Biological Conservation 299 (2024) 110795

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Prioritizing wildlife conservation along habitat gradients in Sumatra

Iding A. Haidir [a,b,*], Oliver R. Wearn [c,d], Nicolas J. Deere [e], Matthew J. Struebig [e], Alue Dohong [a], David W. Macdonald [b], Matthew Linkie [f]

[a] Ministry of Environment and Forestry Republic of Indonesia, Jakarta, Indonesia
[b] WildCRU, The Recanati-Kaplan Centre, University of Oxford, Tubney House, Tubney OX13 5QL, United Kingdom
[c] Institute of Zoology, Zoological Society of London, London, United Kingdom
[d] Fauna & Flora International – Vietnam Programme, Hanoi, Viet Nam
[e] Durrell Institute Conservation and Ecology, University of Kent, Canterbury, United Kingdom
[f] Wildlife Conservation Society, Bogor, Indonesia

ARTICLE INFO

Keywords:
Camera Trapping
Carnivore
Indonesia
Land-use planning
Multi species occupancy
Protected area management

ABSTRACT

Managing protected areas (PAs) requires measurable indicators to assess effectiveness. The status of populations and guilds of multiple species are potential indicators that should be useful in biodiversity-rich tropical countries. We quantified such indicators using data from an intensive camera trap survey of seven sites at the forest-farmland interface of Kerinci Seblat National Park, Sumatra, Indonesia. Surveys between 2014 and 2016 covered 671 camera locations set along habitat gradients comprising primary to degraded forest and lowland to sub-montane forest. We ran Bayesian multi-species occupancy models that incorporated landscape covariates and patrol intensity to generate four population parameters: relative abundance, probability of habitat use, species richness and detection probability. Model-derived beta coefficients summarized at the guild-level were extrapolated using detailed spatially-explicit data on landscape covariates to produce multi-guild occurrence maps to explore the role of habitats in supporting multiple overlapping functional groups. From 55,856 trap nights, we recorded 33 species from six guilds: carnivores; frugivores; granivores; herbivores; insectivores; and omnivores. All guilds were negatively correlated with elevation and positively correlated with primary forest. Five areas with high multi-guild overlap were identified and recommended for increased protection and other conservation measures, such as increasing the frequency of SMART patrols. Our data-driven guild-level approach for improving conservation practice has high relevance to other biodiversity-rich countries. Further utility of this guild approach, with potential future refinement and improvement, should greatly assist PA managers with improving area-based conservation effectiveness, such as higher patrol frequencies and or prioritizing wildlife, and habitat and ecosystem inventory, under-pinned by enhanced research, and cost-efficient budget allocation.

1. Introduction

The United Nations Convention on Biological Diversity (CBD) Target 3 calls for 30 % of the world's terrestrial, inland water, and coastal/marine areas to be effectively conserved and managed by 2030. To assess management performance in these areas, the IUCN-WCPA has applicable guidelines and tools for assessing protected area (PA) management effectiveness, notably the Management Effectiveness Tracking Tool (METT) (Coad et al., 2015; UNEP-WCMC and IUCN, 2016). These guidelines were developed to support site and system processes by improving PA management through: better information sharing; promoting adaptive management; effective resource allocation for management themes identified as being most in need of support (e.g. shifting population monitoring efforts to enforcement); providing accountability and reporting at local, national, and international levels; and, increasing awareness of PA management amongst local communities (Coad et al., 2015).

In prioritizing conservation effort and funds, PA managers need to decide how best to allocate resources for research, patrols, community engagement and other aspects of PA management (Dancer et al., 2022; Chadès et al., 2008). Protected Areas rarely exist in isolation and coordinated species conservation at local (single PA) and landscape (multiple land uses and PAs) scales is, therefore, important to ensure that they are mutually reinforcing (Boyd et al., 2008).

* Corresponding author at: PT Kaltim Lestari Utama | Ecosystem Restoration, Plaza Balikpapan, Borneo Bay City, Kota Balikpapan, East Kalimantan, Indonesia.
E-mail address: iding.haidir@kaltimlestariutama.com (I.A. Haidir).

https://doi.org/10.1016/j.biocon.2024.110795
Received 9 January 2024; Received in revised form 9 September 2024; Accepted 14 September 2024
Available online 30 September 2024

In biodiversity-rich developing countries, where the funds allocated to PA management are often limited, prioritizing themes and areas for further protection is urgently needed to support one of their measures of success: wildlife population viability (UNEP-WCMC and IUCN, 2016). Currently, several indicators of successful conservation area management include maintaining populations of priority species encompassing various taxa at individual and community levels, ensuring habitat intactness, and implementing effective conservation zoning (Hull et al., 2011; Kiffner et al., 2020). However, these indicators need to be regularly updated, especially for relatively small PAs that harbour important umbrella species but are constrained in their ability to allocate resources for population monitoring and maintaining conservation states (Dunn et al., 2016; Roberge and Angelstam, 2004).

In PAs throughout many tropical countries, wildlife monitoring teams have tended to focus on felids (Barlow et al., 2018; Ducarme et al., 2013), given their threat status and high profile as umbrella species (Albert et al., 2018). Felids are important indicator species of hunting pressure because the forest trails they traverse are commonly targeted by poachers, who set snares that may incidentally trap other mammal species. In many of the PAs of Sumatra, rangers gather information on biodiversity indicators, such as presence of priority mammal species and associated threats, and digitally record this in logbooks for further analyses that are useful for management purposes (Risdianto et al., 2016; Linkie et al., 2015). However, funding allocation for such conservation interventions, both in terrestrial and marine PAs, is insufficient in developing countries (Balmford and Whitten, 2003; Bladon et al., 2014; Waldron et al., 2013). In Indonesia, for example, population monitoring received 3.7 % of the Directorate General of Natural Resources and Ecosystem Conservation (KSDAE) of Indonesian MoEF national budget allocation, whilst emphasis is placed on the importance of other management components, such as habitat protection, community development, and conflict resolution (KKH, 2020).

