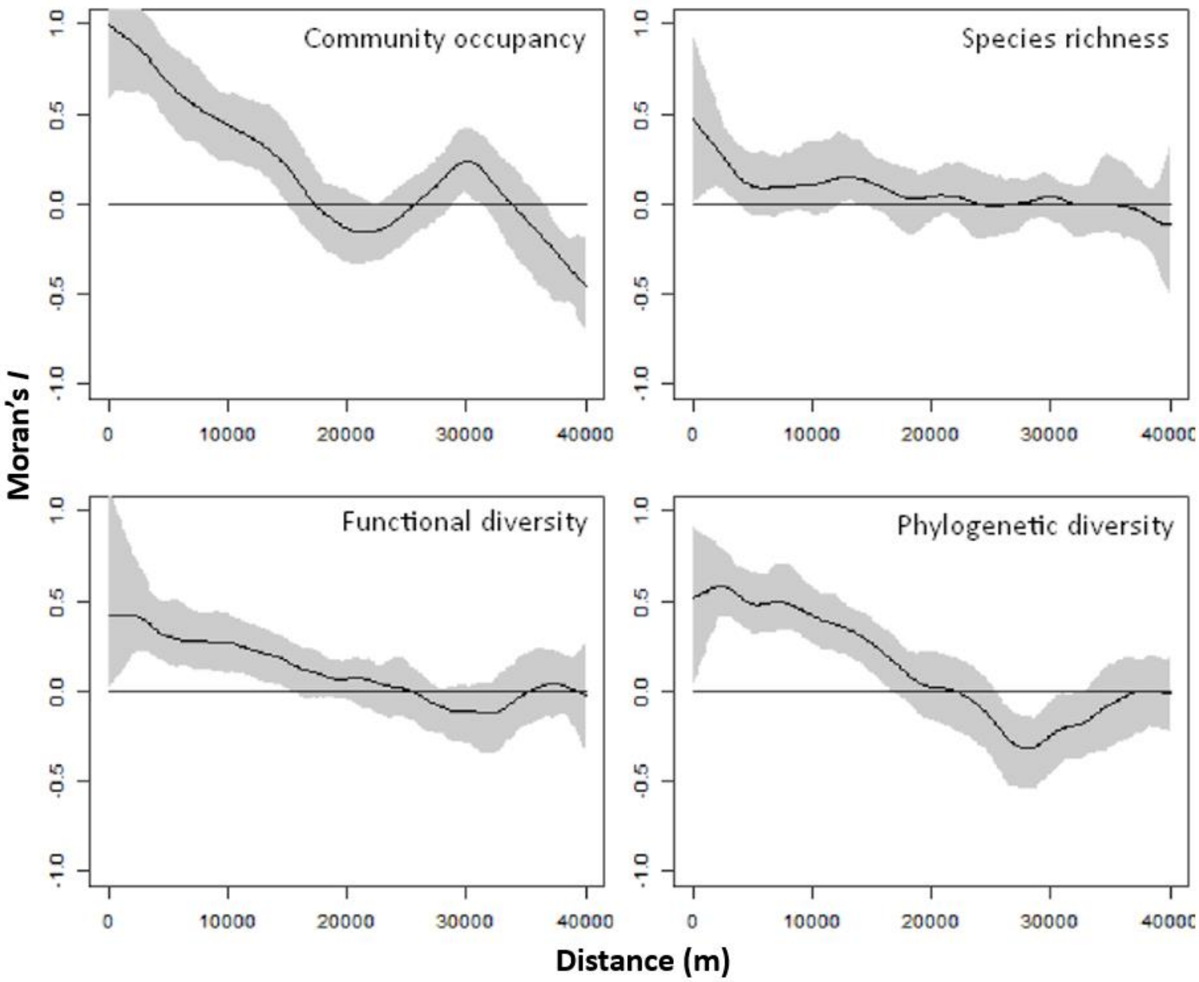
Easily sampled or observed	Easily detected in camera trap, sign survey, direct observation, or combinations in Leuser Landscape. (3) Easy to detect the species or identify their signs (2) Moderate (1) Difficult

No	Species	Total score (max 15)	Natural history & ecology well known (# publications)	Score	Large home range size (km^2)	Score	Management needs benefit other species	Score	Moderate sensitivity to human disturbance	Score	Easily sampled or observed	Score
1	***Panthera tigris***	**15**	**Well-studied species (12)**	**3**	**Large (400)**	**3**	**Priority species**	**3**	**moderate**	**3**	**Easy**	**3**
2	***Dicerorhinus sumatrensis***	**14**	**Well-studied species (3)**	**3**	**Large (13)**	**3**	**Priority species**	**3**	**high**	**2**	**Easy**	**3**
3	***Rusa unicolor***	**14**	**Well-studied species (3)**	**3**	**Large (15)**	**3**	**Management concern (tiger prey)**	**2**	**moderate**	**3**	**Easy**	**3**
4	***Neofelis diardi***	**13**	**Well-studied species (6)**	**3**	**Large (51)**	**3**	**Management concern (large carnivore)**	**2**	**moderate**	**3**	**Moderate**	**2**
5	***Helarctos malayanus***	**13**	**Well-studied species (5)**	**3**	**Large (20.6)**	**3**	**Management concern (large carnivore)**	**2**	**high**	**2**	**Easy**	**3**

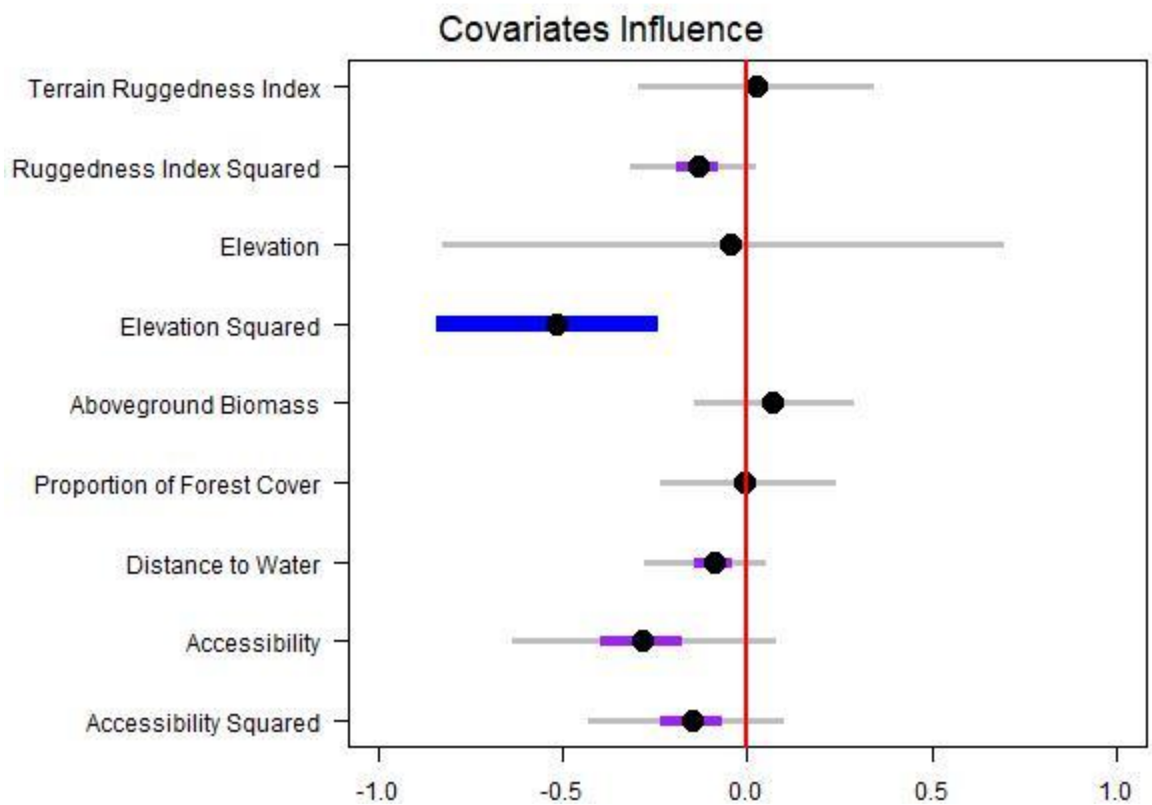
6	***Cuon alpinus***	**12**	**Moderately studied species (1)**	**2**	**Large (83.3)**	**3**	**Management concern (large carnivore)**	**2**	**moderate**	**3**	**Moderate**	**2**
7	***Capricornis sumatraensis***	**11**	**Moderately studied species (2)**	**2**	**Small (2.2)**	**1**	**Management concern (tiger prey)**	**2**	**moderate**	**3**	**Easy**	**3**
8	***Arctonyx hoevenii***	**10**	**Less studied species (0)**	**1**	**Large (12)**	**3**	**Management concern (highland endemic)**	**2**	**moderate**	**3**	**Difficult**	**1**
9	*Catopuma temminckii*	9	Less studied species (0)	1	Large (82.5)	3	Limited attention	1	moderate	3	Difficult	1
10	*Pardofelis marmorata*	9	Moderately studied species (1)	2	Medium (11.9)	2	Limited attention	1	moderate	3	Difficult	1
11	*Sus scrofa*	9	Less studied species (0)	1	Medium (4.46)	2	Management concern (tiger prey)	2	low	1	Easy	3
12	*Macaca fascicularis*	9	Well-studied species (18)	3	Medium (3.65)	2	Limited attention	1	low	1	Moderate	2
13	*Prionodon linsang*	9	Moderately studied species (1)	2	Medium (3)	2	Limited attention	1	moderate	3	Difficult	1
14	*Manis javanica*	9	Well-studied species (3)	3	Small (0.34)	1	Management concern (highly traded)	2	low	1	Moderate	2
15	*Hemigalus derbyanus*	8	Moderately studied species (1)	2	Medium (3)	2	Limited attention	1	high	2	Difficult	1

16	*Martes flavigula*	7	Moderately studied species (2)	2	Medium (7.2)	2	Limited attention	1	low	1	Difficult	1
17	*Herpestes sp.*	7	Moderately studied species (2)	2	Medium (3)	2	Limited attention	1	low	1	Difficult	1
18	*Muntiacus muntjak*	7	Less studied species (0)	1	Small (0.78)	1	Management concern (tiger prey)	2	low	1	Moderate	2
19	*Tragulus kanchil*	7	Less studied species (0)	1	Small (0.062)	1	Limited attention	1	moderate	3	Difficult	1
20	*Tragulus napu*	7	Less studied species (0)	1	Small (0.062)	1	Limited attention	1	moderate	3	Difficult	1
21	*Paguma larvata*	6	Less studied species (0)	1	Medium (8.93)	2	Limited attention	1	low	1	Difficult	1
22	*Macaca nemestrina*	6	Less studied species (0)	1	Small (1.81)	1	Limited attention	1	low	1	Moderate	2
23	*Hystrix brachyura*	5	Less studied species (0)	1	Small (2)	1	Limited attention	1	low	1	Difficult	1

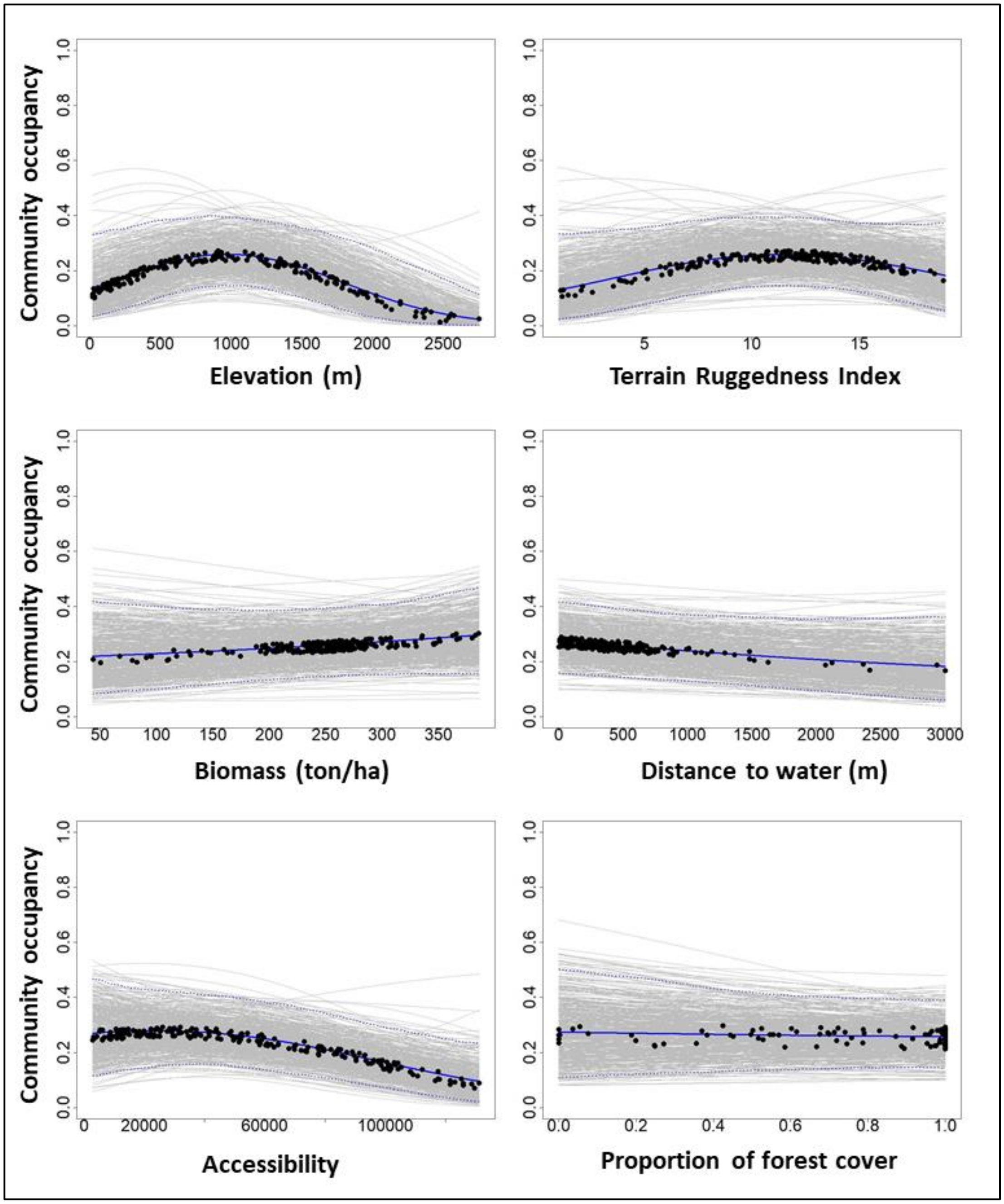
Appendix S3.6. Spline correlograms of Moran's I test output suggested high spatial autocorrelation among biodiversity parameter estimates.



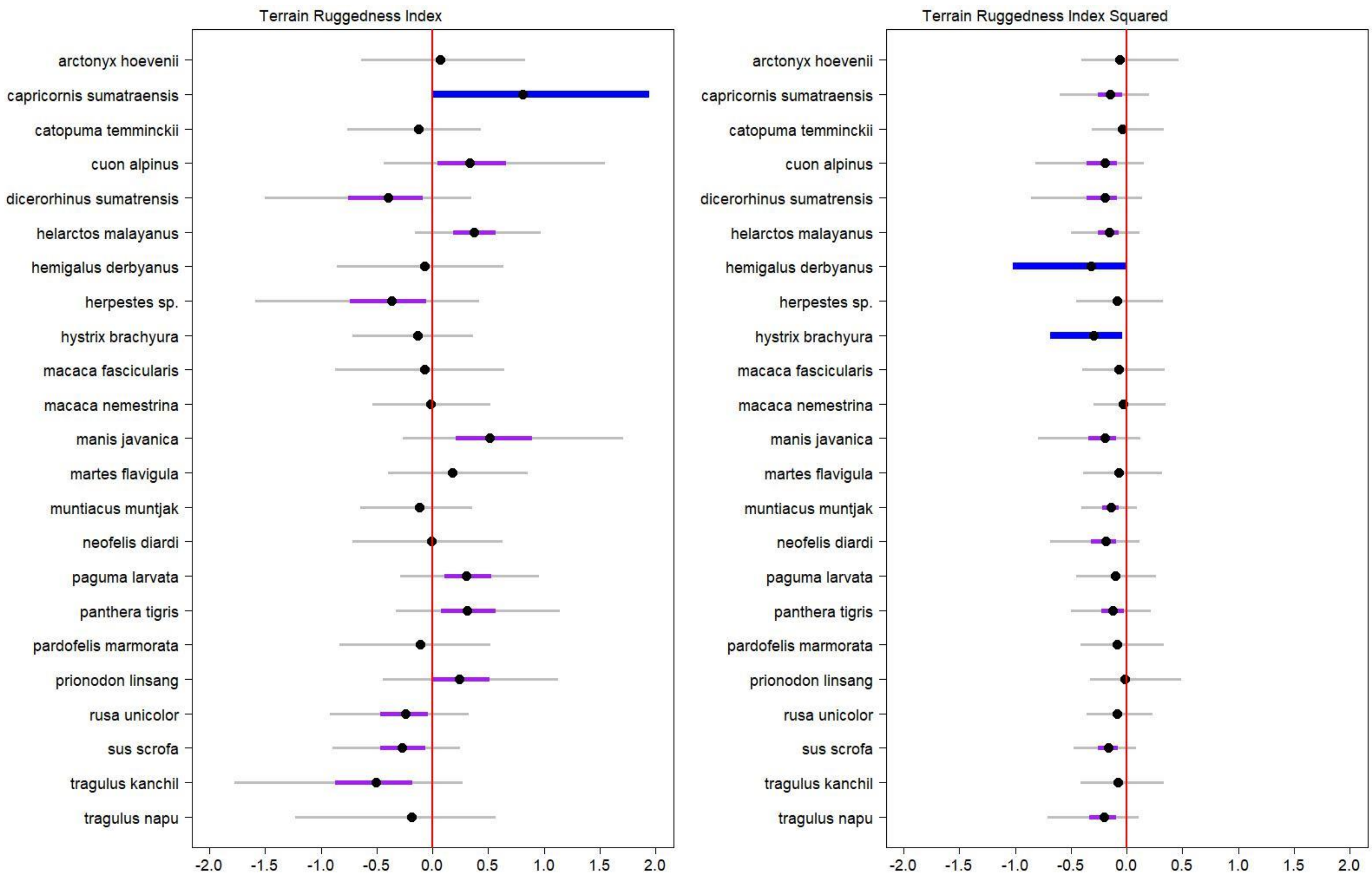
Appendix S3.7. Effect sizes for medium-large mammal community (23 species) responses to selected covariates. Community posterior means are represented in points and Bayesian credible intervals (BCIs) in horizontal lines. Grey colour indicates nonresponse, purple shows limited support of influence (50% BCI), and blue represents substantial influence (95% BCI). Effects of community-covariates are substantial if the BCI does not overlap with zero (vertical red line).



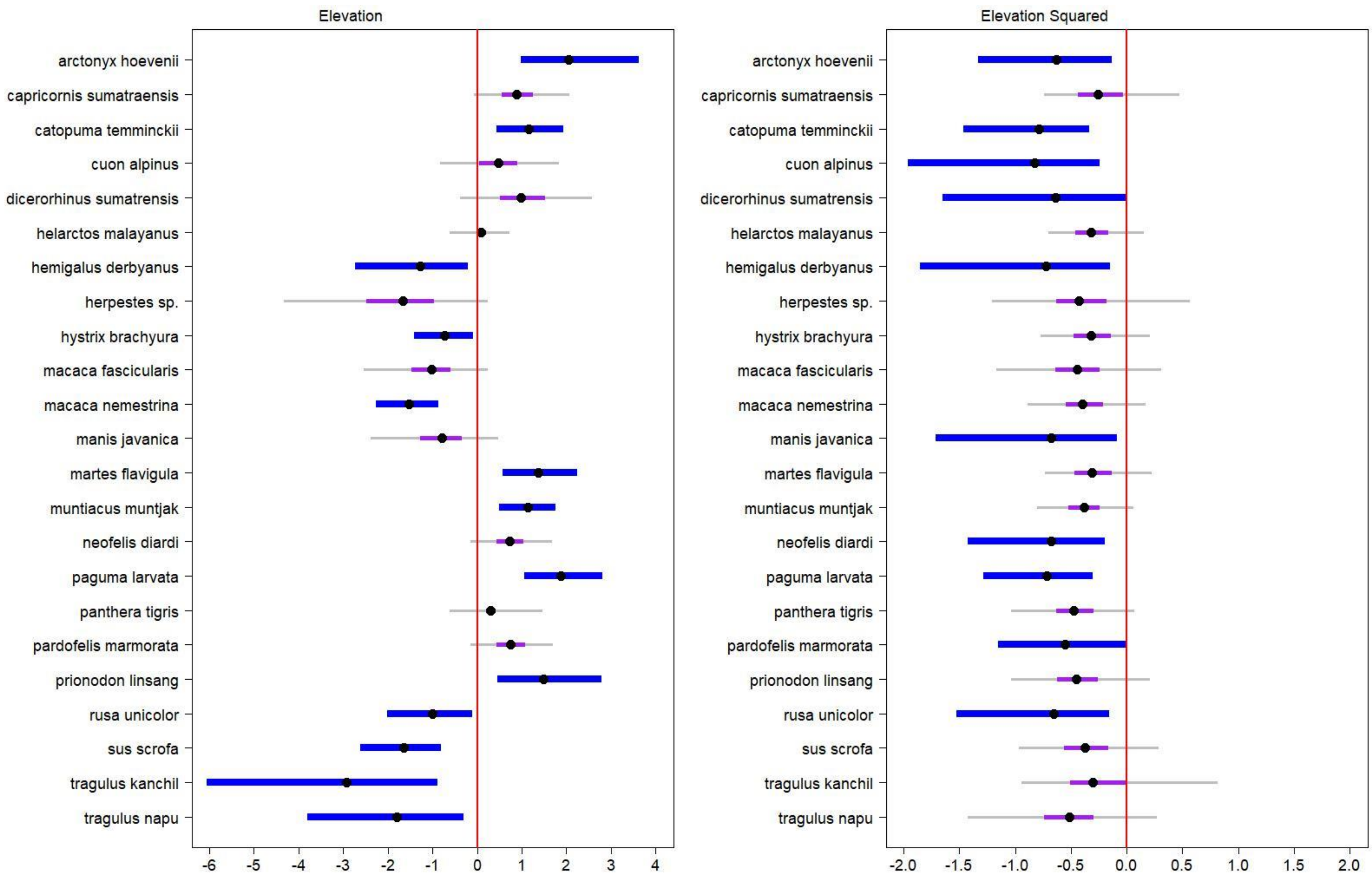
Appendix S3.8. Occupancy probability of medium-large terrestrial mammal community (23 species) in response to six landscape covariates. Blue lines indicate predicted mean posterior distribution values and the dashed lines represent 95% BCIs.

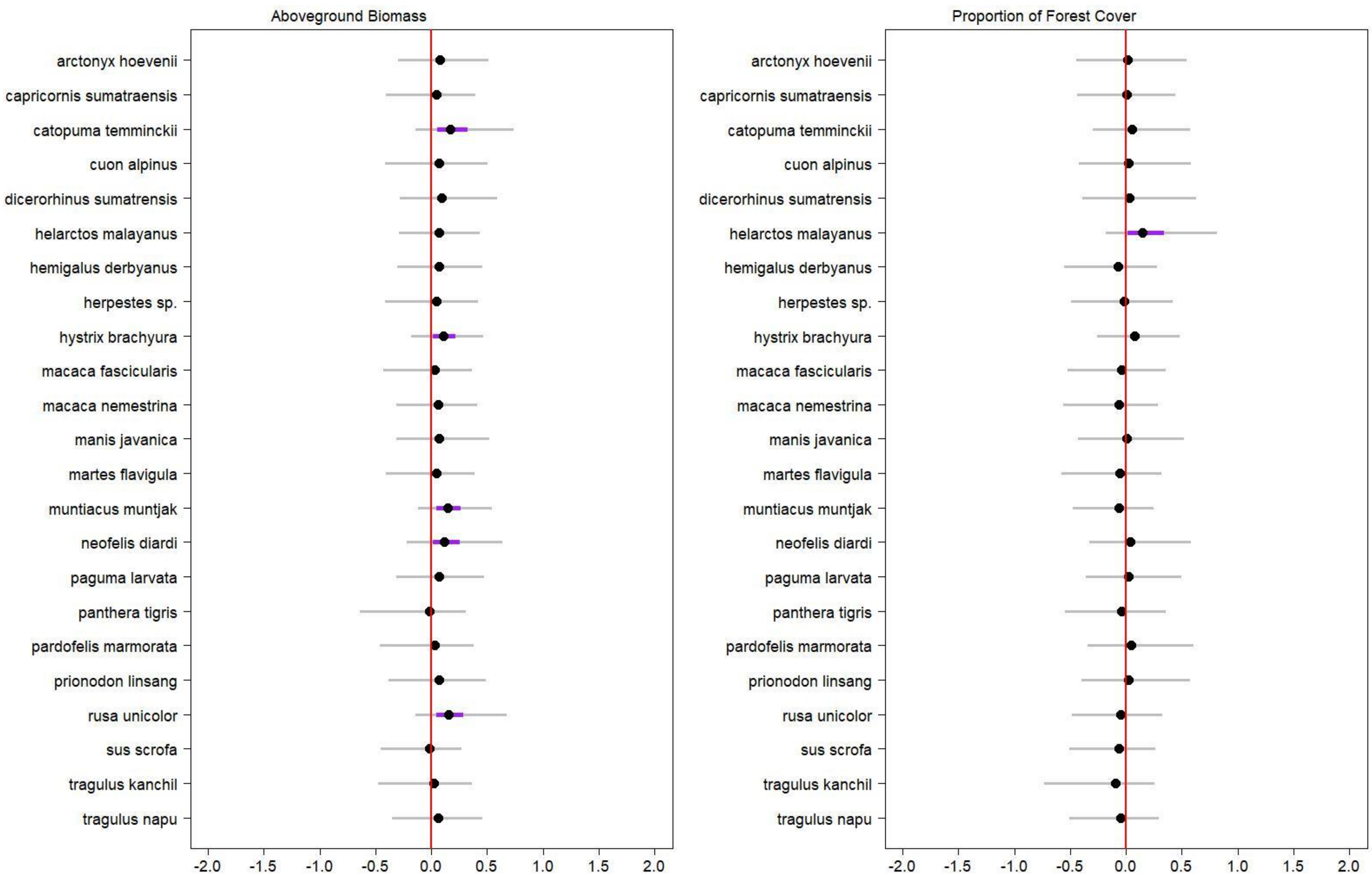


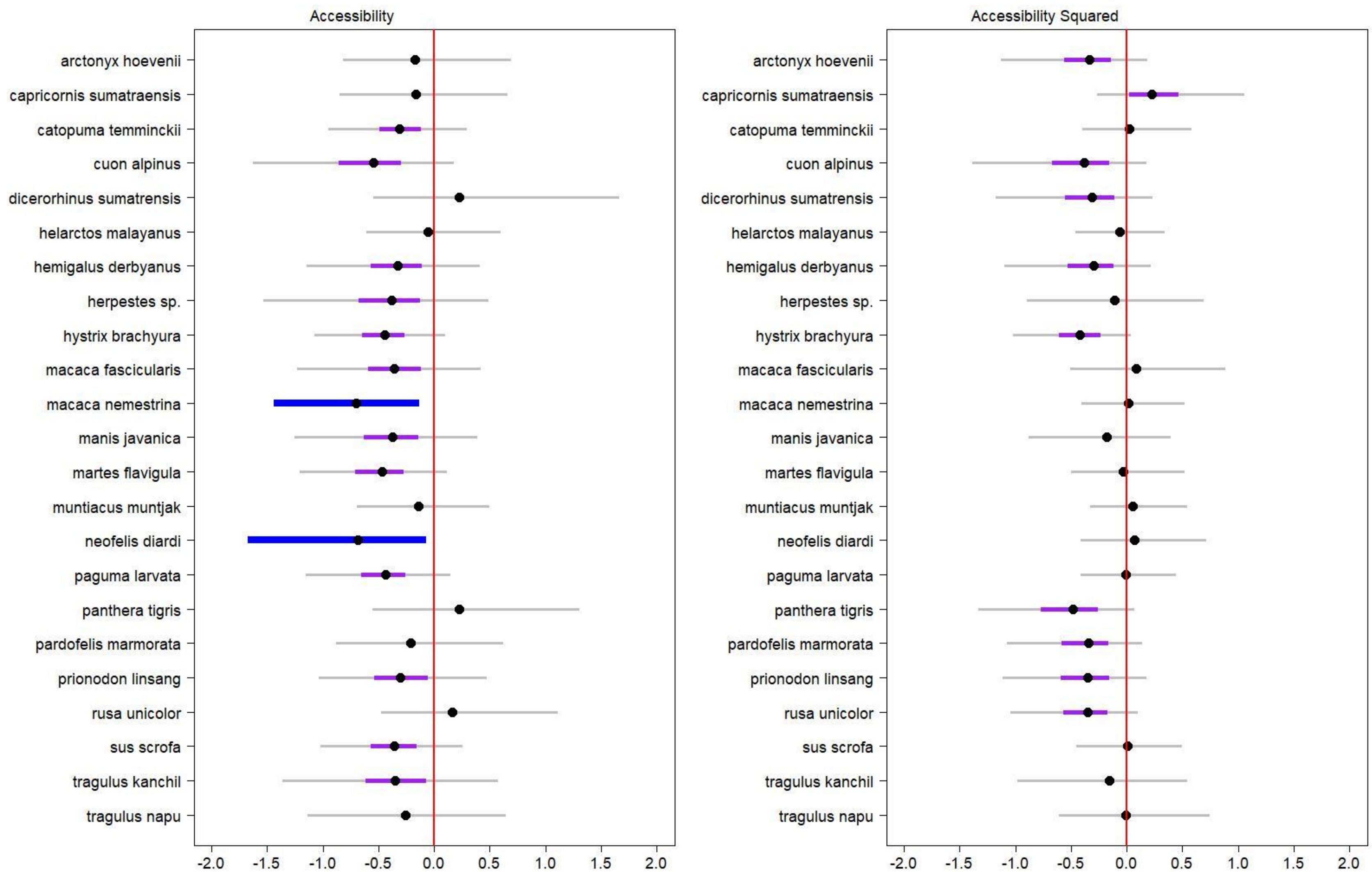
Appendix S3.9. Effect sizes for species-specific responses to selected covariates. Species posterior means are represented in points and Bayesian credible intervals (BCIs) in horizontal lines. Grey colour indicates nonresponse, purple shows limited support of influence (50% BCI), and blue represents substantial influence (95% BCI). Three covariates: elevation, TRI, and accessibility are also presented in second-order polynomial terms that are indicative of nonlinear associations.

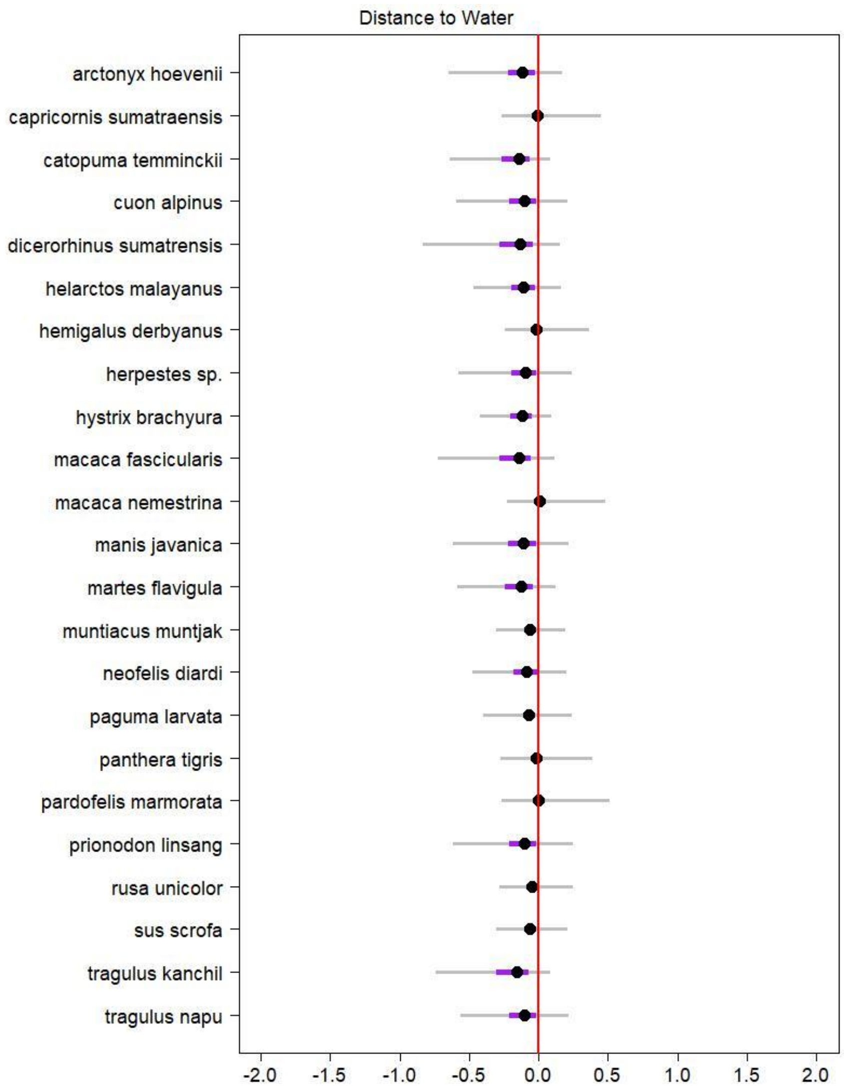


Terrain Ruggedness Index
Terrain Ruggedness Index Squared
arctonyx hoevenii
capricornis sumatraensis
catopuma temminckii
cuon alpinus
dicerorhinus sumatrensis
helarctos malayanus
hemigalus derbyanus
herpestes sp.
hystrix brachyura
macaca fascicularis
macaca nemestrina
manis javanica
martes flavigula
muntiacus muntjak
neofelis diardi
paguma larvata
panthera tigris
pardofelis marmorata
prionodon linsang
rusa unicolor
sus scrofa
tragulus kanchil
tragulus napu
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0

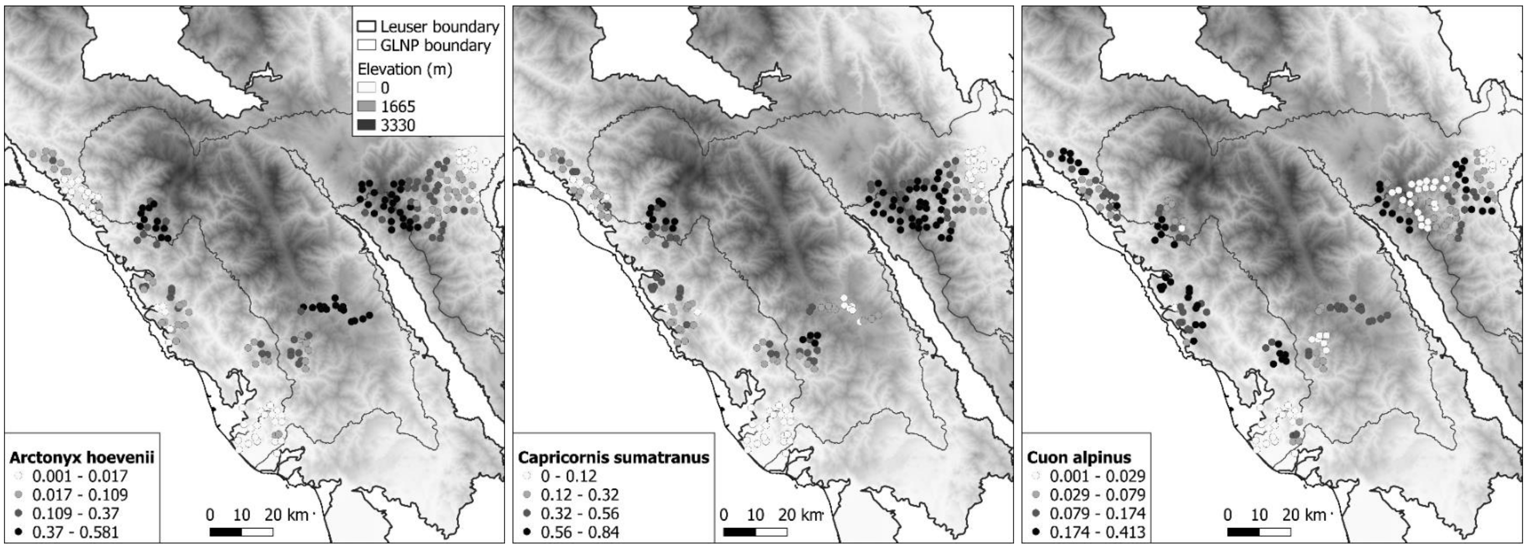

Elevation
Elevation Squared
arctonyx hoevenii
capricornis sumatraensis
catopuma temminckii
cuon alpinus
dicerorhinus sumatrensis
helarctos malayanus
hemigalus derbyanus
herpestes sp.
hystrix brachyura
macaca fascicularis
macaca nemestrina
manis javanica
martes flavigula
muntiacus muntjak
neofelis diardi
paguma larvata
panthera tigris
pardofelis marmorata
prionodon linsang
rusa unicolor
sus scrofa
tragulus kanchil
tragulus napu
-6 -5 -4 -3 -2 -1 0 1 2 3 4
-2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0

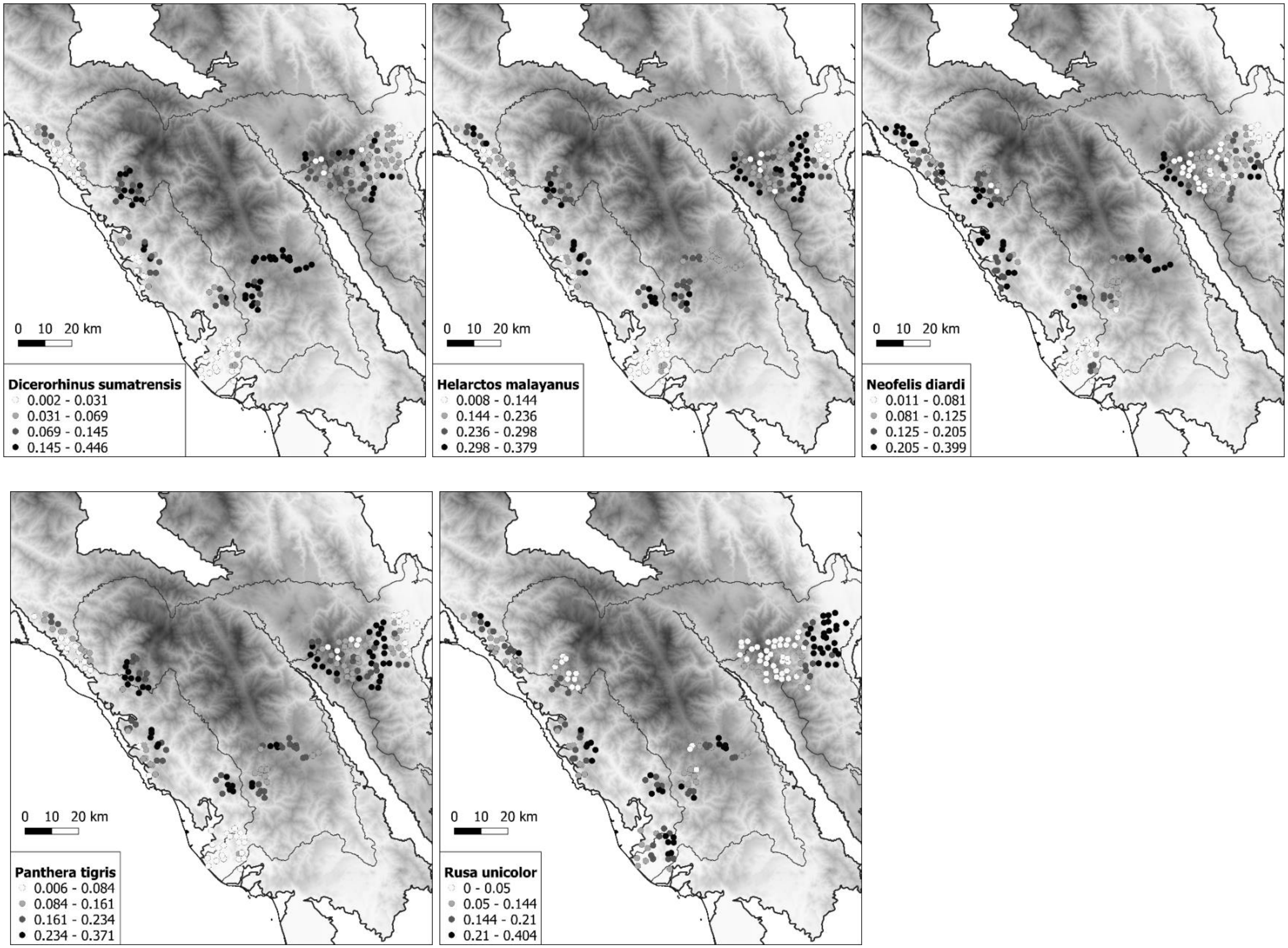

Aboveground Biomass
Proportion of Forest Cover
arctonyx hoevenii
capricornis sumatraensis
catopuma temminckii
cuon alpinus
dicerorhinus sumatrensis
helarctos malayanus
hemigalus derbyanus
herpestes sp.
hystrix brachyura
macaca fascicularis
macaca nemestrina
manis javanica
martes flavigula
muntiacus muntjak
neofelis diardi
paguma larvata
panthera tigris
pardofelis marmorata
prionodon linsang
rusa unicolor
sus scrofa
tragulus kanchil
tragulus napu
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0


Accessibility
Accessibility Squared
arctonyx hoevenii
capricornis sumatraensis
catopuma temminckii
cuon alpinus
dicerorhinus sumatrensis
helarctos malayanus
hemigalus derbyanus
herpestes sp.
hystrix brachyura
macaca fascicularis
macaca nemestrina
manis javanica
martes flavigula
muntiacus muntjak
neofelis diardi
paguma larvata
panthera tigris
pardofelis marmorata
prionodon linsang
rusa unicolor
sus scrofa
tragulus kanchil
tragulus napu
-2.0 -1.5 -1.0 -0.5 0.0 0.5 1.0 1.5 2.0


Distance to Water
arctonyx hoevenii
capricornis sumatraensis
catopuma temminckii
cuon alpinus
dicerorhinus sumatrensis
helarctos malayanus
hemigalus derbyanus
herpestes sp.
hystrix brachyura
macaca fascicularis
macaca nemestrina
manis javanica
martes flavigula
muntiacus muntjak
neofelis diardi
paguma larvata
panthera tigris
pardofelis marmorata
prionodon linsang
rusa unicolor
sus scrofa
tragulus kanchil
tragulus napu
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0

Appendix S310. Occupancy of eight surrogate species across 212 camera traps set in the Leuser Landscape. Occupancy values in legends were divided into four categories based on their quartiles. The upper quartile represents the top 25% values (darkest colour legend).