Recent and more advanced camera trapping studies in Asia and elsewhere have successfully studied the behaviour, ecology, and conservation status of rare and elusive felids (Laurance et al., 2014; Linkie et al., 2013). Other camera-trap studies have advanced our understanding of species abundance along land-use gradients and how this is influenced by various landscape factors (Wearn et al., 2017). From a PA management perspective, the detection of vast arrays of species (Macdonald et al., 2020; Chiaverini et al., 2022) within study areas offers greater opportunities for a science-based, and therefore more effective, decision-making process, whether at the species or community level (Bhagabati et al., 2014). Incorporating multi-species indicators, such as species richness and evenness, in this process has been shown to assist PA managers in making more accurate assessments of different management interventions (Sauer et al., 2013).

Here, we focus on a large biodiversity-rich tropical forest mosaic comprising a relatively intact PA (Kerinci Seblat National Park, KSNP) and degraded buffer zone, offering variations in landscape characteristics (elevation, slope, distance to river, and vegetation index), human impacts (distance to forest core and settlements) and a key conservation intervention (ranger patrols). We used these factors to explore how continuous landscape covariates across KSNP's forest gradients and patrol intensity affected four key biodiversity indicators summarized at the community, guild and species levels: relative abundance, probability of habitat use (akin to occupancy when camera sites are not all strictly independent; Mackenzie and Royle, 2005), species richness, and detection probability.

We aimed to investigate landscape prioritization at the species, guild, and community levels. To do this we first determined whether relative abundance and detection probability for individual species varied in a predictable and ecologically informative way along habitat gradients in the landscapes (for example, it emerged that for some species these measures were higher in the areas that have lower elevation, mild slope and were closer to rivers). We then explored these species-gradient relationships in aggregate by combining the information into guilds and communities, and mapping probability of use at these levels across the study region. The resulting maps were used to identify areas of high species diversity and thereby to infer conservation priorities for multi-species management. Throughout, we aimed to better understand the efficacy of multi-species monitoring in supporting conservation area management effectiveness in the tropics, particularly in Indonesia, and its applicability to PAs in other tropical countries.

2. Materials and method

2.1. Study area

Research was undertaken across seven study areas, purposively sampled 344.8 km^2 over ~16,000 km^2 of the KS landscape in west-central Sumatra, comprising forest in KSNP, adjacent production forests, and a mosaic of various smallholder and large concession plantations (Table S1). The landscape elevation ranges from 0 to 3805 m asl, resulting in the stratification of forest types (lowland, hill, sub-montane, mid-montane and upper montane/sub-alpine) and topography ranging from flat to extremely steep with a varying proportion of terrain ruggedness. The land cover types for the landscape, generated from BAPLAN (Indonesia Ministry of Environment and Forestry's Planning and Mapping Centre), include natural forest (50.5 %), agriculture (30.1 %) (mixed agriculture, paddy fields), monoculture production (9.2 %) (forest plantations and plantations), degraded habitats (swamps, bushes, bare lands, settlements; 9.0 %) and other (1.2 %).

Biodiversity surveys targeted seven study areas (Fig. 1): Kambang in the Pesisir Selatan district, West Sumatra province, which represents lowland forest; four study areas (Bungo, Muara Hemat, Sipurak, and Renah Kayu Embun - RKE) located in three districts (Bungo, Merangin, and Kerinci) in Jambi province, which all represent hill-montane forest; Ipuh in Bengkulu Province, which is dominated by lowland forest and directly borders production forest and palm oil plantations; and the Karang Panggung district of Musi Rawas, South Sumatra, which is dominated by lowland forest and surrounded by smallholder rubber plantations (Fig. S1). The areas have varying levels of land use protection and patrol frequencies.

The KS landscape is designated as a *National Strategic Area*, under Act No 26/2008 regarding National Spatial Planning, in recognition of its high environmental and biodiversity value (MoPWH, 2017). Kerinci Seblat is one of the most biodiverse landscapes in Sumatra, and provides a crucial refuge for the Sumatran tiger (*Panthera tigris sumatrae*; Wibisono et al., 2011) Moreover, this landscape provides crucial ecosystem services to the surrounding area, such as water provision to ~2 million households, which also supports over 50,000 km^2 of agriculture (MoPWH, 2017).

2.2. Sampling design

Field surveys in Bungo, Sipurak, RKE, and Ipuh covered the same areas surveyed by Haidir et al. (2018) and significantly overlapped with previous surveys between 2004 and 2006 by Linkie et al. (2008) and Wong et al. (2013). The minimum convex polygon surrounding the outer array of camera traps for these study areas was 60–70 km^2 from 292 sites, with an inter-trap spacing of 0.8–1.4 km. In the northern (Kambang), central (Muara Hemat) and southern (Karang Panggung) regions of the park, elongated camera trap arrays were implemented, covering 27–32 km^2, 15–18 km in length and 3–5 km in width. These arrays included 143, 130, and 106 camera trap sites (379 in total), respectively, with an inter-trap spacing of 0.4–0.7 km (Supplementary materials, Table S1 and Fig. S1) (Haidir et al., 2020a). Field surveys were designed to cover the interface between forested and non-forested areas. For all surveys, cameras were placed on a pole/tree 2–2.5 m next to low resistance travel routes, such as forest trails, and placed 40–60 cm above the ground. No baits or lures were applied. Cameras were

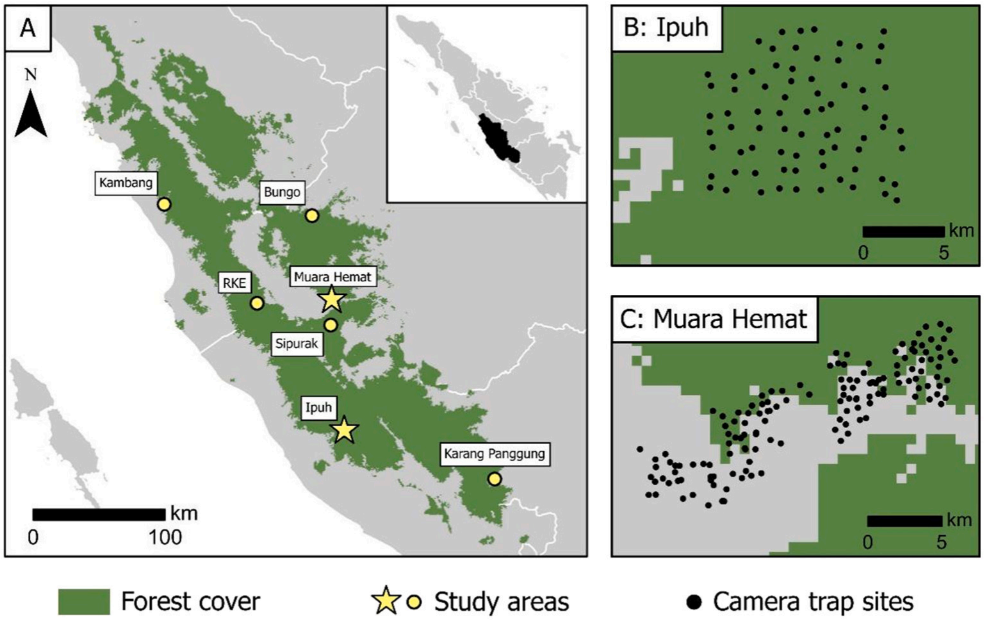

Fig. 1. A) Location of study areas (yellow points) within the Kerinci Seblat Landscape (black polygon, inset) relative to forest cover. Camera trap deployments were strategically positioned to capture a gradient of forest interior habitat (B: Ipuh study area) and transitional zones between forest and non-forest areas (C: Muara Hemat study area). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

deployed for a maximum period of 105 consecutive camera trap nights, though realized survey effort across sites was variable owing to camera malfunctions (EC047, Cuddeback Ambush camera unit), theft and animal damage (~9 % of the total number of camera units, camera sites at survey start was 731 and at at end was 671, with some camera units yielded data from as short as 20 trap nights).

2.3. Covariates

We tested seven landscape covariates that we considered likely to influence the spatial behaviour of medium-large terrestrial mammals in Sumatra (Haidir et al., 2018; McCarthy, 2013), with a particular emphasis on small-medium sized felids (clouded leopard *Neofelis diardi*, golden cat *Catopuma temminckii*, marbled cat *Pardofelis marmorata*, and leopard cat *Prionailurus bengalensis*) and their putative prey (muntjac: *Muntiacus muntjak and M. montanus*; mouse deer: *Tragulus* sp.; pig-tailed macaque: *Macaca nemestrina*; porcupine: *Hystrix brachyura*). Data on elevation (elev) and slope (slope) were obtained from the Shuttle Radar Topographic Mission (SRTM; 30 m resolution) (Rabus et al., 2003); tree cover (treecov) was derived from high resolution satellite imagery (30 m resolution) made commercially available by Global Forest Watch (Hansen et al. (2013); proximity to forest edge (fordist), rivers (rivdist) and villages (vildist) were calculated as Euclidean distances based on official forest cover data from BAPLAN and spatial layers from BAKOSURTANAL (Indonesia Land Survey and Mapping Agency). Distance to water bodies was approximated from third order *Gravelius' streams,* defined as non-seasonal water bodies (Gülgen, 2017). All layers were converted to UTM 47 M Southern Hemisphere Projection and resampled to a 250 m resolution. All covariates were screened for intercorrelation prior to statistical assessment using Pearson's correlation coefficient (r) and variance inflation factors (VIF). To avoid collinearity, we removed covariates that had an $|r| \geq 0.7$ and VIF ≥ 5 (Dormann et al., 2013).

To quantify hunting pressure, we incorporated a measure of patrol intensity, reflecting the frequency of ranger patrols within a 3 km radius of each camera trap site. We assumed that areas routinely visited by patrols were subject to lower hunting pressure due to increased monitoring and enforcement against illegal activities. The KS Tiger Protection and Conservation Units (KS-TPCUs) operate in KSNP and adjacent forest, with the overarching aim of protecting tigers and their habitat from direct and indirect threats (Linkie et al., 2018; Risdianto et al., 2016; Haidir et al., 2020a). We focused on KS-TPCU foot patrols conducted between 2012 and 2016 to detect forest encroachment and dismantle wildlife snares targeting tigers and their typical ungulate prey, songbirds, and other exotic birds like hornbills. Between 2012 and 2016, six units, each led by a national park ranger and three to four well-trained community rangers, operated in two main regions in Bengkulu and Jambi provinces and conducted ~120 patrols each year. Patrol data were archived using Spatial Monitoring and Reporting Tool (SMART) and analysed within an adaptive framework to identify hotspots of illegal activity in the KS landscape and target management to these high risk areas. Monthly patrol efforts were overlaid with camera stations and to calculate the cumulative number of patrols that intersected within a 3 km radius of each deployment site. Further details of camera trap placement relative to covariate attributes are presented in Supplementary Materials (Table S1).