0 10 20 km
Dicerorhinus sumatrensis
0.002 - 0.031
0.031 - 0.069
0.069 - 0.145
0.145 - 0.446
0 10 20 km
Helarctos malayanus
0.008 - 0.144
0.144 - 0.236
0.236 - 0.298
0.298 - 0.379
0 10 20 km
Neofelis diardi
0.011 - 0.081
0.081 - 0.125
0.125 - 0.205
0.205 - 0.399
0 10 20 km
Panthera tigris
0.006 - 0.084
0.084 - 0.161
0.161 - 0.234
0.234 - 0.371
0 10 20 km
Rusa unicolor
0 - 0.05
0.05 - 0.144
0.144 - 0.21
0.21 - 0.404

Appendix S3.11. Species umbrella performance ranking across four biodiversity parameters in medium-large mammal community with beta coefficient values of the linear predictor. Values highlighted in red indicate a significant quadratic relationship.

Rank	Community occupancy		Species richness		Functional diversity		Phylogenetic diversity	
	Species	Mean (95% CI)	Species	Mean (95% CI)	Species	Mean (95% CI)	Species	Mean (95% CI)
1	Sambar deer	0.64 (0.46-0.81)	Sun bear	9.2 (2.47-15.92)	Sambar deer	2.17 (0.74-3.71)	Clouded leopard	9.74 (7.91-11.77)
2	Clouded leopard	0.47 (0.29-0.67)	Clouded leopard	8.68 (3.39-14.39)	Clouded leopard	1.1 (–2.78-3.97)	Sambar deer	8.26 (6.87-9.75)
3	Sun bear	0.45 (0.21-0.71)	Sambar deer	7.43 (2.6-12.65)	Dhole	0.42 (–3.32-3.07)	Dhole	0.99 (–4.38-4.97)
4	Dhole	0.35 (0.22-0.5)	Dhole	6.81 (2.49-10.35)	Mountain serow	–1.29 (–2.61-0.04)	Mountain serow	–2.98 (–4.65 - –1.17)
5	Sumatran rhino	0.25 (0.12-0.39)	Mountain serow	6.54 (2.76-10.53)	Sun bear	–3.01 (–5.04 - –0.86)	Sun bear	–3.95 (–6.67 - –1.23)
6	Sumatran tiger	0.21 (0.03-0.38)	Sumatran tiger	6.19 (1.45-10.87)	Sumatran tiger	–3.51 (–5.1 - –1.89)	Sumatran tiger	–5.6 (–7.09 - –4.13)
7	Mountain serow	0.13 (–0.02-0.29)	Sumatran rhino	4.1 (–1.61-8.52)	Hog badger	–4.46 (–6.06 - –2.85)	Sumatran rhino	–7.16 (–9.28 - –5.08)
8	Hog badger	–0.06 (–0.23-0.13)	Hog badger	–1.76 (–9.93-7.13)	Sumatran rhino	–5.16 (–6.84 - –3.39)	Hog badger	–7.34 (–9.11 - –5.76)

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Chapter 4 Improved cost-effectiveness of species monitoring programs through data integration

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[5]Aceh Natural Resource Conservation Agencies, Banda Aceh, Indonesia;

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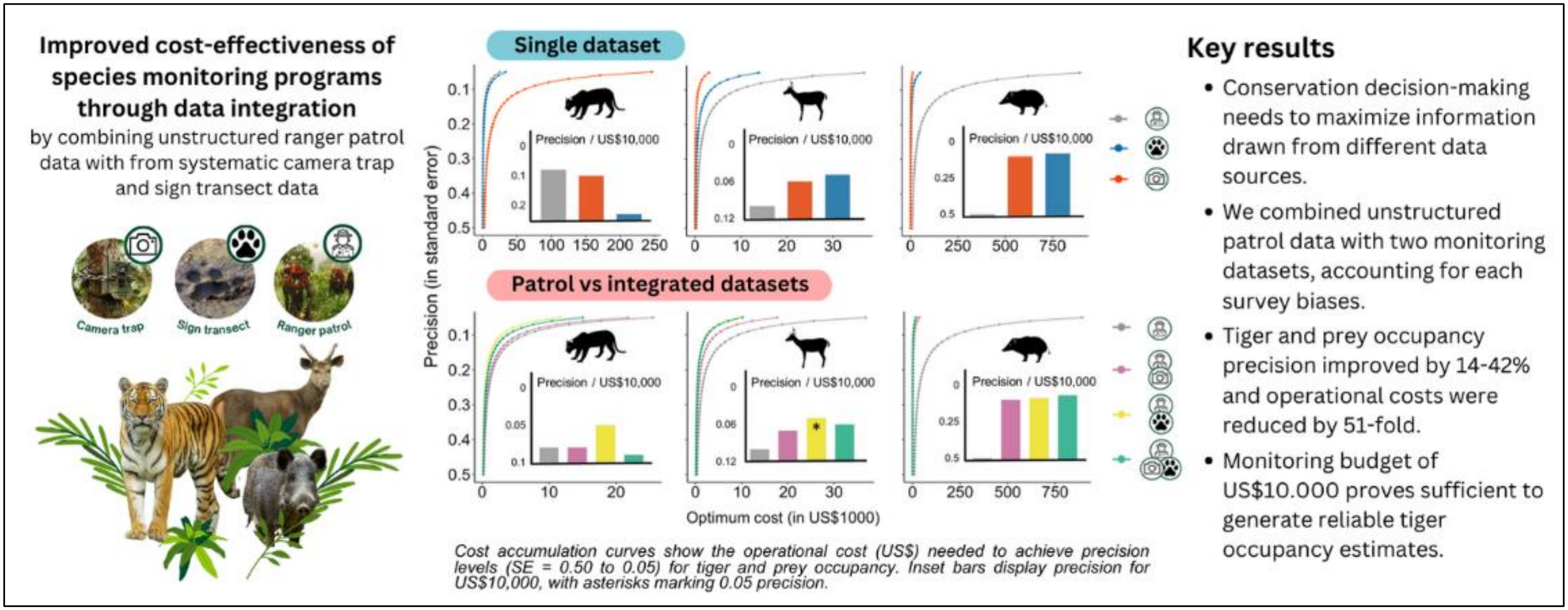

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4.1 Summary

Conservation initiatives strive for reliable and cost-effective species monitoring (Gardner *et al.*, 2008; Voigt *et al.*, 2018; Zwerts *et al.*, 2021). However, resource constraints mean management decisions are overly reliant on data derived from single methodologies, resulting in taxonomic or geographic biases (Isaac *et al.*, 2020). We introduce a data integration framework to optimize species monitoring in terms of spatial representation, the reliability of biodiversity metrics, and the cost of implementation, focusing on tigers (*Panthera tigris sumatrae*) and their principal prey (sambar deer *Rusa unicolor* and wild pigs *Sus scrofa*). We combined information from unstructured ranger patrols, systematic sign transects, and camera traps in Sumatra's largest remaining tropical forest, and used integrated community occupancy models to analyze this multifaceted dataset in a unified way. Data integration improved the precision of species occupancy estimates by 14–42%, expanded the spatial scope of inference to the landscape-level, and cut operational costs up to 51-fold. Our framework demonstrates the underappreciated value of integrating unstructured observations with monitoring data derived from traditional wildlife surveys.

4.2 Results and discussion

How much to spend, and how and where to survey are key questions facing conservation managers when designing species monitoring programs (Santika *et al.*, 2022). Thus, cost-effective approaches to monitor biodiversity are essential for conservation, especially for threatened species. Yet, surveys often involve different methodologies with different aims and so are poorly placed to be analyzed in a unified way (Miller *et al.*, 2019; Isaac *et al.*, 2020). Data integration methods can potentially address this problem by utilizing information from different sources, but to date, few empirical studies have achieved this while simultaneously evaluating the cost-saving implications of these approaches (Sanderlin *et al.*, 2019). Further, there are no such evaluations on multiple taxa in tropical countries that are central to the international conservation agenda.

Here we evaluate the benefits of integrating data from unstructured, but widely implemented ranger patrols with ecological datasets from commonly used wildlife survey methods (sign transects and camera traps), to improve statistical precision, spatial scope of inference, and operational cost-effectiveness of endangered species monitoring. We focus on the Sumatran tiger, which typically occurs at low densities, thus population assessments based on single monitoring methods are plagued by insufficient data to reliably inform conservation management. As resource availability is a key constraint on carnivore populations (Lu *et al.*, 2023), we extend inferences to the tiger's principal prey (Lubis *et al.*, 2023): sambar deer and wild pig. We applied integrated community occupancy models (Doser *et al.*, 2022) to compare species occurrence patterns from ranger patrol, sign transect, and camera trap datasets. We assessed the influence of additional datasets on improving occupancy precision derived from patrol data. Finally, we calculated optimum survey costs to identify the most cost-effective combination of field survey approaches to optimize the precision of species occupancy estimates.

4.2.1 Improved species occupancy precision

Occupancy – the proportion of sites a species inhabits – is a common monitoring metric used by conservation managers to prioritise species recovery (Mackenzie and Royle, 2005). We therefore applied Bayesian community occupancy modelling that accounts for imperfect species detection, performing analyses for each survey dataset separately and in combination. The resulting species occupancy estimates were also used to map the distribution of each species across the Leuser study area. Our data show that these spatial patterns of species occurrence vary substantially depending on the underlying method of data collection (Fig. 5.1B-D). Mapped predictions of tiger, sambar, and pig occupancy derived from the patrol dataset were moderately correlated with those for the transect data (correlation coefficients = 0.45-0.54), but showed opposite trends with camera data (–0.26 - –0.01), except for sambar (0.67).

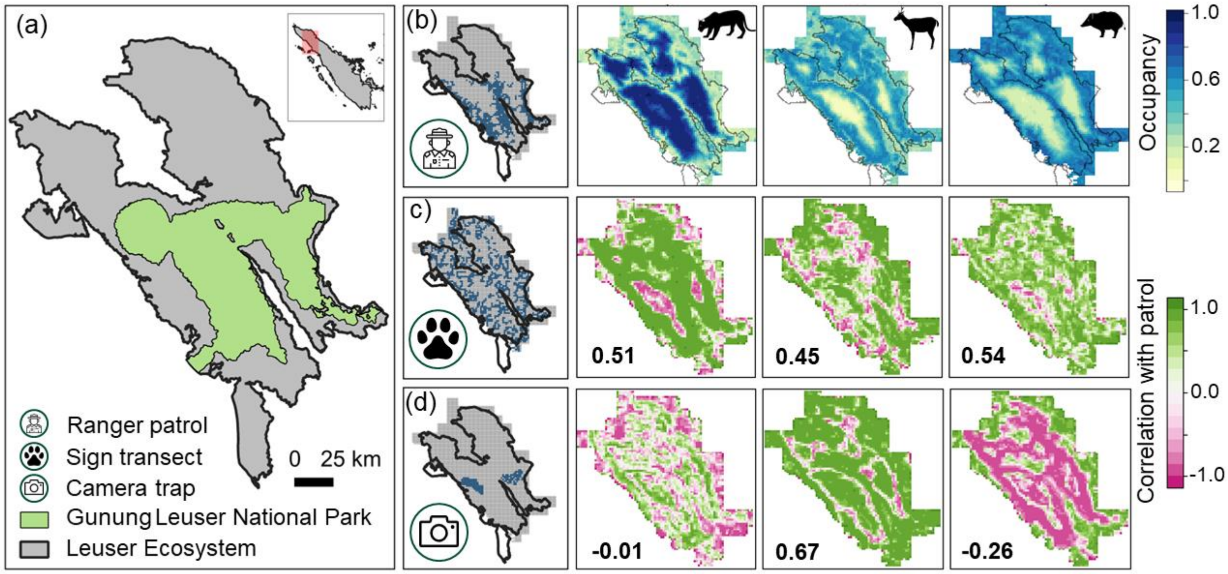

Fig 4.1: (A) Leuser Ecosystem with Gunung Leuser National Park at its core. (B; left to right) Grids cells surveyed (in blue) by ranger patrols and the resulting occupancy probability maps for tiger, sambar, and pig. (C, D; left to right) Surveyed grid cells for transects and cameras followed by spatial correlation maps comparing species occupancy outputs with the patrol maps, with values indicating mean correlation coefficients.

Models derived solely from the unstructured patrol dataset yielded occupancy estimates with low statistical precision, as evidenced by larger 95% Bayesian Credible Intervals (BCIs; Fig. 4.2A). However, integrating the patrol data with other monitoring datasets improved precision for all species (decrease in BCI range; Fig. 4.2B), especially prey (pig: 29-41%; sambar: 24-42%; tiger: 14-22%). Throughout, models combining all three datasets generated the most precise occupancy estimates (also see Appendix S4.1 for species detection probability across models).

4.2.2 Improved monitoring cost-effectiveness

Survey methods needed to detect the elusive and cryptic species typical of tropical forests can incur high costs due to the need for expensive equipment (e.g. camera traps) or skilled observers (e.g. sign transects). For example, the standard annual operational budget for tiger population monitoring in Gunung Leuser National Park (the core conservation area in Leuser Ecosystem) is around US$30,000, but this does not include equipment, personnel salaries, and monitoring activities beyond the park.

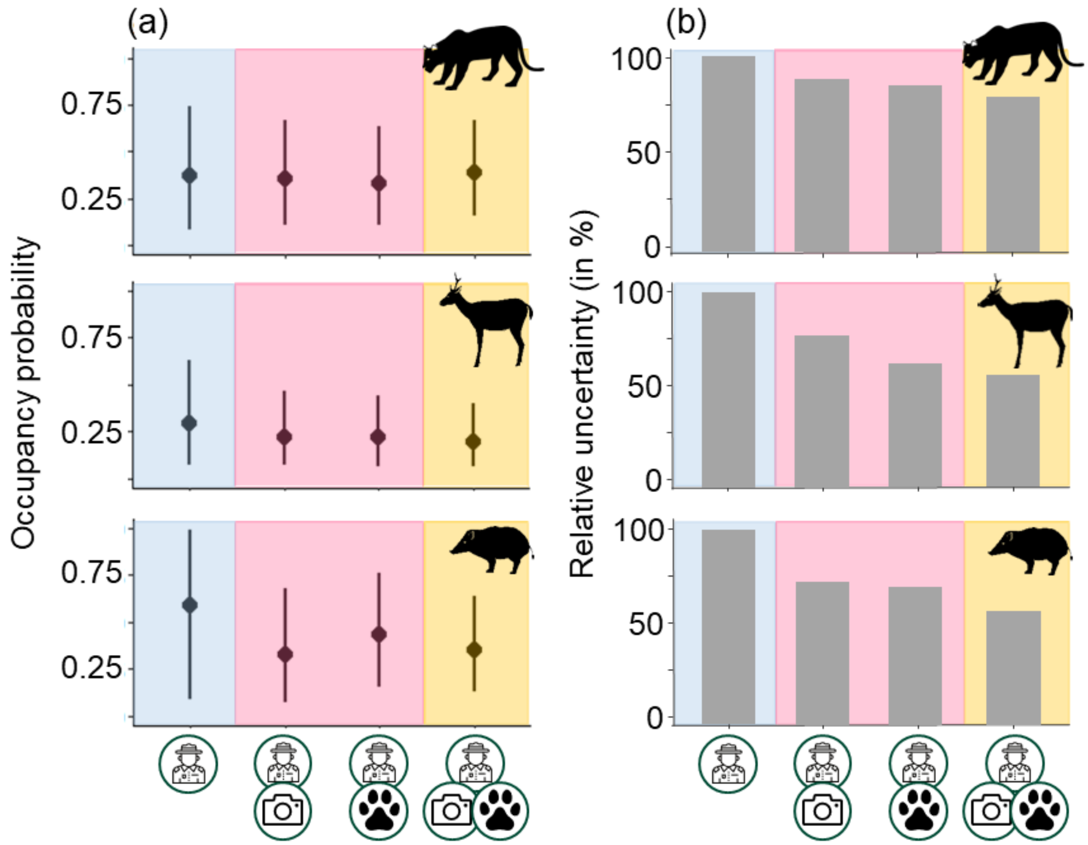

Fig 4.2: (A) Tiger and prey occupancy estimates (points) with 95% Bayesian Credible Intervals/BCIs (vertical lines) represent averages from across Leuser Ecosystem. (B) The percentage of reduced uncertainty (decrease in BCIs range) achieved by combining patrol-derived estimates (reference point with 100% relative uncertainty) with additional datasets.

We estimated the optimum monitoring cost by calculating the operational costs (in US$) for a field team of 4-6 people to survey one 3x3 km grid cell (Appendix S4.2). We then calculated the required number of grid cells (Mackenzie and Royle, 2005) to achieve a species occupancy estimate with a reliable degree of precision (standard error/SE = 0.05) using occupancy and detection estimates derived from the occupancy modelling. When considered as the sole monitoring activity, patrols proved to be the most cost-effective method for achieving the desired level of statistical precision (SE = 0.05) for tiger occupancy (US$25,511; Fig. 4.3), outperforming transects (US$33,472) and cameras (US$246,179). However, for prey species, patrols were considerably more expensive, costing US$36,831 and US$892,674, compared to cameras (US$3,023 and US$12,073 respectively) to generate occupancy estimates for sambar and pig with an equivalent level of precision.

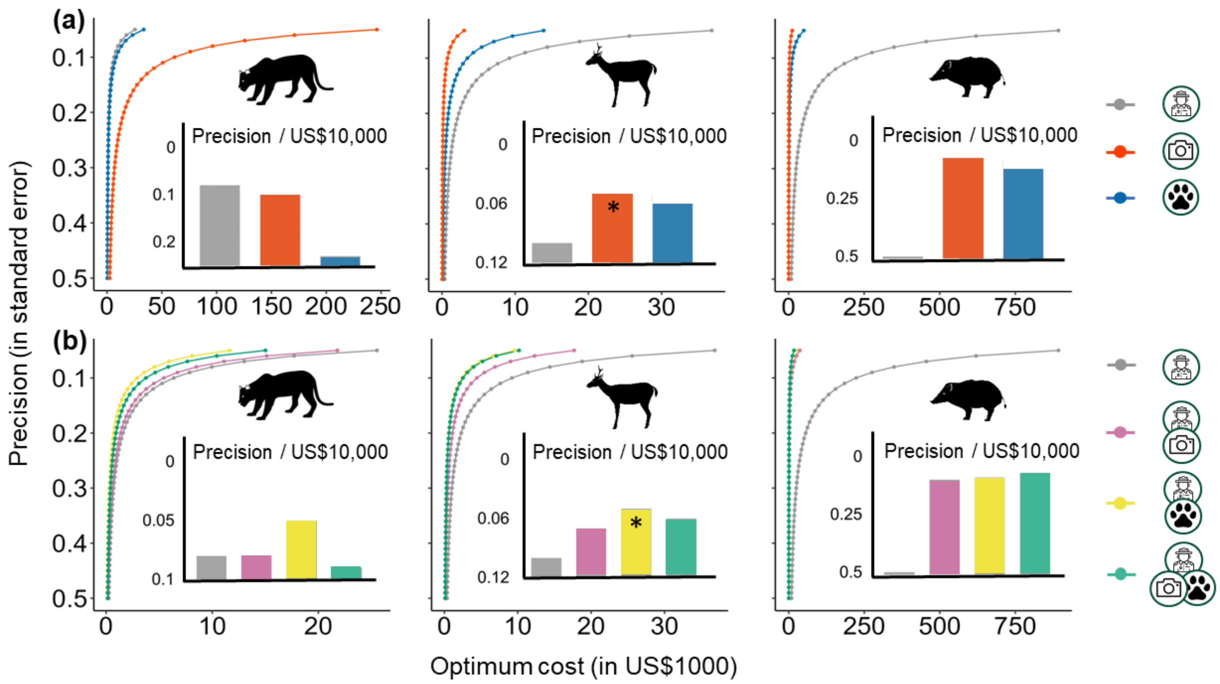

Fig 4.3: The cost accumulation curves present the total operational cost (US$) required to attain specific precision levels (SE = 0.50 to 0.05) for tiger and prey occupancy. Inset bar charts illustrate the precision achieved for US$10,000 spent, with asterisks indicating where precision was achieved at the 0.05 level. (A) Plots compare costs among three activities, while (B) plots compare costs between patrol and integrated datasets.

Importantly, integrating the patrol information with other datasets cut the tiger monitoring cost needed to achieve precise occupancy estimates by more than half (from US$25,511 to US$11,645). For sambar, the cost saving was a 5-fold reduction (US$36,831 to US$9,580), and for pig, it was 51-fold (US$892,674 to US$17,422). When combining patrol and transect datasets, a standard operational cost of US$10,000 was sufficient to produce precise tiger and sambar occupancy estimates.

4.2.3 Advantages of data integration in wildlife monitoring

Globally, protected areas heavily invest in ranger patrols to detect and deter illegal activities (Santika *et al.*, 2022), which are conducted routinely and cover extensive areas. While rangers record species encounters and signs, the unstructured nature of data collection and disproportionate focus on selected species, often charismatic ones, limit the application of patrols in wildlife monitoring programs (Critchlow *et al.*, 2015). Management decisions based on data derived from single survey methodologies, be it unstructured patrols or systematic monitoring, will be subject to taxonomic or geographic biases (Isaac *et al.*, 2020). In our analysis, these biases manifested as imprecise occurrence estimates when patrol data were analyzed in isolation, particularly for prey species that have a lower perceived conservation value. However, even systematic monitoring approaches using traditional survey methodologies can introduce bias into conservation assessments (e.g. small survey area in camera trap (Wearn and Glover-Kapfer, 2019), or species or signs misidentification in transect survey (Lubis *et al.*, 2023)). When extrapolated to landscape scales appropriate to conservation management, these biases may be amplified leading to highly inaccurate wildlife occurrence information. For example, we found limited agreement between spatial occupancy predictions derived from single survey methods especially with camera surveys, highlighting the dangers of designing management strategies based on any single method in isolation.

Integrating unstructured data from patrols with systematically designed transect and camera data offers several advantages to wildlife monitoring programs operating in extensive and challenging environments (Appendix S4.3). First, data integration improves the precision of species occupancy estimates derived from patrol data due to the increased sample size and by borrowing statistical strengths between datasets (Sanderlin *et al.*, 2019). Precise estimates are crucial in conservation management when the goals are to detect long-term species population trends and evaluate conservation program impacts (Zipkin and Saunders, 2018). Second, integrating datasets improves the spatial scope of inference (i.e. here, data coverage increased from 4% to 49.6% of the landscape), which addresses the spatial biases inherited from survey methodologies. For example, given significant logistical constraints in remote and rugged tropical forests, patrols are typically conducted near the forest boundary, while intensive camera campaigns are bounded to the core protected area and sign transects are often more widespread. As we have shown here, data integration generates species occupancy patterns representative of an entire landscape, where conservation interventions are typically staged (Koshkina *et al.*, 2017; Doser *et al.*, 2022).

Our study demonstrates the costs associated with monitoring based on combinations of the various source datasets, which yields broad insights that are applicable for designing more efficient, cost-effective monitoring programs elsewhere. For example, combining the patrol and transect datasets reduced monitoring costs, where a budget of ~US$10,000 is adequate to generate precise estimates of occupancy for tigers and prey. Notably, this is far below the tiger monitoring budget of ~US$30,000 by Gunung Leuser National Park, opening opportunities to assess the feasibility of data integration techniques for future monitoring. Nevertheless, our cost-effectiveness framework highlights the optimum number of sampling locations (e.g. cells to survey), but does not provide detailed information on how surveys should be designed, which will be dictated by the objectives and taxonomic focus of the monitoring program.

4.2.4 Future applications of data integration

Efforts to make more use of disparate monitoring datasets have increased significantly since the 2000s, driven by advances in computational modelling, statistical innovations and the availability of ecological data collected through diverse methods (Zipkin *et al.*, 2021). There is a growing focus on more systematic designs for unstructured monitoring activities, enhancing the potential of utilizing such data for species monitoring. For instance, the establishment of operational procedures for ranger patrols such as the Spatial Monitoring and Reporting Tool (SMART; Taskforce, 2022) and survey designs for citizen science (Callaghan *et al.*, 2019), helps facilitate standardized data collection through grid systems, repeated visits, and recording species detections at set intervals. Our framework shows the hitherto underappreciated value of unstructured observation data when integrated into wildlife survey datasets used for species monitoring. Maximizing the information that can be drawn from all sources is crucial to species monitoring efforts, particularly in tropical regions where timely and cost-effective biodiversity assessments are urgently needed to safeguard threatened wildlife populations and overcome limited operational capacity.

4.3 Method

4.3.1 Study area

We undertook our study in the Leuser Ecosystem (Figure 4.1A), a 25,000 km^2 mosaic of peat swamp, lowland, hill, sub-montane, and montane forest (up to 3,500 m.a.s.l.) in northern Sumatra. Most of the area (75%; 18,673 km^2) is designated for conservation, including the Gunung Leuser National Park (GLNP; 8282 km^2), a UNESCO World Heritage Site. The landscape is well protected, but parts experience some encroachment from agricultural expansion, road development, and human settlements, particularly outside the conservation area (Sloan *et al.*, 2018).

4.3.2 Field data collection

We collected detection data of tigers and prey that are consistently recorded among three survey activities: ranger patrols, sign transects, and camera traps (Appendix S4.3). The patrol dataset comprised 844 patrols in GLNP undertaken between July 2018 and June 2021, totalling 9,593 days (average days per patrol = 14 days [range: 3-30]). Sign transects across Leuser were collected as part of Indonesia's second national tiger occupancy survey, conducted from October 2018 to December 2019. In total, 5,639 km were surveyed within 109, 17x17 km grid cells (average transect length = 51 km [23-79 km]), corresponding to the estimated home range of adult male Sumatran tigers. Systematic camera trap surveys were conducted in the East and West Leuser Ecosystem, between March 2020 and July 2021. These surveys, involving 146 sites, aimed to estimate tiger density, and operated for a total of 14,029 trap days, with an average of 93 consecutive days at each site (11-263 days). Species detections (total detections/survey efforts) were relatively low (range: 0.01-0.03) in transect and camera surveys compared to patrol dataset (0.1-0.44), where tigers were detected most frequently (Appendix S4.3).

4.3.3 Data analysis

To introduce standardized sampling units across datasets, we overlaid a grid comprising 3x3 km cells across Leuser, resulting in patrols covering 658 cells, sign transect 1199 cells, and camera trap 146 cells. The grid size was selected to correspond with tiger population assessments in the region (Pusparini *et al.*, 2017), while providing sufficient detail to inform conservation management. Given the specification of grid cells smaller than Sumatran tiger's home range (Wibisono *et al.*, 2011), the independence assumption underpinning occupancy frameworks may be violated. Therefore, we interpret occupancy as the probability of habitat use, denoting episodic use of areas within the home range to meet ecological demands.

Detection histories were created from each dataset i.e. 0 when a species was not observed and 1 if observed. We generated replicates for the patrol dataset based on the most recent annual data for each grid cell, resulting in a maximum of four 3-month temporal replicates (range: 1-4). For the transect dataset, replicates were defined spatially at 500 m intervals to account for landscape topography (Lubis *et al.*, 2023). To maintain a balanced number of replicates, we restricted the transect length to 6 km corresponding to the average transect length surveyed in 3x3 km cells (1-12.5 km). This resulted in a maximum of 12 replicates (1-12). For the camera dataset, we restricted the sampling period to 90 trap days, yielding a maximum of 18, 5-day replicates per site (3-8).

We applied Bayesian hierarchical integrated community occupancy models to estimate community-level and species-specific occupancy and detection while explicitly accounting for imperfect detection (Doser *et al.*, 2022) (Appendix S4.4). Integrated occupancy modelling combines datasets derived from multiple methodologies within a single statistical framework, addressing potential biases stemming from different survey designs and species detection (Isaac *et al.*, 2020). By utilizing more data, integrated models improve the precision of species occupancy estimates and extend the spatial inference to scales appropriate to conservation management (Doser *et al.*, 2022).

To improve the precision and spatial inference of species occupancy probability, we constructed a common ecological process model to integrate detection information derived from three datasets. Additionally, we developed three observation models specific to each dataset to estimate species detection probability. Throughout, species-specific responses were drawn as random effects from community-level distributions. To account for temporal variability arising from datasets spanning a three-year period, we included year as a random factor in the ecological process model. We then constructed six candidate models featuring each dataset independently and in combination.

To control for environmental variations, we modelled occupancy as a function of habitat quality represented by tree canopy height (m) and its variability (Deere, Guillera-Arroita, *et al.*, 2020). Anthropogenic influences were considered by calculating distance accumulation, the linear distance from human settlements to Leuser, and factoring in topography, access, and barriers (e.g. elevation, roads, rivers, and habitat types) (ESRI, 2023). Species detection was modelled as a function of terrain ruggedness index and habitat types (primary forest, secondary forest, shrubland, wetland, and agriculture). Survey effort and detection tools were also factored in, considering the number of point observations (patrol), transect length (transect), camera models, and total trap days (camera).

We developed tiger and prey occupancy maps using parameter estimates derived from occupancy models and linked these parameters with spatially explicit covariate values across Leuser Ecosystem. We compared patterns among datasets by calculating spatial correlation in the grid cell level between patrol-derived occupancy maps and prediction maps from transect and camera datasets (Sébastien, 2018). To evaluate the benefits of data integration, we compared species occupancy estimates and precision (95% Bayesian Credible Interval; BCIs) derived from the patrol model and integrated models.

4.3.4 Optimum monitoring cost

We evaluated the economic implications of data integration to wildlife monitoring relative to higher levels of statistical precision. Initially, we determined the total operational cost (in US$) of a field team conducting one survey trip. We defined one trip as a 14-day patrol survey, or 30-day for camera or transect surveys, which corresponded to the survey period in Leuser. These costs were divided into four categories based on criteria outlined in Seidlitz et al. (2021): transportation, personnel (e.g. salary, daily fee), meals and lodging, and materials (e.g. field equipment). The budget costs were decided in consultation with the park manager and partner organizations. For long-term equipment like cameras and global positioning system devices, we spread the cost over the device’s lifetime (e.g. 36 months for camera traps based on consultation with field practitioners in Sumatra). The total costs were then divided by the average number of cells surveyed per trip by one team: patrol (8 cells), transect (30), trap (12), and the sum of cells for integrated datasets (Appendix S4.2).

We used Mackenzie and Royle's (Mackenzie and Royle, 2005) formula to calculate the required number of grid cells to achieve a desired level of statistical precision within a 10% deviation of species occupancy estimates (Standard Error/SE = 0.05) (Appendix S4.5). This is calculated based on model-derived estimates of occupancy and detection probability, a user-defined threshold for precision, and the mean number of temporal/spatial survey replicates associated with each dataset: patrol (4 replicates), camera (18), and transect (12), and sum of replicates for integrated datasets. We then estimated the optimum monitoring cost by multiplying the cost to survey a grid cell with the required number of cells to achieve a range of precisions from SE 0.50-0.05, at intervals of 0.01. Finally, we compared the total costs and gained precision at a common economic cost reference (US$10,000) to determine the most cost-effective survey activity or combination to reliably inform tiger and prey occupancy.

4.4 Acknowledgements

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4.5 Data availability

Example datasets and model codes associated with this manuscript can be accessed at https://github.com/Ardiantiono/Data-integration.git.

4.6 References

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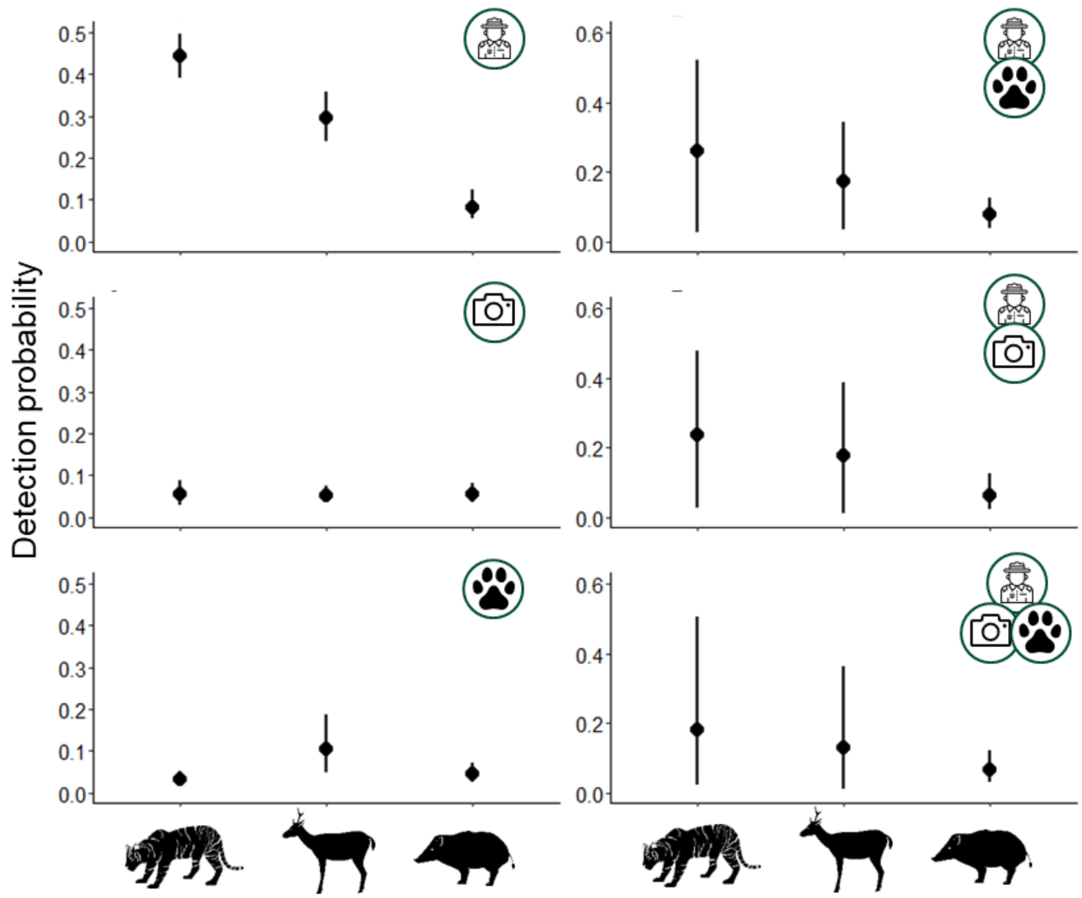
4.7 Supplementary information

Appendix S4.1: Species detection probability across single and integrated datasets based on the occupancy model outputs.



Appendix S4.2: Detailed operational cost (in US$: US$1 = IDR15,000) for one team per survey trip across three activities. One trip is defined as either 14 days (patrols) or 30 days (transects and cameras). For long-term equipment, the costs were spread across device's lifetime which was determined based on consultation with field practitioners in the region. Operational costs for a team to survey one grid cell were calculated by dividing the total operational cost by the number of grid cells surveyed in one survey trip.

Operational cost in US$ (one team per trip)	Usage period in months	Survey activity		
		Ranger patrol	Sign transect	Camera trap
Materials		**125**	**137**	**336**
Camera trap	36			167
Camera trap security (e.g. lock and cases)	60			13
Memory card for camera traps	36			4
Battery (e.g. camera traps, GPS)	1	33	33	53
Digital camera	60	4	4	4
GPS	60	6	6	6
Power bank	24	2	2	2
Densiometer	60		5	
Personal equipment (e.g. bag, sleeping bag, uniform, rain coat)	24	67	67	67
Team equipment (e.g. compass, cooking utensil, dry bag, tent, stationary)	24	14	21	21
Meals and lodging		**600**	**1,200**	**1,200**
Meals	1	600	1,200	1,200

Personnel		**900**	**1,420**	**1,420**
Team leader salary (employee)	1		267	267
Team leader salary (non-employee)	1	140		
Team members salary (employee)	1		233	233
Team members salary (non-employee)	1	373	800	800
Staff salary (employee, e.g. database officer)	1	267		
Medical support (e.g. insurance and medicine)	1	120	120	120
Transportation		**100**	**333**	**167**
Local transport (vehicle rental, fuel)	1	100	333	167
Grand Total		**1,725**	**3,090**	**3,123**
Number of grid cells surveyed per trip		**8**	**30**	**12**
Operational cost to survey one grid cell		**216**	**103**	**260**

Appendix S4.3: Survey design, data characteristics, and potential strengths (in blue) and biases (in orange) of three datasets used in this study.

	Ranger patrol	Sign transect	Camera trap
Aim	Detect and reduce illegal activities	Estimate tiger density	Estimate tiger occupancy
Species recorded	Tiger, prey species, and other species of conservation concerns (e.g. elephant, rhinoceros, and orangutan)	Tiger, prey species, and other species of conservation concerns (e.g. elephant, rhinoceros, and orangutan)	Terrestrial mammal
Survey design	Semi-structured. Assigned into 3x3 km grid.	Originally structured in 17x17 km grid. Resized to 3x3 km grid.	Structured in 3x3 km grid.
Data type	Species encounter and sign data	Species encounter and sign data	Species photograph data.
Species detections (total detections / total replicates)	Tiger: 429 (0.44) Sambar: 246 (0.25) Pig: 98 (0.10)	Tiger: 161 (0.02) Sambar: 165 (0.02) Pig: 94 (0.01)	Tiger: 70 (0.03) Sambar: 20 (0.01) Pig: 44 (0.02)
Number of 3x3 km grid cells	658	1199	146
Number of replicates per grid cell	Temporal: 4	Spatial: 12	Temporal: 18

Potential strengths and biases			
Survey design	Opportunistic species record No reference grid	Grid size based on tiger ecology (17x17 km). Grid was large for prey species.	Grid size based on tiger ecology (3x3 km). Grid was large for some prey species.
Observer	Misidentification and lower detection ability.	Misidentification and lower detection ability.	Camera active for 24 hours; photograph evidence
Species	Focus on large charismatic species e.g. tiger, rhinoceros, and elephant.	Tiger, prey species, and other species of conservation concerns (e.g. elephant, rhinoceros, and sun bear)	Terrestrial mammals
Location	Within Gunung Leuser National Park, mostly in forest boundary where the threats occur	Whole Leuser Ecosystem	Restricted in the core area of Leuser Ecosystem
Frequency	Monthly	Every 10 year	Every three year

Appendix S4.4: Integrated community occupancy model framework

We employed a Bayesian hierarchical integrated community occupancy model (ICOM) to estimate community-level and species-specific occupancy and detection developed by Doser et al. (2022). Species-specific responses were drawn as random effects from community-level distributions in both occupancy and detection models with estimable hyper-parameters that represent community patterns (Kery and Royle, 2016).