2.4. Multi-species occupancy model

Prior to analysis, we created a multi-species detection matrix whereby sampling periods were collapsed into five-day temporal replicates, resulting in a maximum of 25 sampling occasions for each of the 671 camera trap sites. Within each temporal replicate, we denoted a “1” if the species was detected during the five-day interval, and a “0” if it was not. We excluded species with fewer than five detections from the modelling process as it is difficult to disentangle changes in abundance and detection, when observation data are sparse.

We implemented a Bayesian hierarchical multi-species occupancy model (Kéry and Royle, 2015) to elucidate the environmental and anthropogenic determinants of mammal persistence across the KS landscape. Occupancy models are a powerful analytical tool to monitor wildlife populations due to their capacity to explicitly account for bias arising from imperfect detection (Guillera-Arroita, 2017). Multi-species applications of occupancy frameworks are particularly advantageous for monitoring rare or elusive species, as they specify species-specific parameters as random effects drawn from a common, community-level distribution, which improves estimation precision for species infrequently detected during sampling (Devarajan et al., 2020; Pacifici et al., 2014). Accordingly, multi-species occupancy models permit inferences at multiple taxonomic scales, such as individual species, entire mammal communities, or any particular grouping of interest (i.e. guilds: Deere et al., 2020; Wearn et al., 2017). In this study, we estimated species-level responses to all variables, but restricted our inferences at a higher taxonomic scale to three groupings: small-medium sized felids, potential prey for felids (defined according to Haidir et al., 2018), and trophic guild (carnivores, frugivores, herbivores, insectivores, omnivores: (Table S2)).

We implemented the Royle-Nichols multi-species occupancy model (Royle and Nichols, 2003), which outperforms the standard occupancy approach when variation in local abundance imparts variation in detection probability (Tobler et al., 2015). Specifically, the Royle-Nichols approach allows species detection probability to increase at sites where the species is more abundant, as we would expect from first principles. For group-living species, the specific parametric form of the Royle-Nichols detection process was further modified (following Royle and Dorazio, 2009 and Wearn et al., 2017) by including an additional overdispersion parameter, which allowed the model to have a relaxed assumption of independent detection amongst individuals.

For the purposes of mapping our results, we converted abundance to probability of habitat use (see below). The zero-inflation component was included to allow for instances where a species did not occur at all in a part of the landscape. The Poisson process alone is only able to model low abundances, but not zero abundance. More specifically, the zero-inflation parameter was a function of the broad land-use type (old growth forest, secondary forest, agroforestry) that a particular camera was placed in. This approach has been used previously with the Royle-Nichols model (Tobler et al., 2015; Wearn et al., 2017) and zero-inflation is a widespread approach in ecological modelling (e.g. Zuur, 2012).

We calculated probability of habitat use by a species (ψ) as a deterministic function of local abundance, which expresses the probability that abundance is greater than zero: ($\psi = 1 - exp(-\lambda)$. This function is equivalent to one minus the Poisson probability of getting a zero abundance ($N = 0$) given the local abundance parameter (Royle and Nichols, 2003). To map probability of habitat use at the guild level, we generated 3000 spatial predictions drawn from the posterior distribution based on model-derived associations with landscape and anthropogenic covariates. For each guild, we express probability of habitat use and uncertainty as the median and standard deviation, respectively, across all spatial predictions estimated from the posterior. Probability of habitat use predictions for each guild were reclassified based on a conservative 75th percentile threshold. Cells were converted into binary values, depending on whether they were above ('1') or below ('0') the threshold. To define areas with the highest number of overlapping guilds, binary predictions of guild occurrence were summed to accumulate the number of guilds that overlap in a given area (Dunn et al., 2016).

2.5. Species richness

We derived a bias-corrected measure of species richness from our model, to estimate species diversity at each camera trap site while accounting for imperfect detection (Berry et al., 2010). We calculated metacommunity richness incorporating detection probability by summing the abundance-derived latent occurrence state across species for each site (Kéry and Royle, 2016). We used continuous spatial covariates and patrol intensity at each camera site to understand their relationships with species richness. To make this information more accessible to PA management, we also present species richness in several pertinent categories: forest types (lowland/0–300 m asl, hill/300–800 m asl and sub montane/ >800 m asl; the maximum elevation of a camera trap site was ~1900 m asl), distance to forest (outer ≥2000 m outside forest edge, periphery = 0–2000 m outside forest edge, interior = 0–2000 m towards forest core, and core ≥2000 m towards forest core), three classes for distance to village (close ≤5000 m, medium = 5000–8000 m, and far ≥8000 m), distance to river (close ≤1000 m, medium = 1000–2000 m, and far ≥3000 m), three classes of vegetation cover (secondary degraded ≤0.38, primary degraded = 0.38–0.42, and primary ≥0.42), and patrol intensity (low = 0–1, medium = 2–3, and high ≥4).