In the ICOM framework, we used joint likelihood to combine temporal and spatial replicated data from different sources into a single model (Miller *et al.*, 2019). We assume the detection process of tiger and prey is independent in each data source with a shared ecological process of species occurrence (Doser *et al.*, 2022).

We built the ecological process model common among all three sets in the ICOM to estimate tiger and prey occupancy probability (ψ) with the following form:

$$\text{logit}(\psi_{i,j}) = \beta_{0i} + \beta_{1i}Accessibility_j + \beta_{2i}Accessibility^2_j + \beta_{3i}CanopyHeight_j + \beta_{4i}CanopyHeight^2_j + \beta_{5i}CanopyHeightVariability_j + xi_i * eps_i Year_j \quad \textbf{(1)}$$

Where β_0 is species-specific intercept, $\beta_{2\text{-}5}$ are species-specific effects of multiple occupancy covariates, and *xi * eps* represent the temporal random factor (year). All of these parameters were shared across three datasets in the ICOM framework.

We also built the observation model specific to each data source to estimate species detection probability (p) with the following form:

$$\text{logit}(p.camera_{i,j,k}) = \alpha_{0i}CameraType_j + \alpha_{1i}TRI_j + \alpha_{2i}TrapNights_j$$

$$\text{logit}(p.transect_{i,j,k}) = \gamma_{0i}HabitatType_j + \gamma_{1i}TRI_j + \gamma_{2i}TransectLength_j$$

$$\text{logit}(p.patrol_{i,j,k}) = \delta_{0i}HabitatType_j + \delta_{1i}TRI_j + \delta_{2i}Num.Observation_j$$

(2)

Where α_0, γ_0, δ_0 are species-specific intercepts for each dataset and $\alpha_{1\text{-}2}$, $\gamma_{1\text{-}2}$, $\delta_{1\text{-}2}$ are effects of covariates influencing species detection across spatial/temporal replicates.

We specified six models (three for single datasets and three for integrated datasets using JAGS (v1.5.1 in R; Kellner 2019). Three parallel Markov chains were run with 400,000 iterations with the first 100,000 iterations removed as burn-in, and the rest thinned by 300. Model performance was evaluated using Gelman-Rubin statistics and Bayesian p-values (Gelman *et al.*, 1996). Occupancy and detection estimates for tiger and prey across Leuser were extracted from the model outputs.

Appendix S.4.5: Survey effort calculation

We applied model-derived occupancy (ψ) and detection (*p*) probabilities using a formula by Mackenzie & Royle (2005) to estimate the optimum number of grid cells (*s*) to achieve certain precision. Here we calculated the number of grid cells required to gradually reach standard error within 10% of the species occupancy estimates (var($\hat{\psi}$) = 0.05).

$$s = \frac{\psi}{var(\hat{\psi})}\left[(1 - \psi) + \frac{(1 - p^*)}{p^* - Kp(1 - p)^{K-1}}\right]$$

The p^* denotes the probability of detecting focus species at least once during *K* sampling replicates. The values of *K* were adjusted for each survey method: ranger patrol (4 replicates), camera trap (18), and sign transect (12). For integrated models, we sum the number of replicates of combined surveys i.e. ranger patrol and sign transect together has a total 4 + 12 = 16 replicates.

References for supplementary information

Doser, J. W. et al. (2022) 'Integrated community occupancy models: A framework to assess occurrence and biodiversity dynamics using multiple data sources', Methods in Ecology and Evolution, 13(4), pp. 919–932. doi: 10.1111/2041-210X.13811.

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Chapter 5 Targeting conservation actions for tigers based on multiple monitoring and anthropogenic threat data

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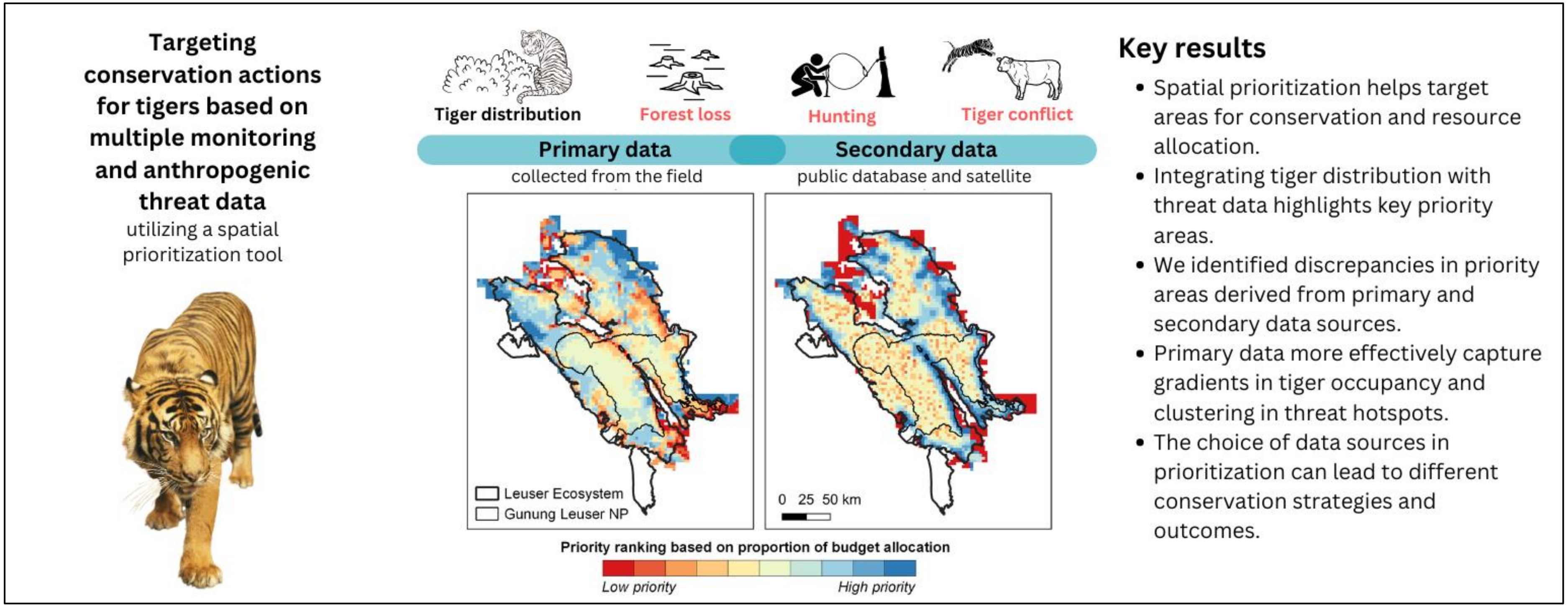
Manuscript in preparation

5.1 Abstract

Systematic conservation planning helps identify priority areas for the strategic allocation of resources and interventions, and can be particularly useful in biodiverse tropical nations where resources are limited. The effectiveness of such planning relies on the quality of available data. We explore the utility of multiple monitoring and threat data sources in spatially allocating resources for Sumatran tiger (*Panthera tigris sumatrae*) conservation in Sumatra, incorporating information on tiger distribution, forest loss, hunting, and human-tiger conflict. We compared prioritisation outcomes using primary data collected through field surveys and secondary data from the public database and satellite imagery. A significant discrepancy emerged between priority areas identified through primary versus secondary datasets, highlighting that different data sources can lead to substantially different conservation interventions and outcomes. We show that primary data provides a more nuanced identification of high-priority areas for tiger conservation that better captures gradients in tiger occupancy and clustering patterns in threat hotspots. We advocate for the use of the best available monitoring and threat data and recommend broader-scale, multispecies prioritisation approaches that consider costs and actively involve stakeholders to enhance biodiversity conservation efforts.

Keywords: Biodiversity management, conservation priority, effective conservation, resource allocation, tropics



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5.2 Introduction

Targeted conservation efforts are essential to effectively halt global biodiversity loss (Walls, 2018; Díaz *et al.*, 2019). Tropical nations, with their high numbers of threatened species and ecosystems, are renowned as biodiversity hotspots and so are critical for conservation (Allan *et al.*, 2019; Gallego-Zamorano *et al.*, 2020). However, these nations frequently face challenges with limited resources impacting their ability to effectively manage biodiversity (Graham *et al.*, 2021). Systematic conservation planning offers operational models to help decision-makers allocate scarce resources effectively (Kukkala and Moilanen, 2013). Embedded within this framework, spatial prioritisation explicitly identifies critical areas for conservation intervention (Kukkala and Moilanen, 2013; Kujala, Moilanen and Gordon, 2018), considering factors such as biodiversity features (Sibarani *et al.*, 2019), threats (Veach, Moilanen and Minin, 2017; Du *et al.*, 2024), and costs of action (Schuster *et al.*, 2023).

The effectiveness of conservation planning depends on the quantity and quality of input data (Kujala *et al.*, 2018). Large-scale prioritisation studies often use readily available secondary data sources, such as the IUCN Red List of threatened species range data (Nori, Loyola and Villalobos, 2020; Pusparini *et al.*, 2023) or satellite imagery as proxies for environmental and anthropogenic threats (Allan *et al.*, 2019; Cui, Carmona and Wang, 2024). Primary data that are collected from the field, such as species detections from monitoring programs, has the potential to significantly enhance the quality of input data for prioritisation. Utilizing primary data should allow more accurate and representative conditions in the field to be captured. Therefore, conservation planning based on primary data is particularly relevant at local and landscape scales, where monitoring and conservation programmes are typically implemented.

Large carnivores are disproportionately impacted by anthropogenic pressures (e.g. habitat loss, overexploitation, and human-wildlife conflict) due to traits like slow reproductive rates, low population densities, and substantial overlap with human populations. Due to their charismatic nature, large carnivores are often selected as flagship species for their ability to attract public interest and funding (Caro, 2010;

Macdonald *et al.*, 2015). Consequently, conservation planning often focuses on large carnivores and develops prioritisations based on considerations of their ecology and threats (see examples in Di Minin *et al.* 2016; Long *et al.* 2021; Vasudeva *et al.* 2022).

Here we conducted a spatial prioritisation analysis to identify priority areas for the conservation of a threatened apex predator, the Sumatran tiger (*Panthera tigris sumatrae*). The Sumatran tiger is highly threatened and serves as an important flagship species, making it a priority species for conservation efforts in Indonesia (MoEF, 2015). Our spatial prioritisation was developed by combining tiger distribution data with prominent threats impacting tiger populations, including forest loss, hunting, and human-tiger conflict (Wibisono and Pusparini, 2010; Linkie *et al.*, 2015; Lubis *et al.*, 2020). We applied our prioritisation using two data sources: 1) primary data, which applied datasets collected from the field to characterise tiger distribution and threats layers and 2) secondary data, which developed proxies for these layers using IUCN Red List range maps and satellite imagery respectively. By comparing the inferences drawn from these two data sources, we aimed to identify high-risk areas of anthropogenic threats within the tiger's distribution to inform priority zones for interventions and ensure the future survival of vulnerable tiger populations. By comparing inferences drawn from primary and secondary data, we sought to determine the reliability of widely available data to make accurate conservation recommendations.

5.3 Method

5.3.1 Study area

We conducted our study in the Leuser Ecosystem (25,000 km^2; Fig. 5.1A). Leuser is the largest continuous area of tropical forest in Sumatra and the most extensive of the eleven priority landscapes for Sumatran tiger conservation (Sanderson *et al.*, 2023). The area is characterized by a habitat mosaic encompassing a gradient of lowland and peat swamp forest, with hill, sub-montane, and montane forests ranging to an elevation of 3,500 m a.s.l. Most of the Leuser Ecosystem is designated for conservation (75%; 18,673 km^2), including the Gunung Leuser National Park (GLNP; 8,282 km^2), a UNESCO World Heritage Site. The landscape has experienced encroachment from agricultural expansion, road development, and human settlements, particularly outside the conservation area (Sloan *et al.*, 2018).

5.3.2 Input layers for prioritisation: primary data sources

1) Tiger occupancy

We collected tiger detection data from three survey activities: ranger patrols, sign transects, and camera traps (Appendix S5.1; also see Chapter 4 for detailed methodology). The patrol dataset included 844 patrols in the GLNP from July 2018 to June 2021, totalling 9,593 days (average per patrol = 14 days). Sign transects were obtained from Indonesia's second national tiger occupancy survey, conducted between October 2018 and December 2019 (Chandradewi *et al.*, 2019), and covering 5,639 km within 109, 17x17 km grid cells (average transect length per cell = 51 km). Camera trap surveys were conducted in the East and West Leuser Ecosystem from March 2020 to July 2021 across 146 sites and totalled 14,029 trap days (an average of 93 active days per site).

To standardize sampling across datasets, we overlaid a grid of 3x3 km cells over the Leuser Ecosystem, resulting in patrols, sign transects, and camera traps covering 658, 1199, and 146 cells, respectively. The grid size was selected to correspond with previous tiger population assessments in Sumatra (Pusparini *et al.*, 2017) and to inform conservation management at a finer scale. Detection histories were created for each dataset, where 0 was assigned when tiger encounters or signs were not observed and 1 if observed. We generated replicates for the patrol dataset based on the most recent annual data for each grid cell, resulting in a maximum of four 3-month temporal replicates (range: 1-4). For the transect dataset, replicates were defined spatially at 500 m intervals to account for landscape topography (Lubis *et al.* 2023). To maintain a balanced number of replicates, we restricted the transect length to 6 km corresponding to the average transect length surveyed in 3x3 km cells (range: 1-12.5 km). This resulted in a maximum of 12 replicates. For the camera dataset, we restricted the sampling period to 90 trap days, yielding a maximum of 18 5-day replicates per site (range: 3-8).

We applied Bayesian hierarchical integrated occupancy models to estimate tiger occupancy and detection while accounting for imperfect detection (Doser et al. 2022; Appendix S5.2). To improve the precision and spatial inference of species occupancy probability, we constructed a common ecological process model to integrate detection information derived from three datasets. We modelled tiger occupancy as a function of habitat quality indicated by tree canopy height (Deere *et al.*, 2020a) and resource availability represented by prey biomass. We calculated prey biomass as a function of relative abundance using integrated Bernoulli N-mixture models for the tiger's principal prey species (sambar deer *Rusa unicolor* and wild pig *Sus scrofa*; see Appendix S5.3 for full methodological details. We also consider anthropogenic influence represented by accessibility or distance from human settlements accounting for difficulty or ease of moving across habitat types, elevational gradients, roads, and rivers (Deere *et al.*, 2020b; ESRI, 2023).

Additionally, we developed three observation models specific to each dataset to estimate species detection probability to account for differences in survey designs and detection abilities. Species detection was modelled as a function of terrain ruggedness index, habitat types (primary forest, secondary forest, shrubland, wetland, and agriculture), and survey effort (patrol: number of point observations; transect: transect length; camera trap: total trap days). Finally, we developed tiger occupancy maps by linking parameter estimates derived from occupancy models to spatially explicit covariate values across the Leuser Ecosystem.

As the grid cell size of 3x3 km is smaller than the Sumatran tiger's home range of an estimated 289 km^2 (Wibisono *et al.*, 2011), the independence assumption underlying occupancy frameworks may be violated i.e. tigers can travel across multiple grid cells during the survey period. Therefore, we interpret tiger occupancy as the probability of habitat use, indicating preferential use of areas within the home range to meet ecological demands.

2) Forest loss

We developed a forest loss model for the Leuser Ecosystem, including a 25 km buffer from its boundaries, at a resolution of 90 m. Forest was defined as tall evergreen dipterocarp-dominated vegetation with closed canopies (>90% cover), including both intact, degraded and mangrove forests (Margono *et al.*, 2014). Forest loss was defined as the absence of tree foliage cover without regrowth for at least three years in undisturbed forests and one year in degraded forests, within a 30-meter pixel (Vancutsem *et al.*, 2021). Our analysis tracked changes in forest cover between 2000 and 2021 using the Tropical Moist Forest datasets (https://forobs.jrc.ec.europa.eu/TMF).

Using a framework by Rosa et al. (2013) and modified by Voigt et al. (2021), we projected future forest loss risk in Leuser to 2045. This data-driven probabilistic model, based on past patterns of forest loss and a neighbourhood function around deforested pixels (Rosa et al., 2013), accounted for 14 non-correlated ecological, landscape, and social covariates associated with forest loss (Appendix S5.4; correlation coefficient < 0.7) (Voigt *et al.* 2021, 2022). The models were trained using six years of the most recent forest loss data (calibration period of 2016-2021) and the best model was selected using forward step-wise regression and fitted with Markov Chain Monte Carlo (MCMC) sampling implemented in "Filzbach" (Lyutsarev, 2023).

We validated the model predictions using observed forest change data from 2016-2021, calculating the percentage of cells with a perfect match, *commission* errors (i.e. forest pixels predicted to be deforested, but not observed as forest loss), and *omission* errors (i.e. forest pixels observed, but not predicted to be deforested) (Rosa *et al.*, 2013). The best-performing model was used to predict forest loss risk in subsequent six-year periods — to capture forest change patterns within the period — from 2016 to 2045 and over 100 iterations to estimate forest loss probability for each pixel. The probability of forest loss was visualized by aggregating the binary forest loss maps across all iterations, resulting in a summed probability map (e.g. a pixel deforested in 50 out of 100 iterations was assigned a 0.5 forest loss probability).

3) Hunting pressure

We applied a Bayesian hierarchical single-species occupancy model to estimate the probability of snare occurrence across Leuser. Snare detections were collected from 844 ranger patrols conducted in GLNP between July 2018 and June 2021, focusing on metal cable and nylon snares that are known to trap tigers (Linkie *et al.*, 2015). We generated temporal replicates based on the most recent annual data for each grid cell (July 2018-June 2019, July 2019-June 2020, July 2020-June 2021), resulting in a maximum of four 3-month replicates, using the approach by Ghoddousi *et al.* (2022). To control for environmental variations, snare occupancy was modelled as a function of habitat quality used for tigers, represented by tree canopy height (m) and its variability (Deere *et al.*, 2020a); anthropogenic influences indicated by accessibility or travel time from human settlements accounting for difficulty or ease of moving across habitat types, elevational gradients, roads, and rivers (Deere et al., 2020b; ESRI, 2023); and a multidimensional well-being index that tracks education, health, living standards, infrastructure, environment, and social cohesion at the village level (Morgans *et al.* 2024). Snare detection was modelled using the same set of covariates used in patrol detection models embedded within tiger occupancy and prey abundance hierarchical models. The snare occupancy map was generated using parameter estimates derived from the occupancy model and extrapolated across Leuser.

4) Human-tiger conflict

We developed a Bayesian spatial log-Gaussian Cox process model using presence-only data and incorporating a detection function (Martino *et al.*, 2021) that was implemented in the inlabru R package (Bachl *et al.*, 2019). We compiled locations of human-tiger conflict (HTC) across Leuser from January 2018 to December 2021, focusing on incidents involving human and livestock attacks, as these often led to the removal or translocation of problem tigers (Lubis *et al.*, 2020). Conflict information was collected by five Wildlife Response Unit teams consisting of personnel from the Wildlife Conservation Society-Indonesia Program, local government, communities, and NGOs, located in different regencies to ensure complete coverage across the ecosystem.

To explain conflict intensity, we considered factors such as proximity to settlements, represented by accessibility; community wellbeing and economic status, represented by a village-level multidimensional well-being index (Morgans *et al.*, 2024); livestock biomass combining cattle (Gilbert *et al.*, 2022b), buffalo (Gilbert *et al.*, 2022a), and goats (Gilbert *et al.*, 2022c), and; human population density (Rose *et al.*, 2019). We generated a log-intensity map of sampling intensity without covariates as an input layer for the detection model, using all observation points collected by Wildlife Response Unit teams including conflicts incidents with other species, species encounters, and conflict mitigation activities like patrols. The probability of HTC occurrence (0-1) was then derived by inversing the log-intensity output of the model parameters.

5.3.3 Input layers for prioritisation: secondary data sources

We used the tiger geographic range developed in the 2021 IUCN Red List assessment for global tiger species (Goodrich *et al.*, 2022). From the IUCN range, we created a binary map of the Sumatran tiger distribution in Leuser, where a value of 1 was assigned for areas of tiger presence or 0 where tigers are locally extinct or their presence uncertain.