2.6. Model specification and performance

To obtain samples of the joint posterior distribution, models were specified within a Bayesian framework using JAGS routed through R using 'jagsUI' (RStudio, 2015). Throughout, we consider statistical associations to be substantial if 95 % Bayesian Credible Intervals (2.5th and 97.5th percentile of the posterior distribution) did not overlap zero and moderate if the 75 % BCI (12.5th and 87.5th percentile of the posterior distribution) did not overlap zero. Unless stated otherwise, outputs are presented as posterior means with uncertainty expressed as 95 % BCIs. We provide further details of model specification, convergence diagnostics and posterior predictive checks in the Supplementary Materials (Tables S3, S4, and Fig. S2).

3. Results

From a combined sampling effort of 55,856 camera trap nights, 33 mammal species were detected from our 671 trap sites. From this species list, we excluded eight species with limited detections (<5), resulting in a mammal community consisting of 25 species. Inspection of detection histories revealed that group-living species were more prevalent than solitary taxa (Table S2).

3.1. Relative abundance, detection probabilities and guild occupancies

The relative abundance of the mammal community and respective species clusters increased towards the forest interior and, to a lesser extent, in areas of denser vegetation and further from rivers. Community-level trends obscured considerable variation in the response to covariates at the species level. For example, while patrol intensity had limited impact on community abundance, several threatened taxa, including the sun bear and sambar, showed clear increases in relative abundance (95 % BCI did not overlap zero) in areas afforded security from poaching by more frequent ranger patrols. Graphical summaries of covariate effects at the species level are presented in Supplementary Materials S Data2. The five species with the highest relative abundance across the study areas were wild boar, muntjac, porcupine, pig-tailed macaque and Sumatran tiger. Accordingly, the five species with the highest detection probability were bearded pig, muntjac, sambar, Hoogerwerf's Sumatran rat and the Malayan sun bear (see Fig. 2 for a posterior estimate of relative abundance and detection probability for all species).

Associations between environmental and anthropogenic covariates imply that felids had higher relative abundances in forest interior locations further from rivers, whilst prey tended towards lowland habitats characterized by dense vegetation. Patrol intensity had a neutral relationship with the relative abundance of small-medium felids and a moderate positive affect on the relative abundance of prey species (a visual relationship of hypothesis testing for these relationships is shown in Fig. 3). Habitat associations across other species groups were found to be highly variable (Fig. 4). IUCN threatened taxa, carnivores, and to a lesser extent, omnivores and frugivores all demonstrated a preference for core forest habitat, while guilds characterized by a wide dietary spectrum also preferred low elevation areas. Gentler slopes and higher patrol intensity facilitated moderately higher herbivore and insectivore abundance respectively, whereas the other guilds had a relatively neutral relationship with these covariates. Herbivores also demonstrated a moderate preference for dense vegetation, likely reflecting lower disturbance in these areas.

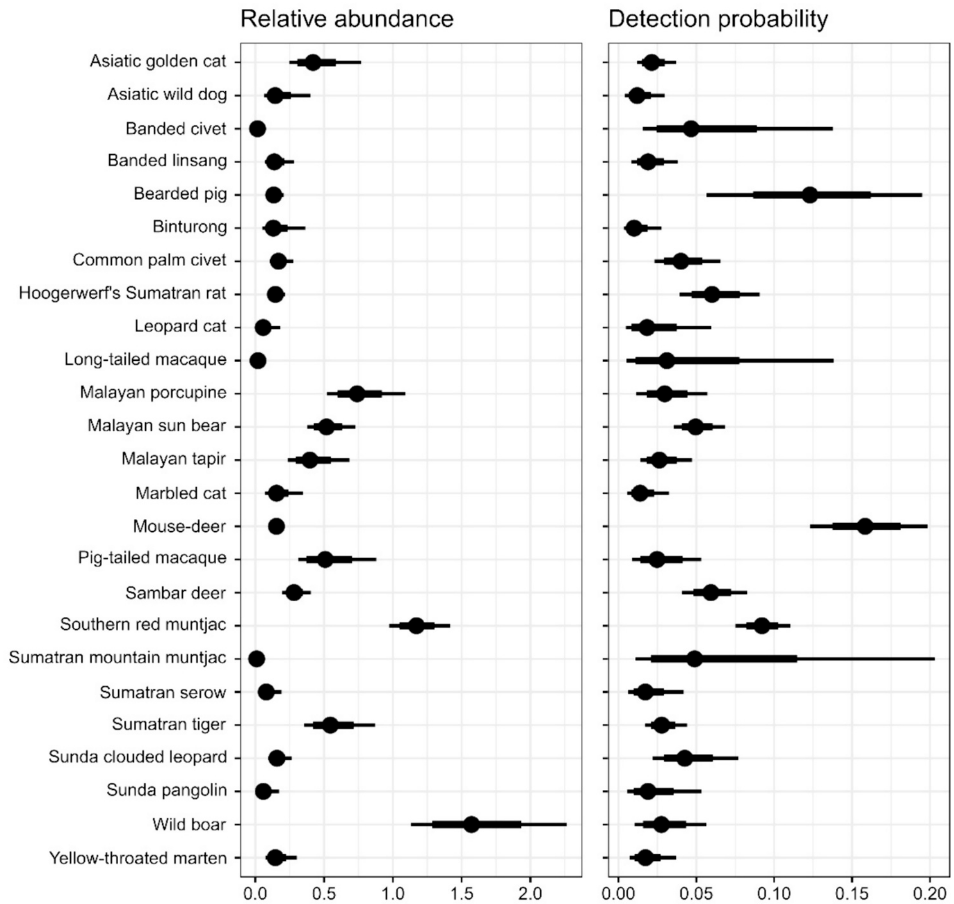

Fig. 2. Posterior estimates of relative abundance and detection probability of species detected by camera traps in the Kerinci Seblat landscape at mean levels of all covariates. Points represent the median of the posterior distribution and horizontal lines denote 75 and 95 % Bayesian Credible Intervals (thick and thin lines respectively).

At the land-use scale, mammals were sensitive to disturbance, as indicated by proportional changes in occurrence when disturbance classes were compared (See Fig. 5 for community/guild level changes and Fig. S3 for species-wise changes). Across the entire mammal community, declines in abundance from old growth forest were comparable between secondary forest (posterior mean: −6.7 %; 95 % BCI: −10.4 % to −3.0 %) and agroforest (−7.3 %, −11.0 % to −4.0 %) but demonstrated no statistical difference between secondary forest and agroforest. Declines in abundance were most pronounced for IUCN threatened species (old growth to secondary forest: −12.3 %, −16.8 % to −8.0 %; old growth to agroforest: −10.6 %, −15.3 % to −6.5 %), indicating that vulnerable species are most heavily impacted by land-use change. Trends of decline relative to old growth forest were consistent across most species groups, with transitions between the disturbed forest classes being more variable. While some guilds moderately increased in abundance between secondary forest and agroforest (threatened taxa, carnivores, omnivores, small felids: 2.4–4.9 % average increases across guilds), groups demonstrating a degree of dependence on forest resources were more heavily impacted (up to 4.9 % declines in herbivores, insectivores and prey species). At the species level, Asiatic wild dog, sun bear, Asian tapir and Sunda clouded leopard demonstrated the most severe declines relative to land-use change, declining between 20.3 % and 30.37 % on average across species. Several species appeared to benefit from the ecological opportunities presented in disturbed habitat, most notably wild boar, which increased in abundance by up to 50.34 % (16.4–89.9 %) in the more disturbed habitat classes when compared to old growth forest.

Spatial predictions of probability of habitat use across functional guilds indicated that carnivore occurrence peaked at 0.38 at a 250 m cell resolution. The highest extrapolated probability of habitat use recorded for frugivores, granivores, herbivores, insectivores, and omnivores was 0.05, 0.15, 0.22, 0.14, and 0.29, respectively. Overlaid binary maps of guild representation identified that Ipuh accommodated the highest number of co-occurring guilds (median: 6; 95 % CI: 3–6), followed by Sipurak (4; 0–5), RKE (3; 0–6) and Karang Panggung (2; 0–2). The remaining study areas were found to be of lesser ecological value, supporting no overlapping guilds on average. Amongst the areas containing the highest number of guilds, Ipuh demonstrated the most precise predictions with the lowest error (mean prediction error: 0.069; 95 % BCI: 0.054–0.098), providing a greater degree of confidence that this is a regionally important area for mammal conservation. Across the KS landscape, guild retention was found to be high in hill forests and we identified six areas where guilds were highly overlapped: five within KSNP and one in Batang Hari Protection Forest (Fig. 6).

3.2. Species richness

To draw baseline information on species diversity, we created median species richness predictions for all seven study areas (Fig. 7). Ipuh had the highest predicted mammal species at 11 (6–16), followed by Sipurak at eight (3−13), Karang Panggung at seven (3−11), Bungo at six (2−12), RKE at six (2−13), Muara Hemat at six (2−11), and Kambang at five (BCI 2–9). Species richness was most pronounced between 300 and 900 m a.s.l. (equating to lowland and hill forest), in areas with gentle and moderate slopes, and towards the forest interior (montane forest >2000 m inside KSNP). This indicates that primary lowland-hill forest