Spatial proxies for multiple threats were prepared from satellite imagery. For forest loss, we generated an Euclidean distance map from deforested areas during the 2000-2016 period using Tropical Moist Forest datasets utilized in the modelling. We assumed that future forest loss is more likely to occur near previously deforested areas (Rosa *et al.*, 2013; Voigt *et al.*, 2021). For hunting, two Euclidean distance maps from access areas such as human settlements and roads were generated as proxies for hunting, considering higher hunting risks in areas that are easily accessible (Benítez-López *et al.*, 2019; Ghoddousi *et al.*, 2022). These two maps were then combined, by assigning the lowest values — indicating shorter distances to access points — to the pixels (Benítez-López *et al.*, 2019). For HTC, we used a proxy of distance from the forest edge, assuming that conflicts are more likely to occur outside the forest and decrease as the distance from the forest increases, with negligible conflicts in the forest itself due to the absence of settlements. We calculated the Euclidean distance from the edge of continuous forest patches that can sustain a viable tiger population (minimum size: 1000 km^2; Luskin *et al.* 2017). We then rescaled these Euclidean layers into a probability map (0-1) with higher values indicating a higher risk of threats i.e. near deforested areas, access points, and forest edge.

5.3.4 Spatial prioritisation

To identify conservation priority areas for tigers facing high threat levels, we utilized the prioritzr R package to generate spatial prioritisations across various budget levels, ranging from 0.1 to 0.9 (Hanson *et al.*, 2024). This approach assumes that areas selected under smaller budgets are of higher importance. We used 3x3 km grid cells that contained a minimum of 50% forest cover (reference forest in 2016) as planning units (PU) — the spatial units at which efforts are implemented. Units were selected to align with the resolution of the tiger occupancy map. We assigned a uniform budget of 1 to all PUs, therefore, the prioritisation settings can be interpreted as the incremental selection of priority PUs from 0.1 (10%; highest importance) to 1.0 (100%; lowest importance) of the total area of all PUs.

Our prioritisation incorporated four feature layers: tiger distribution, probability of forest loss, hunting, and HTC. We ran two prioritisation scenarios based on primary data and secondary data sources. For each budget setting, we employed a minimum shortfall objective to identify the set of PUs that would effectively reduce the conservation target shortfalls (Jung *et al.*, 2021). We assigned a weight and relative target of 1 to the tiger feature, and a lower weight and target of 0.5 to the threat features, based on the premise that areas with higher tiger occupancy or within tiger range should be prioritised. Finally, we generated maps of selected PUs based on criteria across the different budget settings, giving higher rankings to PUs selected under a lower budget.

To compare the inferences from the two data source scenarios, we calculated the correlation between PU rankings from the primary and secondary data maps using Spearman's rank correlation test. We also calculated the correlation between high-priority PUs in primary data scenario, those selected under budgets of 0.5 and below, and with high-priority PUs from secondary data scenario.

5.4 Results

5.4.1 Tiger and threat layers from multiple data sources

Feature layers derived from primary data sources revealed contrasting patterns between tiger occupancy and threat layers across the Leuser Ecosystem (Fig. 5.1B-C; see Appendix S5.5 for details on covariates and their influence). Tigers were more likely to occupy the core area of the Leuser, characterized by less disturbed forests, higher prey availability, and greater distance from human access points. Conversely, hunting pressure was higher within the forest and near these access points. Deforestation and HTC risks were predominantly clustered along the landscape's boundary. Forest was most likely to be lost in areas near already deforested regions, villages with low well-being scores, relatively flat topography, and areas outside of conservation areas. Conflict occurrences were also more frequent near human access points.

Secondary data from the IUCN Red List database indicated that the tiger range comprised most of Leuser. However, this layer differs from the map derived from primary data, which shows gradients of tiger occupancy probability, whereas the secondary data map only indicates the presence or absence of tigers. Spatial proxies highlighted elevated threats near human activity points (e.g. roads, settlements, deforested areas) and along forest edges.

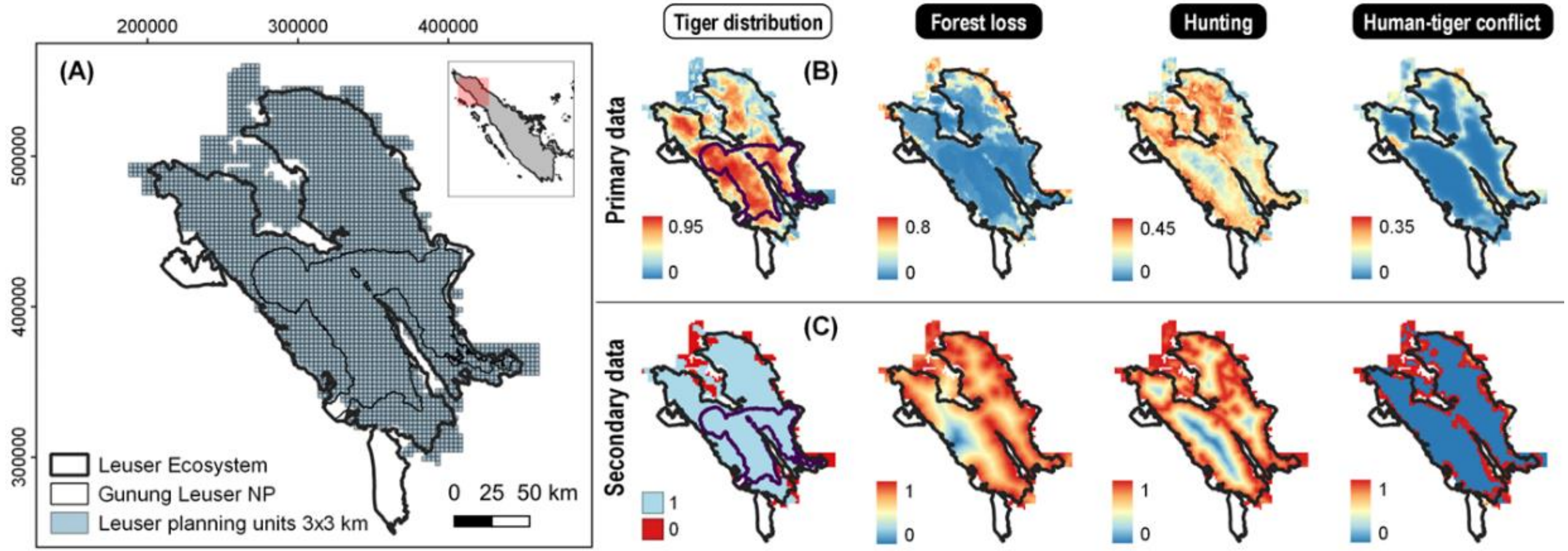

Fig 5.1: (A) Leuser Ecosystem with Gunung Leuser National Park at its core and PUs (grid cells of 3x3 km with minimum 50% forest cover and excluding peatland) that accounted in the prioritisation. (B-C; left to right) Four feature layers used in spatial prioritisation in primary data scenario (B) and secondary data scenario (C).

5.4.2 Tiger conservation priority regions according to data sources

Spatial prioritisations across different data source scenarios revealed that high-priority PUs — selected within budget settings ranging from 0.1 to 0.5 — were predominantly located along the boundary of the Leuser Ecosystem, where tiger presence coincided with elevated threat levels (Fig. 5.2 (Top); also see Appendix S5.6). Priority layers derived from primary data sources displayed distinct clusters of high-priority areas along the boundary, particularly in the northern and southeastern parts of the landscape. In contrast, priority layers from secondary data sources exhibited a more continuous gradient from the boundary, with PUs outside the tiger IUCN range assigned as non-priority. Notably, when the budget allocation exceeded 0.5 in secondary data scenario, the prioritisation began randomly selecting PUs, reflecting a loss of clear spatial prioritisation. The differences in identified priority regions between the data scenarios were underscored by the lack of correlation between priority rankings (ρ = -0.03, $p < 0.08$) (Fig. 5.2, Bottom). When the focus was narrowed to higher priority PUs, the correlation between unit rankings turned positive but remained weak (ρ = 0.18, $p < 1e-6$).

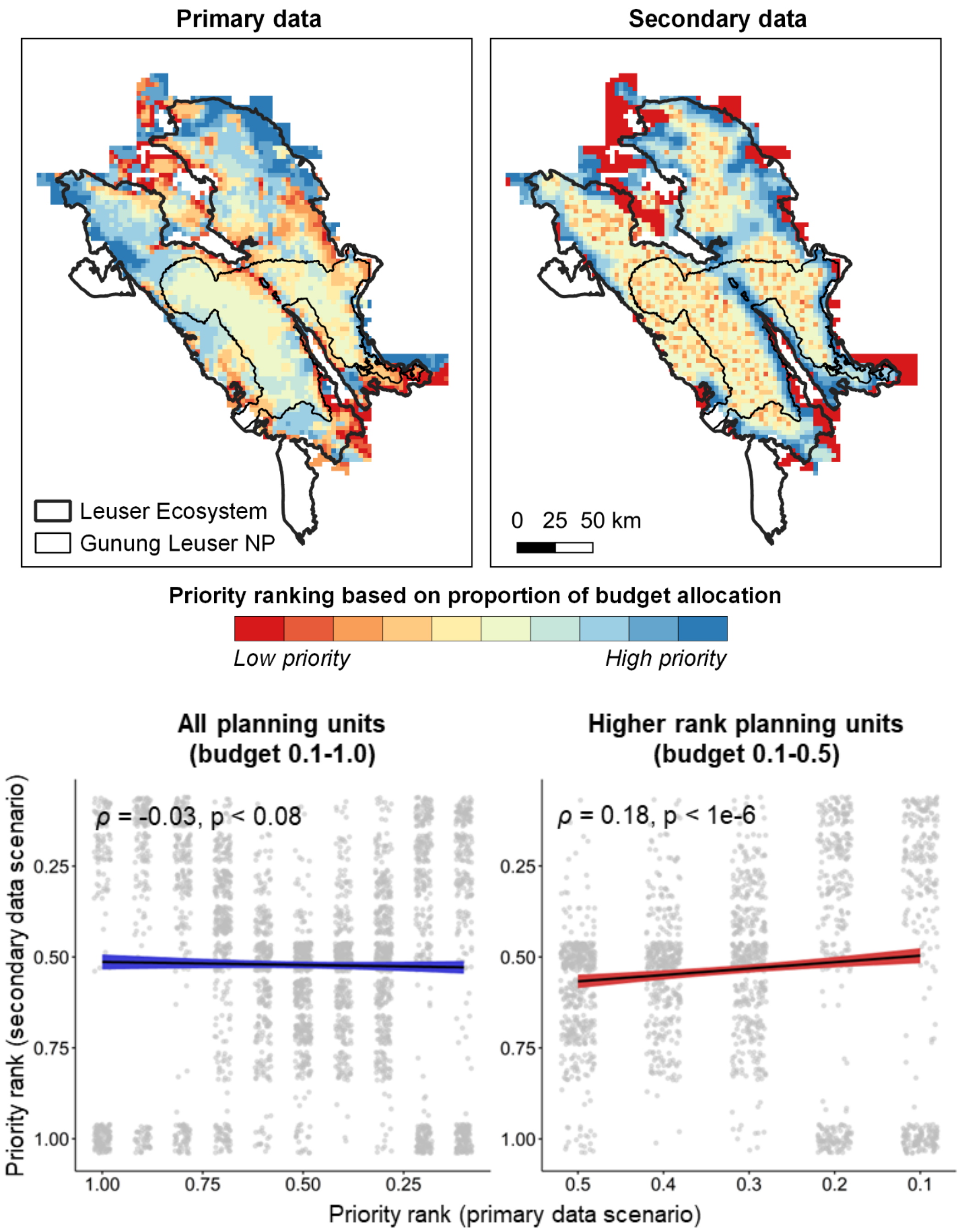

Fig 5.2: (Top) The priority ranking maps of primary and secondary data scenarios. The PUs selected in lower budget settings received higher priority ranks (0.1 > 0.5 > 1.0). (Bottom) Priority ranking correlations between data scenarios. Grey points indicate PUs rankings. The black line represents the linear regression line, with a 95% confidence interval shown in red. The x and y-axis values were reversed to indicate that higher ranks correspond to low-budget settings.

5.5 Discussion

Conservation managers often face challenges in deciding how to allocate limited resources effectively when designing and implementing conservation programs. Spatial prioritisation offers a valuable tool for guiding the strategic allocation of these resources. However, the outcome of prioritisation exercises can vary depending on the scale at which they are conducted and the data sources used, with important implications for the identification of priority areas and resource allocation decisions (Hermoso and Kennard, 2012; Kujala *et al.*, 2018). Our study underscores the sensitivity of spatial prioritisation to the availability and quality of input data. The disparity in high-priority areas across different data scenarios indicates that the choice of data source substantially influences spatial prioritisation outcomes, potentially leading to different conservation interventions and outcomes.

5.5.1 Comparing different data sources in prioritisation

We found that the priority map derived from primary data sources identified three main clusters of high-priority regions in the northern and southeastern parts of the Leuser Ecosystem. These regions, characterized by remaining forests surrounded by palm oil plantations and human settlements, are predominantly located outside established conservation areas, therefore conservation intervention is lacking in these areas. The prioritisation patterns align broadly with threat distributions in Leuser reported in previous studies including forest loss (Sloan *et al.*, 2018; Lubis *et al.*, 2023), hunting (Figel *et al.*, 2021), and human-tiger conflict (Lubis *et al.*, 2020), highlighting the selection of regions facing high levels of threats. Notably, the top priority regions did not coincide with areas of high tiger occupancy. This apparent discrepancy can be explained by the fact that the core areas of Leuser with high tiger occupancy are in mountainous regions with rugged topography, making them difficult to access. As a result, tiger populations in these areas are relatively safe from human threats and less likely to need active protection and conservation interventions (Wibisono *et al.*, 2011; Lubis *et al.*, 2023).

In scenarios based on secondary data, PUs outside the IUCN Red List tiger range were classified as non-priority, based on the assumption that tigers were absent in those areas. Additionally, under lower budget settings, PUs were randomly selected within the tiger range due to the uniform value applied across the range, allowing for a flexible selection of remaining PUs. This highlights the challenges of using coarse biodiversity data like the IUCN species range maps and underscores the advantages of incorporating detailed biodiversity data into spatial prioritisation exercises. Although additional analyses—such as focal statistics, which smooth spatial data by averaging values within a defined window (e.g. 9x9 PUs) to capture range continuity (ESRI 2025)—could be used to create a gradient of tiger occurrence probabilities, particularly in PUs outside the defined tiger range.

Using species occupancy data derived from primary sources proved to be more informative than relying solely on presence/absence data from species range maps. The priority map generated from primary data scenario accounted for the potential occurrence of tigers in areas classified as non-priority in secondary data scenario. Occupancy distribution can identify where tigers occur in suboptimal environments (MacKenzie *et al.*, 2018), such as populations under severe anthropogenic threats where they might be at significant risk of local extinction and require immediate intervention.

Moreover, the primary data prioritisation revealed continuous patterns across lower-ranked PUs, as the tiger occupancy layer contains continuous probability values, allowing prioritisation to consider these gradients. These more structured patterns, as opposed to the random patterns observed in secondary data scenarios, are crucial when management resources allow for prioritising lower-ranked regions as well. In addition, the threat layers derived from primary data sources exhibited more clustered patterns, facilitating a more focused prioritisation of high-risk regions. This approach is particularly beneficial when resources are limited, as it avoids the less efficient strategy of selecting all areas along the boundary, as suggested by secondary data.

Nevertheless, primary datasets require dedicated efforts and considerable resources to collect, which can be particularly challenging in tropical forests (Gardner *et al.*, 2008; Wearn and Glover-Kapfer, 2019). Collecting and processing these data with appropriate sampling designs and robust analytical methods can yield accurate and detailed information on species distributions and anthropogenic threats within study regions — details that might be missed when relying on inferences derived from secondary data. However, these steps require specialized expertise, which is often lacking in many tropical nations (Ardiantiono *et al.*, 2024).

On the other hand, secondary data are more accessible and often cover larger geographical areas. They are readily available in public databases widely used in conservation studies, such as the IUCN Red List or Key Biodiversity Areas (Stephenson and Stengel, 2020), or from satellite imagery. These data are typically ready for immediate use in prioritisation exercises (e.g. the IUCN Red List species range) or require minimal processing (e.g. calculating Euclidean distance from features like roads or settlements). Yet, secondary data may be outdated (e.g. older IUCN species assessment or satellite imagery) or lack the high-resolution spatial information necessary for fine-scale conservation planning (e.g. the IUCN tiger range map which only indicates their presence or absence across the landscape).

5.5.2 Future directions

We note several opportunities to expand and improve our prioritisation framework for species conservation planning. First, expanding prioritisation to other landscapes on a larger scale. Considering multiple landscapes in prioritisation can facilitate the development of more holistic conservation strategies to secure national to global species populations (e.g. through connectivity planning or joint management) and help governments to reach international commitments like Kunming-Montreal Global Biodiversity Framework targets (Lessmann, Muñoz and Bonaccorso, 2014; Schoen *et al.*, 2022; Pusparini *et al.*, 2023).

Second, explicitly accounting for action cost. At the moment, costs for conservation programs are usually provided at the management unit level, such as at the national park level, not at finer scale details like zonation or unit area (Nugraha *et al.*, 2024). Incorporating action costs (e.g. higher costs in hard-to-access areas or costs specific to management zonation within conservation areas) instead of the uniform area costs can enhance the prioritisation by considering the availability of resources (Kukkala and Moilanen, 2013).

Third, shifting focus from single species to broader wildlife communities. The proliferation of hierarchical multispecies models and data integration presents opportunities to generate multispecies occupancy or abundance layers across large landscapes for integration into prioritisation exercises (Isaac *et al.*, 2020). Additionally, integrating threats that broadly impact biodiversity, such as habitat loss and overexploitation (Dirzo *et al.*, 2014), provides flexibility for developing multispecies prioritisation. For instance, our prioritisation framework can be adapted by either running separate prioritisation exercises for different species or integrating various species population maps into the current model.

Fourth, actively engage multiple stakeholders in prioritisation exercises. The participatory modelling framework is increasingly advocated to ensure this process is not exclusive to scientists and conservation practitioners who are involved in this study, but actively engaging local communities and other stakeholders (Wall, McNie and Garfin, 2017; Crevier and Parrott, 2019; Ibbett *et al.*, 2024). Therefore, promoting the participatory development of spatial prioritisation will ensure a complete understanding of the system and increase the acceptance and opportunity of the model to be adopted by stakeholders, thus ensuring science is translated into decision-making (Enquist *et al.*, 2017; Crevier and Parrott, 2019).

The quality of data significantly influences the effectiveness of conservation planning. Our appraisal highlights the substantial impact that different data sources can have on spatial prioritisation for species conservation. Given the substantial disparities in inferences drawn from primary and secondary data sources, we advocate for the use of accurate, locally relevant data collected from the field whenever possible. In situations where such data are unavailable, secondary data can serve as a viable alternative, providing preliminary insights — especially when conservation actions must be implemented urgently or across large scales where on-the-ground data are lacking. However, it is crucial to exercise caution when relying solely on secondary data, as this may result in prioritisation and potential misallocation of resources. Ultimately, while spatial prioritisation is a valuable tool for identifying high-priority areas for conservation intervention, successful implementation requires collaboration and strategic allocation of available resources to achieve the best outcomes in protecting biodiversity, ecosystems, and communities.

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5.7 Data availability

Example datasets and model codes associated with this manuscript can be accessed at https://github.com/Ardiantiono/Tiger-prioritization.git.

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5.9 Supplementary information

Appendix S5.1: Survey design, data characteristics, and potential strengths (in blue) and biases (in orange) of three datasets used in this study.

	Ranger patrol	**Sign transect**	**Camera trap**
Aim	Detect and reduce illegal activities	Estimate tiger density	Estimate tiger occupancy
Species recorded	Tiger, prey species, and other species of conservation concerns (e.g. elephant, rhinoceros, and orangutan)	Tiger, prey species, and other species of conservation concerns (e.g. elephant, rhinoceros, and orangutan)	Terrestrial mammal
Survey design	Semi-structured. Assigned into 3x3 km grid.	Originally structured in 17x17 km grid. Resized to 3x3 km grid.	Structured in 3x3 km grid.
Data type	Species encounter and sign data	Species encounter and sign data	Species photograph data.
Species detections (total detections / total replicates)	Tiger: 429 (0.44) Sambar: 246 (0.25) Pig: 98 (0.10)	Tiger: 161 (0.02) Sambar: 165 (0.02) Pig: 94 (0.01)	Tiger: 70 (0.03) Sambar: 20 (0.01) Pig: 44 (0.02)
Number of 3 km grid cells	658	1199	146
Number of replicates per grid cell	Temporal: 4	Spatial: 12	Temporal: 18
Potential strengths and biases			
Survey design	Opportunistic species record No reference grid	Grid size based on tiger ecology (17x17 km). Grid was large for prey species.	Grid size based on tiger ecology (3x3 km). Grid was large for some prey species.
Observer	Misidentification and lower detection ability.	Misidentification and lower detection ability.	Camera active for 24 hours;

			photograph evidence
Species	Focus on large charismatic species e.g. tiger, rhinocero, and elephant.	Tiger, prey species, and other species of conservation concerns (e.g. elephant, rhinoceros, and sun bear)	Terrestrial mammals
Location	Within Gunung Leuser National Park, mostly in forest boundary where the threats occur	Whole Leuser Ecosystem	Restricted in the core area of Leuser Ecosystem
Frequency	Monthly	Every 10 year	Every three year

Appendix S5.2: Integrated community occupancy model framework

We employed a Bayesian hierarchical integrated community occupancy model (ICOM) to estimate community-level and species-specific occupancy and detection developed by Doser et al. (2022). Species-specific responses were drawn as random effects from community-level distributions in both occupancy and detection models with estimable hyper-parameters that represent community patterns (Kery and Royle, 2016).

In the ICOM framework, we used joint likelihood to combine temporal and spatial replicated data from different sources into a single model (Miller *et al.*, 2019). We assume the detection process of tiger and prey is independent in each data source with a shared ecological process of species occurrence (Doser *et al.*, 2022).

We built the ecological process model common among all three sets in the ICOM to estimate tiger and prey occupancy probability (ψ) with the following form:

$$\text{logit}(\psi_{i,j}) = \beta_{0i} + \beta_{1i}Accessibility_j + \beta_{2i}Accessibility^2_j + \beta_{3i}CanopyHeight_j + \beta_{4i}CanopyHeight^2_j + \beta_{5i}CanopyHeightVariability_j + xi_i * eps_iYear_j \quad \textbf{(1)}$$

Where β_0 is species-specific intercept, β_{2-5} are species-specific effects of multiple occupancy covariates, and *xi * eps* represent temporal random factor (year). All of these parameters were shared across three datasets in the ICOM framework.

We also built the observation model specific to each data source to estimate species detection probability (p) with the following form:

$$\text{logit}(p.camera_{i,j,k}) = \alpha_{0i}CameraType_j + \alpha_{1i}TRI_j + \alpha_{2i}TrapNights_j$$

$$\text{logit}(p.transect_{i,j,k}) = \gamma_{0i}HabitatType_j + \gamma_{1i}TRI_j + \gamma_{2i}TransectLength_j$$

$$\text{logit}(p.patrol_{i,j,k}) = \delta_{0i}HabitatType_j + \delta_{1i}TRI_j + \delta_{2i}Num.Observation_j \quad \textbf{(2)}$$

Where α_0, γ_0, δ_0 are species-specific intercepts for each dataset and α_{1-2}, γ_{1-2}, δ_{1-2} are species effects of covariates influencing detection across spatial/temporal replicates.

We specified six models (three for single datasets and three for integrated datasets using JAGS (v1.5.1 in R; Kellner 2019). Three parallel Markov chains were run with 400,000 iterations with the first 100,000 iterations removed as burn-in, and the rest thinned by 300. Model performance was evaluated using Gelman-Rubin statistics and Bayesian p-values (Gelman *et al.*, 1996). Occupancy and detection estimates for tiger and prey across Leuser were extracted from the model outputs.

Appendix S5.3: Integrated single-species Bernoulli/N-mixture model framework

We employed Bayesian hierarchical integrated single species Bernoulli/N-mixture models to estimate the relative abundance of the Sumatran tiger's main prey species: sambar deer and wild pigs (Royle and Nichols 2003, adapted into Doser *et al.* 2022; Appendix S5.3). We utilized prey detection data from ranger patrols, sign transects, and camera trap surveys. Prey abundance was modelled as a function of habitat quality represented by the Normalized Difference Vegetation Index (NDVI), anthropogenic activity indicated by distance to roads, and topographic influence of the terrain ruggedness index. Species detection models, unique to each dataset, were built based on the same set of covariates used in tiger occupancy models. Prey abundance maps across Leuser were generated from model parameters. We then multiplied the abundance of sambar and pigs with their mean adult body mass (sambar = 177.5 kg, pig = 84.5 kg; Jones *et al.* 2009) and summed species-specific layers to estimate total prey biomass.

Detection histories were created from each dataset i.e. 0 when a species was not observed and 1 if observed. We generated replicates for the patrol dataset based on the most recent annual data for each grid cell, resulting in a maximum of four 3-month temporal replicates (range: 1-4). For the transect dataset, replicates were defined spatially at 500 m intervals to account for landscape topography (Lubis *et al.* 2023). To maintain a balanced number of replicates, we restricted the transect length to 6 km corresponding to the average transect length surveyed in 3x3 km cells (1-12.5 km). This resulted in a maximum of 12 replicates (1-12). For the camera dataset, we restricted the sampling period to 90 trap days, yielding a maximum of 18, 5-day replicates per site (3-8).

We employed a Bayesian hierarchical integrated single-species Bernoulli/N-mixture model to estimate species-specific relative abundance and detection (Royle and Nichols 2003, adapted into Doser *et al.* 2022). We built the ecological process model common among all three datasets to estimate wild pig and sambar deer relative abundance (λ) with the following form:

$$\log(\lambda_{i,j}) = \beta_{0i} + \beta_{1i}DistRoad_j + \beta_{2i}DistRoadI^2_j + \beta_{3i}NDVI_j + \beta_{4i}NDVI^2_j + \beta_{5i}TRI_j + xi_i * eps_iYear_j \quad \textbf{(1)}$$

Where β_0 is species-specific intercept, β_{2-5} are species-specific effects of multiple occupancy covariates, and *xi * eps* represent temporal random factor (year). All of these parameters were shared across three datasets in the ICOM framework.

We also built the observation model specific to each data source to estimate species detection probability (p) with the following form:

$$\begin{aligned} \text{logit}(p.camera_{i,j,k}) &= \alpha_{0i}CameraType_j + \alpha_{1i}TRI_j + \alpha_{2i}TrapNights_j \\ \text{logit}(p.transect_{i,j,k}) &= \gamma_{0i}HabitatType_j + \gamma_{1i}TRI_j + \gamma_{2i}TransectLength_j \\ \text{logit}(p.patrol_{i,j,k}) &= \delta_{0i}HabitatType_j + \delta_{1i}TRI_j + \delta_{2i}Num.Observation_j \end{aligned} \quad \textbf{(2)}$$

Where α_0, γ_0, δ_0 are species-specific intercepts for each dataset and α_{1-2}, γ_{1-2}, δ_{1-2} are species effects of covariates influencing detection across spatial/temporal replicates.

We specified the integrated model using JAGS (v1.5.1 in R; Kellner 2019). Three parallel Markov chains were run with 200,000 iterations with the first 100,000 iterations removed as burn-in, and the rest thinned by 100. Model performance was evaluated using Gelman-Rubin statistics and Bayesian p-values (Gelman *et al.*, 1996). Relative abundance and detection estimates for prey across Leuser were extracted from the model outputs.

Appendix S5.4: The selected predictors of deforestation.

No	Predictor	Description	Rationale
1	Slope	Slope in 2000 derived from the digital elevation model (30 m).	The gentle slope is associated with higher deforestation due to easy access.
2	Forest cover and loss	Forest cover and loss before the calibration period (2001-2016) and within the calibration period (2017-2021).	Forest patches closer to deforested areas are highly vulnerable to deforestation.
3	Distance to rivers	Distance to rivers based on Open Street Map to represent accessibility.	Forest clearance activities are likely to occur close to the river due to improved access.
4	Accessibility	Accessibility is defined as time to travel from human settlements and considering the influence of roads, slopes, and land cover.	Forest clearance activities are likely to occur when easily accessible.
5	Main commodity: Subsistence	Distance to Indonesian villages that primarily derive income from farming staple foods, plantation agriculture, or non-agricultural livelihoods. Village boundaries include human settlements and surrounding land mapped by the Indonesian Bureau of Statistics.	Forest clearance activities occur more near settlements. The extent of this depends on livelihood activities (higher deforestation near subsistence agricultural activities).

6	Main commodity: Plantation	Distance to Indonesian villages that primarily derive income from farming staple foods, plantation agriculture, or non-agricultural livelihoods. Village boundaries include human settlements and surrounding land mapped by the Indonesian Bureau of Statistics.	Forest clearance activities occur more near settlements. The extent of this depends on livelihood activities (higher deforestation near plantation activities).
7	Main commodity: Non-agriculture	Distance to Indonesian villages that primarily derive income from farming staple foods, plantation agriculture, or non-agricultural livelihoods. Village boundaries include human settlements and surrounding land mapped by the Indonesian Bureau of Statistics.	Forest clearance activities likely occurred near settlements, but potentially depend on their main source of income (lower deforestation if not dependent on agricultural activities).
8	Transmigrant settlements	Distance to transmigrant settlements (defined as a class in the landcover layer)	Forest patches closer to transmigrant settlements are highly vulnerable to deforestation
9	Mining	Categorical variable (three classes): - **Non-mining areas (reference)** - **Mining concessions (exploration)** - **Mining concessions (production)**	Forest patches closer to mining areas are highly vulnerable to deforestation
10	Land-use	Categorical variable (six classes): - **Non-forest areas (APL-reference)** - **Strict protected forests (IUCN 1 & 2 – National Parks)** - **Other protected (other IUCN classes)** - **Watershed protection forests (HL)** - **Production forests (HP, HPT)** - **Conversion forests (HPK)**	Different land uses influence the deforestation pressures i.e. highly protected areas would experience less forest loss, while areas gazetted for conversion will inevitably be deforested.

11	Social forest	Categorical variable (three classes): - **Absence of social forests (reference)** - **Social forests (implemented: HPHD and IUPHKM)** - **Social forests (proposed)**	The presence of social forestry is expected to improve local communities' welfare, thus reducing deforestation pressure.
12	Oil palm concessions	Smallholder and industrial closed-canopy oil palm plantations	Areas vulnerable to deforestation were associated with the expansion of oil palm plantations.
13	Peat	Peat areas	Peatland forests are typically more vulnerable to uncontrolled fire and clearing for plantation.
14	Socioeconomic deprivations	A multidimensional well-being index including 15 indicators of village well-being from Indonesia's PODES census in 2018. The index is calculated at the village level from the same BPS administration boundaries as other layers.	Poor communities tend to rely on forests for their livelihood e.g. to clear forests for agriculture as they have less opportunity to earn income outside their village area.

Appendix S5.5: Influence of predictors on the probability of tiger and threats occurrence/intensity. Mean values below 0 show negative influence (i.e. lowering tiger occupancy) and otherwise. For forest loss, the effect of peat is relative to the effect of no peat, mining to no mining, and protected areas and forests to non-forests.

Tiger occupancy probability

Parameters	Mean	2.50%	50%	97.50%
Intercept	-0.14	-1.65	-0.15	1.43
Accessibility (*linear*)	1.14	0.72	1.11	1.75
Accessibility (*quadratic*)	0.11	-0.21	0.05	0.74
Canopy height (*linear*)	0.40	0.00	0.40	0.82
Canopy height (*quadratic*)	0.28	0.06	0.27	0.54
Prey biomass	0.42	0.20	0.42	0.65

Forest loss probability

Parameters	Mean	2.50%	50%	97.50%
Intercept	-2.75	-2.86	-2.72	-2.69
Past deforestation	3.34	3.29	3.34	3.40
Slope	-0.04	-0.04	-0.04	-0.04
Subsistence livelihood	0.00	0.00	0.00	0.00
Plantation livelihood	0.00	0.00	0.00	0.00
Oil palm	0.00	0.00	0.00	0.00
Socioeconomic deprivation	0.19	0.00	0.08	0.60
Peat	0.04	0.00	0.04	0.09
Mining (exploration)	0.46	0.42	0.46	0.49
Mining (production)	0.28	0.24	0.29	0.32
Strict protected area	-1.33	-1.39	-1.34	-1.28
Other protected area	-1.19	-1.27	-1.19	-1.13
Watershed protection forest	-0.37	-0.38	-0.37	-0.36
Production forest	-0.14	-0.15	-0.14	-0.14
Conversion forest	0.01	-0.02	0.01	0.03

Snare occupancy probability

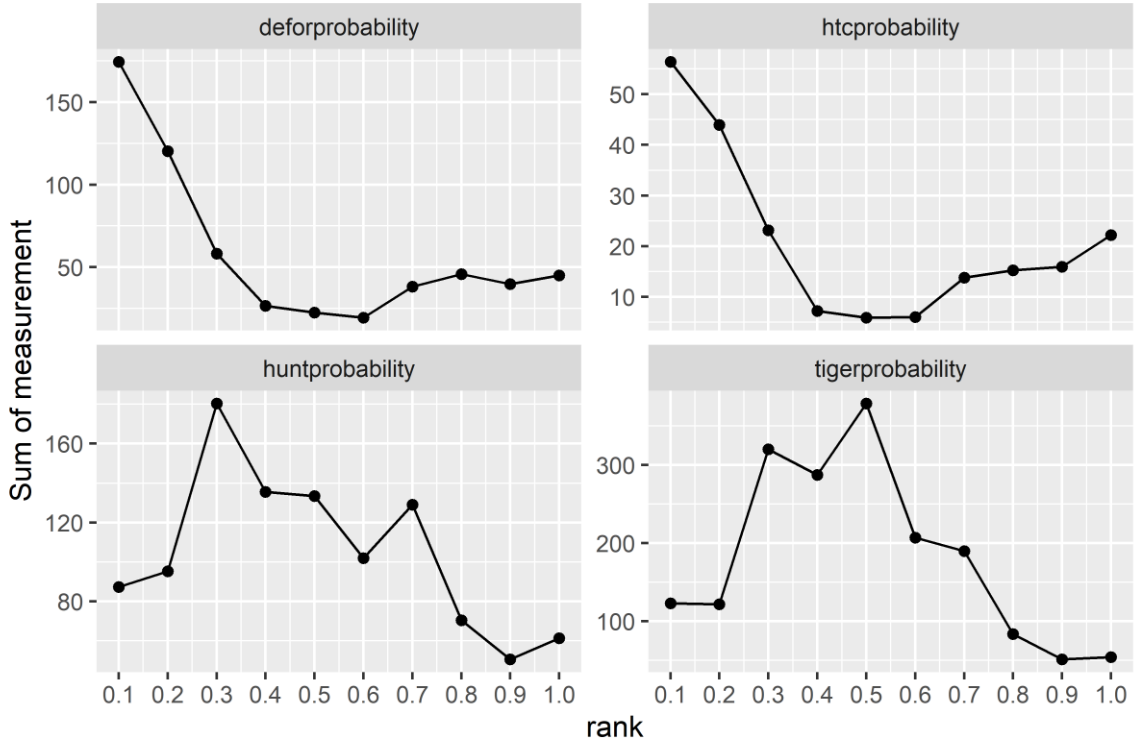
Parameters	Mean	2.50%	50%	97.50%
Intercept	-0.87	-1.3	-0.88	-0.37
Accessibility	-0.15	-0.57	-0.15	0.25
Canopy height	0.43	-0.05	0.42	0.95
Canopy height variability	0.07	-0.39	0.07	0.53
Multidimensional well-being index	0.11	-0.2	0.11	0.42

Human-tiger conflict intensity probability

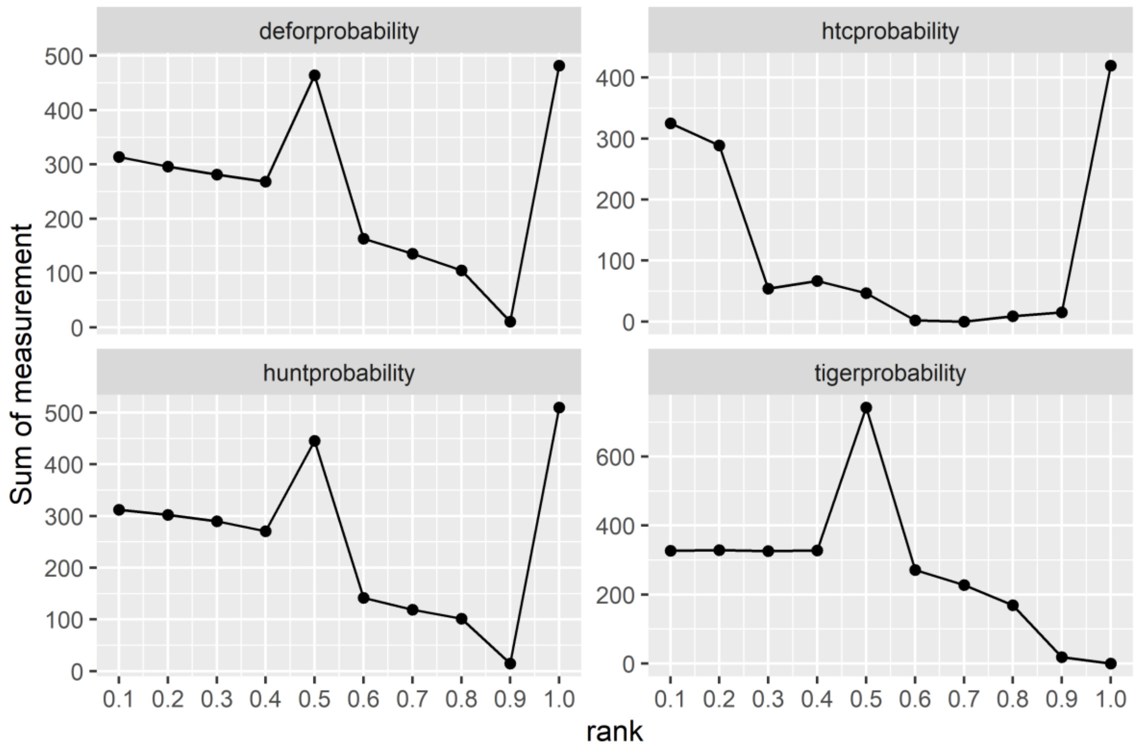
Parameters	Mean	2.50%	50%	97.50%
Intercept	-3.56	-6.07	-3.57	-0.99
Accessibility	-0.26	-4.51	-2.61	-0.94
Multidimensional well-being index	-0.18	-0.5	-0.18	0.14
Livestock biomass	-0.05	-0.51	-0.04	0.36
Human density	-0.56	-0.96	-0.56	-0.17

Appendix S5.6: Sum of conservation feature values in planning units selected under different budget settings for scenarios:

A) Primary data



B) Secondary data



Reference for supplementary information

Doser, J. W. et al. (2022) 'Integrated community occupancy models: A framework to assess occurrence and biodiversity dynamics using multiple data sources', Methods in Ecology and Evolution, 13(4), pp. 919–932. doi: 10.1111/2041-210X.13811.

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Chapter 6 Discussion

This thesis explores approaches to enhance terrestrial mammal monitoring in tropical forests and integrates comprehensive ecological datasets into species systematic conservation planning. Based on the findings of my research I proposed cost-effective methods to assess mammal occupancy and biodiversity across Sumatra's largest tropical forest landscape by leveraging data from diverse sources and applying innovative statistical modelling techniques. With a focus on the Sumatran tiger (*Panthera tigris sumatrae*), I developed a case study aimed at identifying key areas for intervention, thereby directly informing conservation decision-making.

In this discussion chapter, I will evaluate how the research aligns with the thesis' two primary objectives: 1) improving the effectiveness of biodiversity monitoring, and 2) targeting conservation actions through systematic conservation planning. The discussion will then extend to the broader implications of the research findings for global and national environmental policies.

6.1 Improving the effectiveness of biodiversity monitoring in the tropics

Monitoring biodiversity in tropical forests presents significant challenges such as the remote and often inaccessible nature of these areas, combined with the elusive and cryptic behaviour of many species (Mulatu *et al.*, 2017). Our review of mammal population research in Chapter 2 highlights the broader challenges of monitoring wildlife in Indonesia. Although the focus is on Indonesia, these challenges are common across tropical nations, which despite their rich biodiversity, often face significant limitations in resources and expertise necessary for effective monitoring (Mulatu *et al.*, 2017; Schmeller *et al.*, 2017). Through this research, I demonstrate how some of these critical issues can be addressed and offer potential solutions to improve wildlife monitoring efforts.