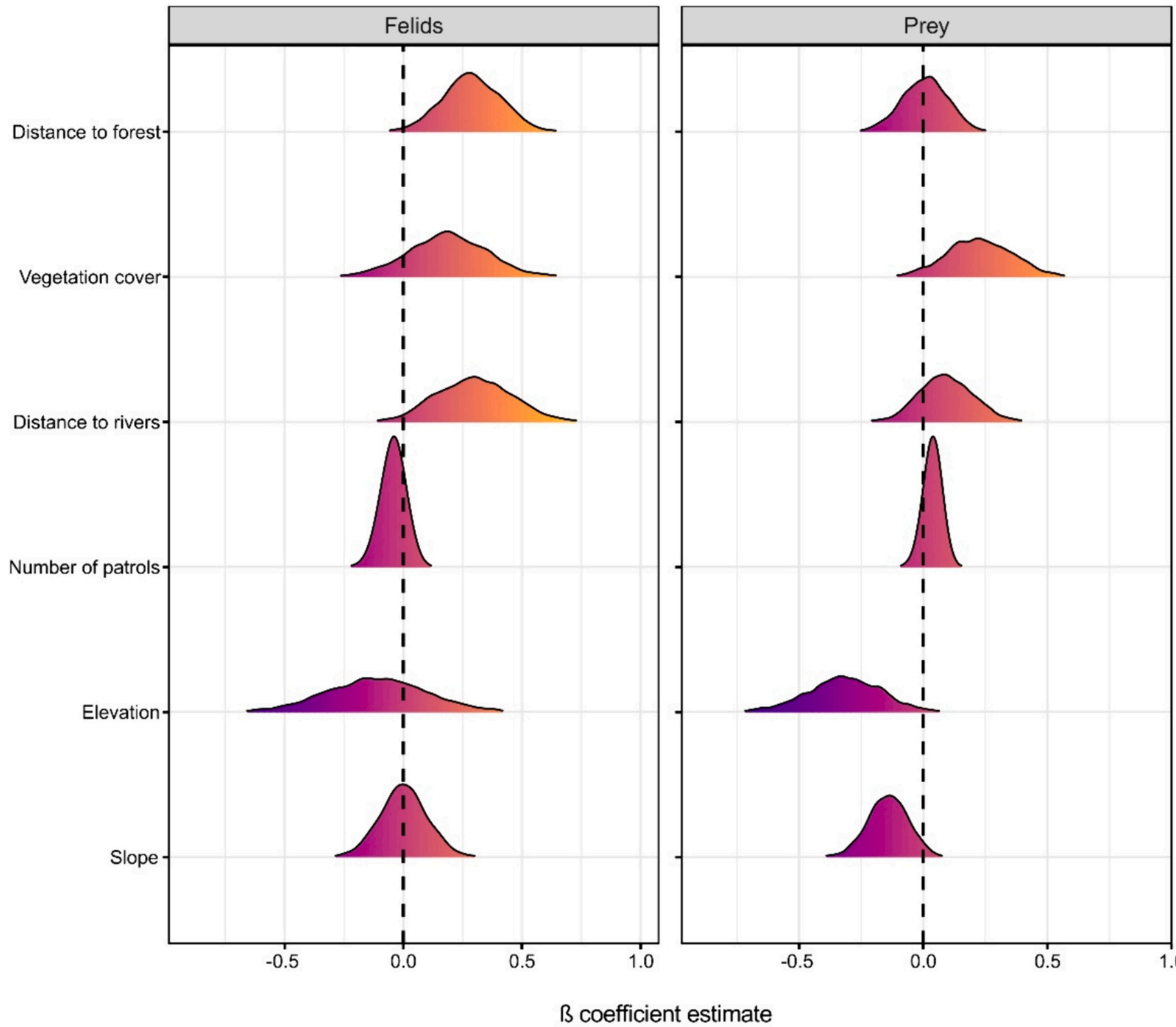

Fig. 3. Hyper-parameter estimates for small-medium sized felids (clouded leopard, golden cat, marbled cat, and leopard cat) and prey (muntjac, Sumatran muntjac, Malayan porcupine, and pig-tailed macaque) hyper-parameter estimates and probability of relationships between species group abundance and site covariates in the Kerinci Seblat landscape.

further from the forest edge with relatively relaxed slopes have a greater number of mammal species than secondary forest. Presumably, there are variations between species composition in all richness clusters. However, the overall richness estimate was higher in areas >8 km away from the nearest village, with no significant difference between areas close to village (<5 km) and at a medium distance (5–8 km) away. Most of our camera trap sites were placed in locations with low patrol intensity, where the model predicted a mean richness of seven species (4.9–10.2). While mean species richness was nine (6.4–11.81) in areas with medium and high patrol intensity. Lastly, our model predicted that areas within an 8 km radius from the rivers had a mean species richness of eight (5.7–11.2), which is slightly higher than areas further (>8 km) from the rivers, which had a mean of seven species (5.4–10.5).

4. Discussion

Studying wildlife through multi-species approaches is an effective means of providing useful information for science, such as how predator species richness impacts ecosystem function (Finke and Snyder, 2010) and conservation and policy interventions (Rayan and Linkie, 2016). It also provides important management insights into how tropical forest degradation and loss impact wildlife communities, and more generally ecosystem health and resilience. Using data from a mammal community assessment, with specific reference on small-medium felids (Haidir et al., 2020b), our study generated multi-species population indicators – relative abundance, probability of habitat use, species richness and detection probability - along continuous habitat gradients in Sumatra. This provides a multidimensional measure of ecosystem health that can be used to improve PA management effectiveness through monitoring non ‘flagship species’ or a non-tiger-centric approach (Ardiantiono et al., 2024). Our methodology also provides a template for performing multi-species population monitoring from intensive camera trapping efforts, which has wide applicability to other tropical landscape settings (Macdonald et al., 2018).

For all functional guilds in our study, a clear pattern emerged along the habitat gradient, whereby higher habitat use was found in areas deeper inside the forest, with higher vegetation cover and at lower elevation. This emphasizes the importance of intact forest within the national park in safeguarding these multi-species groups, because all guilds exhibited significant declines from old growth forest to secondary forest and agroforest, which was most pronounced for the IUCN threatened species. It also highlights that rehabilitating degraded lands through restoration efforts, as well as preventing further degradation, could yield substantial biodiversity benefits, as has been demonstrated elsewhere in the tropics (Williams et al., 2017; Atkinson et al., 2022; Bhatia et al., 2023). Encouragingly, our model revealed high relative