The first issue is the disproportionate emphasis on a limited number of species, typically those that are charismatic or easier to study, such as habituated animals. While data gathered from monitoring these species can offer targeted management recommendations, it risks being unrepresentative of broader biodiversity and may overlook less well-known species that could also be in decline (Jetz *et al.*, 2019). As a result, there is a growing shift in conservation efforts from species-centred approaches to those that encompass broader biodiversity, aiming to monitor Essential Biodiversity Variables (EBV) at higher levels (Jetz *et al.*, 2019; Chaudhary *et al.*, 2022). The EBV are important global metric for tracking changes in biodiversity, including species populations, genetic composition, and community composition (Pereira *et al.*, 2013; Jetz *et al.*, 2019).

Chapter 3 demonstrates the effectiveness of camera traps in generating data on multiple species that enable community-level analyses. These analyses can provide valuable insights into mammal occupancy, taxonomic, functional, and phylogenetic diversities, particularly in tropical regions where such data are often scarce. Even in species-specific surveys, such as those targeting large cats, camera traps often capture data on a wide range of species, facilitating comprehensive community-level analysis (Mena *et al.*, 2020; Chaudhary *et al.*, 2022; Sibarani *et al.*, 2022).

This chapter also extends the application of these biodiversity metrics to evaluate the effectiveness of umbrella species as indicators of broader ecological communities — a conservation strategy that is widely used but rarely evaluated (Lindenmayer and Westgate, 2020; Steenweg *et al.*, 2023). Additionally, I introduce the concept of "umbrella fleets", a group of top-performing umbrella species that can act as proxies for broader biodiversity. While further research is needed to solidify these findings, the strategic use of umbrella fleets could significantly reduce the need for exhaustive community-level monitoring, particularly when resources, time, and expertise are limited. This approach also presents opportunities to utilize data from human observation, such as ranger patrols or transect surveys, by focusing on the detection of these key umbrella species.

The second major challenge lies in the limitations of study design and analysis. Chapter 3 and 4 introduce innovative analytical frameworks that address these issues, particularly the biases inherent in data collection and analysis. I built the analyses under the Bayesian framework because of its ability to handle complex model structures and provide flexibility in model specification — both essential, for instance, in performing data integration (Kery and Royle, 2016; Doser *et al.*, 2022). Additionally, the Bayesian approach is particularly powerful in dealing with the challenges of small sample sizes and low detection rates, which are common in tropical monitoring efforts (Kery and Royle, 2016).

In Chapter 3, I employed the Bayesian Hierarchical Multispecies Occupancy framework, which specifically accounts for imperfect detections — an aspect often neglected in mammal population research in Indonesia (see Chapter 2). Imperfect detection implies that true species occupancy is not always observed, necessitating careful consideration to ensure accurate inferences, especially for rare species that are frequently missed in surveys (MacKenzie *et al.*, 2018). I further integrated the outputs of the occupancy model to generate robust estimates of functional and phylogenetic diversity, while also accounting for imperfect detection — an element typically overlooked in such calculations (Penjor *et al.*, 2022).

In Chapter 4, I developed a Bayesian Integrated Community Occupancy Modelling framework that synthesizes data from multiple surveys. This framework explicitly addresses imperfect detections and potential biases related to study design and data collection. By improving precision and expanding spatial inference, the framework underscores the value of leveraging all available data and enhances the utility of unstructured data in species monitoring programs. Notably, previous literature on data integration has often overlooked the direct assessment of its potential cost-effectiveness, limiting its broader application in conservation practices (Zipkin and Saunders, 2018; Miller *et al.*, 2019; Isaac *et al.*, 2020). I address this gap by explicitly calculating the financial benefits of data integration, thereby demonstrating its significant potential in species monitoring.

While this thesis does not delve into detailed sampling design strategies, this is an important consideration for planning effective monitoring efforts. Clearly defined monitoring goals are essential to selecting the most appropriate strategy. For example, spatial occupancy surveys may prioritise either maximizing survey coverage for spatial interpolation by uniformly selecting sampling locations across the study area or enhancing covariance estimates through clustered sampling designs (Miller *et al.*, 2019). Optimizing sampling design — such as determining the number of sites or replicates within a given budget, as discussed in Chapter 4 or through power analysis (Guillera-Arroita and Lahoz-Monfort, 2012) — is crucial for obtaining meaningful survey results. In the context of data integration, it is also important to compare the effectiveness of different methods in detecting various species, ensuring that the data integration process explicitly accounts for potential biases, for example through the exclusion of species not detectable across all methods (Abrams *et al.*, 2019; Lyet *et al.*, 2021).

Together, Chapters 3 and 4 also contribute to addressing other critical issues in wildlife monitoring. Robust occupancy and biodiversity profiles are essential baselines for long-term population studies, where the management goals include detecting species population trends and evaluating the impact of conservation programs (Zipkin and Saunders, 2018). The use of all available data not only aligns with the recommendations for improving species monitoring in Chapter 2, but also offers solutions to geographic biases in monitoring efforts. In data-deficient regions lacking systematic surveys, incorporating or combining unstructured, observational data — such as local knowledge, citizen science, and protection patrols — can inform crucial baseline population estimates for conservation management (Miller *et al.*, 2019; Dobson *et al.*, 2020).

6.2 Targeting conservation actions through systematic conservation planning

Effective conservation planning relies on high-quality data to inform management strategies. Chapter 5 reveals significant discrepancies between priority maps generated from all primary versus secondary data, highlighting the critical importance of selecting appropriate input data for analysis. I advocate for the use of the best available data, particularly data that are collected in the field, whenever possible. This must be paired with rigorous analyses to ensure accurate inferences. Chapter 5 exemplifies the application of various robust analytical approaches to generate spatial layers for tiger distribution and associated threats, utilizing a wide array of data inputs.

For instance, I calculated tiger occupancy using the hierarchical integrated occupancy modelling framework from Chapter 4, incorporating prey biomass as a covariate. This approach effectively integrates detection/non-detection data from both unstructured (like ranger patrols) and systematic surveys (such as camera traps and sign transects) to provide more precise, landscape-wide species occupancy estimates (Doser *et al.*, 2022). I also extended the application of hierarchical modelling to estimate snare occupancy that indicates hunting distribution. This highlights the broader applicability of occupancy modelling beyond traditional wildlife studies, using snares as indirect indicators of hunter presence and activity (Moore *et al.*, 2021; Ghoddousi *et al.*, 2022).

Furthermore, I employed a probabilistic model to analyse satellite imagery depicting forest change, categorizing the data as binary (forest: 1, non-forest: 0) to predict forest loss over time (Voigt *et al.*, 2021). By accounting for various socio-ecological drivers of forest loss, we were able to identify areas at high risk of future deforestation. Additionally, for human-tiger conflict incidents, we applied a spatial log-Gaussian Cox process model, which effectively handles presence-only data commonly obtained from reports (Bachl *et al.*, 2019). The model effectiveness can be further enhanced by integrating presence-absence data, leading to more robust inferences on a larger scale (Grattarola, Bowler and Keil, 2023; Morera-Pujol *et al.*, 2023).

Since all these models consider the influence of spatial covariates on the tiger distribution and threats, they enable the creation of spatial layers using the most predictive spatial proxies that can be expanded to other landscapes. These layers may offer superior performance compared to those derived from secondary data sources, highlighting the chapter's contribution to advancing conservation planning through the use and integration of diverse data.

Conservation planning requires well-defined management objectives to effectively guide both the planning process and the implementation of actions (Kukkala and Moilanen, 2013). In Chapter 5, I established a protection-oriented objective for our spatial prioritisation exercises, aligning with management goals at both local and national levels. The adaptability of spatial prioritisation tools allows for the continuous refinement of objectives and strategies to achieve these goals (Hanson *et al.*, 2024). For example, in the context of tiger conservation in Leuser, we could prioritise protecting at least 30% of the area within each management unit — such as national parks, protection forests, or community forests.

Since most threats to biodiversity are human-driven, relying solely on ecological models is insufficient for identifying conservation priority areas (Milner-Gulland, 2012; Enquist *et al.*, 2017). Developing a social-ecological prioritization model that integrates human dimension — such as behaviours, attitudes, or social values related to wildlife and forests — with ecological factors like biodiversity profiles and threat risks offers a more holistic approach to account for complex interactions between humans, wildlife, and forests (Struebig *et al.*, 2018; Williamson, Schwartz and Lubell, 2018; Carter *et al.*, 2020). This approach is crucial not only to identify areas of high conservation values, but also to consider the social realities that influence conservation outcomes.

Importantly, setting objectives and conducting prioritisation through a participatory approach is strongly encouraged to ensure all stakeholder voices are heard and everyone is actively involved in the process (Wall, McNie and Garfin, 2017). While this may be time-consuming, the inclusive approach fosters a sense of ownership and collaboration, which is essential for the successful implementation and long-term sustainability of conservation efforts. It also significantly enhances the acceptance and likelihood of adopting the prioritisation results, thereby facilitating the translation of science into decision-making (Enquist *et al.*, 2017; Crevier and Parrott, 2019).

Establishing well-defined management objectives, developing socio-ecological prioritisation model, and conducting participatory prioritisation are critical steps that would significantly enhance systematic conservation planning. These enhancements would lead to more targeted, robust, and socially accepted conservation plans that are better equipped to address the complexities of real-world conservation challenges.

6.3 Implications for environmental policy

From a policy perspective, optimizing biodiversity monitoring through the measurement of community-level biodiversity metrics (Chapter 3) and data integration (Chapter 4) provides more robust baselines and trends for assessing biodiversity status in a cost-efficient manner. This enhanced approach allows for more effective monitoring of policy targets at both national to international levels. On the international policy commitments, this research can complement existing biodiversity indicators, such as the Living Planet Index, by supporting the monitoring of targets within Kunming-Montreal Global Biodiversity Framework (GBF), including Target 4 which aims to "Halt species extinction, protect genetic diversity, and manage human-wildlife conflicts" (UNEP, 2022). The data integration framework proposed in Chapter 4 provides methods for combining diverse datasets, including an unstructured one, thereby improving data utilization and expanding spatial representation, especially in data-sparse regions like the global south (Ledger *et al.*, 2023).

At the national level of Indonesia, these policy implications are equally relevant. My thesis highlights ways to make species monitoring in conservation areas more cost-effective, as promoted in initiatives such as Indonesia's Biodiversity Strategy and Action Plan 2025-2045 (IBSAP), which seeks to "Survey and monitor populations of target species (predominantly mammals) and assess their habitat suitability" (Target 4.1) (MoEF, 2015; Bappenas, 2024).

Regarding area-based conservation policies, this thesis contributes to the identification of high biodiversity areas by considering multiple facets of biodiversity (Chapter 3) and the development of a spatial prioritisation framework (Chapter 5). The insights from these chapters can be instrumental in identifying priority areas for biodiversity conservation to achieve Kunming-Montreal GBF Target 3, which aims to "Conserve 30% of land, waters, and seas" (UNEP, 2022). The same principles apply to Indonesia's national biodiversity conservation policies, such as IBSAP and the Ministry of Environment and Forestry Strategic Plan, which collectively aim to identify and protect areas of high biodiversity value (Nurzaini *et al.*, 2020; Bappenas, 2024).

These area-based targets can be further integrated with Other Effective Area-Based Conservation Measures (OECMs), which contribute to long-term, in-situ biodiversity conservation outside formally protected areas (Alves-Pinto *et al.*, 2021). A prime example of potential OECMs is Indonesia's flagship social forestry programme, which seeks to allocate 12.7 million hectares of forest land (10% of the state's forest areas) to local communities for sustainable management (Moeliono *et al.*, 2023). OECMs, collectively covering nearly 56% of the world's land, play a critical role in complementing existing conservation efforts by recognizing and supporting the rights of local communities to manage their lands, sustain their livelihoods, and preserve their cultural practices (Alves-Pinto *et al.*, 2021; Gurney *et al.*, 2021). To effectively monitor the impacts of OECMs schemes on biodiversity, reliable and cost-effective biodiversity indicators are needed — an area where this thesis's work on optimizing biodiversity monitoring can make a significant contribution.

6.4 Conclusion

The research presented in this thesis offers valuable pathways to enhance biodiversity conservation by optimizing monitoring efforts and strategic conservation planning for threatened mammals in tropical forests. Although the geographic focus is on the Sumatran rainforest of Leuser, the study findings and recommendations have broader applicability to other tropical regions. The study insights are particularly valuable in areas with limited resources and operational capacity, where timely and cost-effective biodiversity assessments and strategic resource allocations are urgently critical to safeguard threatened biodiversity.

Effective biodiversity conservation hinges on a robust capacity for monitoring and systematic conservation planning (Schmeller *et al.*, 2017; Elliott, Ryan and Wyborn, 2018). While there has been progress in building this capacity in tropical countries — evident in the growing number of conservation-focused degree programs, training workshops, and the publication of protocols and guidelines — there remains an urgent need for further capacity building to keep pace with the accelerating loss of biodiversity. Collaboration between stakeholders will be crucial in these efforts, enabling the sharing of knowledge, resources, and expertise across institutions and regions. Additionally, the analytical frameworks developed in the thesis are publicly available, with detailed guidance provided in the "Data Availability" sections of each chapter. This ensures they can be easily learned and applied in future research and management efforts.

Finally, to truly improve the state of biodiversity, it is crucial to make strong commitments not only to implement environmental policies but also to ensure the allocation of adequate financial resources (Langhammer *et al.*, 2024). Protecting biodiversity is not only just a scientific and policy challenge, but it is also a moral imperative. Therefore, we must foster a sense of optimism and determination to drive forward effective, evidence-based conservation actions (Pienkowski *et al.*, 2022). By staying committed, well-equipped, and optimistic in our conservation efforts, we can aspire to a future where biodiversity thrives, and humans and wildlife coexist in harmony.

6.5 References

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Co-authored publications

Below are the peer-reviewed journal articles that I contributed throughout my PhD programme and relevant to the broad theme of my thesis. The titles and abstracts of the publication are presented in reverse chronological order and the full-text copies can be found online.

Research article: Safeguarding Asian tapir habitat in Sumatra, Indonesia

Irene M.R. Pinondang, Nicolas J. Deere, Maria Voigt, **Ardiantiono**, Agus Subagyo, Alexander Moßbrucker, Antika Fardilla, Desy S. Chandradewi, Fahrudin Surahmat, Febri A. Widodo, Gabriella Fredriksson, Hariyo T. Wibisono, Jatna Supriatna, M. Irfansyah Lubis, Nuri Asmita, Sunarto, Tengku Lidra, Tomi Ariyanto, Wido R. Albert, Wilson Novarino, Wulan Pusparini, Yoan Dinata, Matthew J. Struebig

Oryx: July 2024

First View; Pages: 1:11; DOI: https://doi.org/10.1017/S0030605323001576

Abstract: The Asian tapir *Tapirus indicus* is the only tapir species in Southeast Asia. It is declining across its range and is categorized as Endangered on the IUCN Red List. The forests of Sumatra are critical to Asian tapir conservation as they contain some of the last remaining populations of the species, yet conservation efforts are hindered by a lack of information on habitat suitability. We collated camera-trap data from nine landscapes across 69,500 km^2 of Sumatran rainforest to help predict suitable habitat for Asian tapirs on the island. Predictions from Bayesian occupancy models demonstrated that tapir occupancy was greatest in forests below 600 m elevation and exclusively in forests with high aboveground biomass. Forests around the Barisan Mountains on the west of Sumatra provide the most suitable habitat for the species. Only 36% of the most critical habitat (i.e. 80th percentile of predicted occupancy values, or above) for tapirs is formally protected for conservation, with much of the remainder found in forests allocated to watershed protection (35%) or logging (23%). We highlight several key areas in Sumatra where tapir conservation could be bolstered, such as by leveraging existing conservation efforts for other charismatic flagships species on the island.

Perspective: Reflecting on the role of human-felid conflict and local use in big cat trade

Melissa Arias, Peter Coals, **Ardiantiono**, Joshua Elves-Powell, Jessica Bell Rizzolo, Arash Ghoddousi, Valeria Boron, Mariana da Silva, Vincent Naude, Vivienne Williams, Shashank Poudel, Andrew Loveridge, Esteban Payan, Kulbhushansingh Suryawanshi, Amy Dickman

Conservation Science and Practice: 2024

Volume: 6; Issue: 1; DOI: https://doi.org/10.1111/csp2.13030

Abstract. Illegal trade in big cat (*Panthera spp*.) body parts is a prominent topic in scientific and public discourses concerning wildlife conservation. While illegal trade is generally acknowledged as a threat to big cat species, we suggest that two enabling factors have, to date, been under-considered. To that end, we discuss the roles of human-felid conflict, and "local" use in illegal trade in big cat body parts. Drawing examples from across species and regions, we look at generalities, contextual subtleties, ambiguities, and definitional complexities. We caution against underestimating the extent of "local" use of big cats and highlight the potential of conflict killings to supply body parts.

Research article: Planning for megafauna recovery in the tropical rainforests of Sumatra

Muhammad I. Lubis, Janice S. H. Lee, U.M. Rahmat, Tarmizi, Eka Ramadiyanta, Dewi Melvern, Sasha Suryometaram, Ahtu Trihangga, Muhammad Isa, Dedy Yansyah, Ridha Abdullah, **Ardiantiono**, William Marthy, Kendall R. Jones, Noviar Andayani, Matthew Linkie

Frontiers in Ecology and Evolution: September 2023

Volume: 11; DOI: https://doi.org/10.3389/fevo.2023.1174708

Abstract. Human-induced forest loss has had devastating impacts on biodiversity. Mammal populations in the tropics have been hit particularly hard by the resulting habitat loss, fragmentation and degradation, as well as by overhunting which often goes hand-in-hand. While declines in these populations are generally well documented, few studies offer a pathway for their recovery. Here, we test the association between changes in forest habitat and occupancy trends of Sumatran megafauna (elephant and tiger) and key tiger prey species (wild boar and sambar) in the Leuser Ecosystem: a large forest landscape on the Indonesian island of Sumatra. For elephant and tiger, we develop additional occupancy models to predict their respective spatial distribution under different scenarios of forest loss and gain (through restoration and increased connectivity) to provide a blueprint for avoiding future species loss and assisting with their population recovery. From 2000 to 2019, 254,722 ha (6.7%) of natural forest was converted, primarily to plantations and shrubs. The species-specific responses over the study period revealed that the occurrence of elephant declined along the west, with a range shift to the northeast of Leuser, whereas wild boar underwent a dramatic widespread decline and although sambar experienced losses around the forest edge, it remained widespread in the interior forest, while tiger occupancy remained stable. Modelling habitat loss and fragmentation led to an unsurprising demise of Sumatran megafauna, whereas strategic investments that reconnected several forest patches provided disproportionately large benefits for their recovery through the recolonization of former parts of their range. Indonesia has achieved six consecutive years of declining forest loss rates, and our study's findings can build off this conservation success by supporting improved provincial spatial planning and field-based restoration efforts

that avoid declines of threatened megafauna species and act as a catalyst for rewilding a landscape of global importance.

Research article: Integrating social and ecological information to identify high-risk areas of human-crocodile conflict in the Indonesian Archipelago

Ardiantiono, Sujan M. Henkanaththegedara, Brandon Sideleau, Sheherazade, Yogie Anwar, Iding A. Haidir, A.A. Thasun Amarasinghe

Biological Conservation: March 2023

Volume: 280; DOI: https://doi.org/10.1016/j.biocon.2023.109965

Abstract. Crocodile attacks on humans and subsequent retaliations are a pressing issue for saltwater crocodile conservation. As human-crocodile conflict is complex, integrating social and ecological information better explains the drivers and patterns of these interactions. Our study aims to incorporate ecological factors associated with the intensity of crocodile attacks together with social factors of mass media reports to identify high-risk areas of human-crocodile conflict in Indonesia. We compiled reports of crocodile attacks in the 2010–2019 period from media reports, field surveys, and local informants. The presence of attack was estimated by evaluating the influence of habitat, climate, human, and reporting effort. As tone of media coverage can reflect and shape reader's tolerance about a certain issue, we assessed the headline's tone from each media article that reported crocodile attacks from 2017 to 2019. A total of 665 crocodile attacks were recorded and mainly distributed in western and central Indonesia. The estimated number of crocodile attacks was higher in areas with lower forest biomass and human density, and wider cellular network coverage. Negative media coverages were frequently reported in western Indonesia. By combining social information of negative media reporting and the ecological information of crocodile attacks hotspots, we identified 170,500 km^2 priority risk areas in the western part of Indonesia, a notable 65.8 % reduction in area size compared to the attack hotspots. We highlight the application of socio- ecological information in risk prioritisation to address the rising trends of negative human-wildlife interactions.