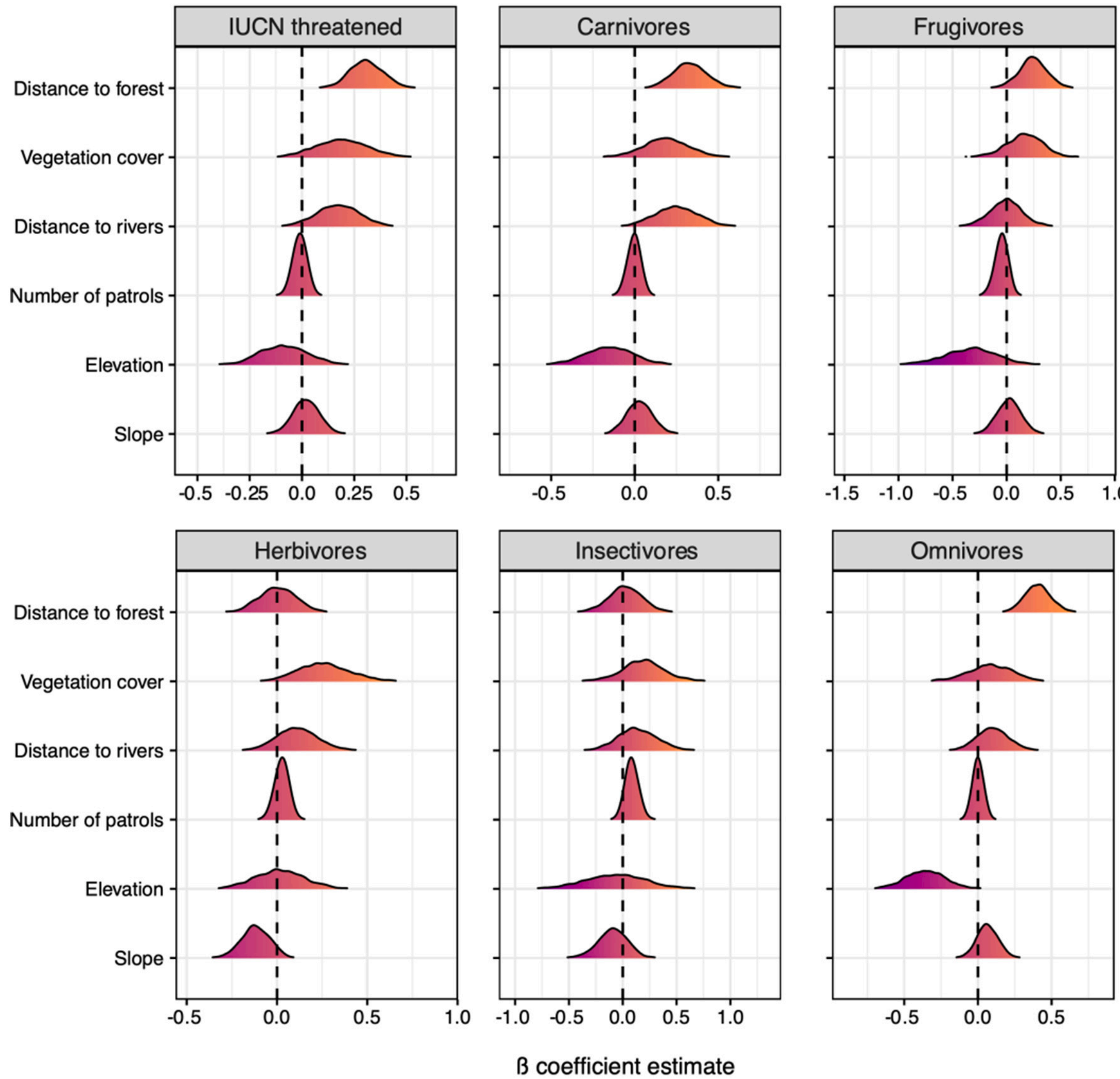

Fig. 4. Guild hyper-parameter estimate and probability of relationships between species' guild abundance and site covariates in the Kerinci Seblat landscape.

abundances for the Critically Endangered Sumatran tiger and its principal prey (wild boar) and several other important prey species (muntjac and pig-tailed macaque), further underlining the status of KSNP and surrounding forest as a global priority tiger conservation landscape (Sanderson et al., 2023).

We emphasize that both sun bear and sambar deer demonstrated higher abundances in areas routinely patrolled, remembering that both of these species could be considered targets owing to bear bile trade and bushmeat, respectively. Further, there is abundant evidence that wildlife may shift habitat use to avoid areas accessible by people and thus subject to increased hunting pressure (Benítez-López et al., 2017; Brodie et al., 2023; Deith and Brodie, 2020). We found that felids, and other carnivores, tended to be more abundant in interior forest habitat, while prey species favoured densely vegetated areas. These nuanced habitat preferences confound interpretation of the efficacy of ranger patrols insofar as these favoured habitats are less accessible to both poachers and rangers.

Identifying areas with higher species richness along habitat gradients can direct PA managers to shift the focus of their conservation interventions. Our model indicates that lowland areas that had intact forest and were further from villages had a higher species richness and greater variety of trophic guilds (i.e. Ipuh), highlighting the importance of such areas for retaining biodiversity in the landscape. More broadly, extrapolations beyond the study landscapes highlight the importance of five areas within KSNP (highest guild overlapped areas) and an area in the adjacent Batang Hari Protection Forest for supporting guild richness. Both these new guild analyses and a previous examination of felids and prey (Haidir et al., 2020a) emphasize the crucial role of lowland and hill forest areas inside KSNP (annotated #1 to #5 in Fig. 6), and Batang Hari Protection Forest (#6) as biodiversity strongholds (IUCN, 2004). Our study also found that peripheral and less intact forests, such as Muara Hemat, could support a relatively high number of mammal species (~10 at each camera trap location), if receiving sufficient protection.

Our study did not find that higher patrol intensities were associated with higher species abundance overall at the community level. Certain species groups did, however, apparently benefit from patrolling, with the abundance of prey species, herbivores and insectivores all positively associated with patrol intensity. We did not find an effect of patrolling overall, likely due to the fact that there is a latent process – the behaviour of hunters and the resulting spatial variation in hunting pressure – that remained unmodelled. This latent process has the potential to undermine any straightforward comparison of patrol intensity and wildlife abundance. For example, we suspect that in our landscape there are areas which are subject to very low hunting levels and that have relatively high wildlife abundance. Patrol teams may decide not to visit these areas and, because background hunting levels are not controlled

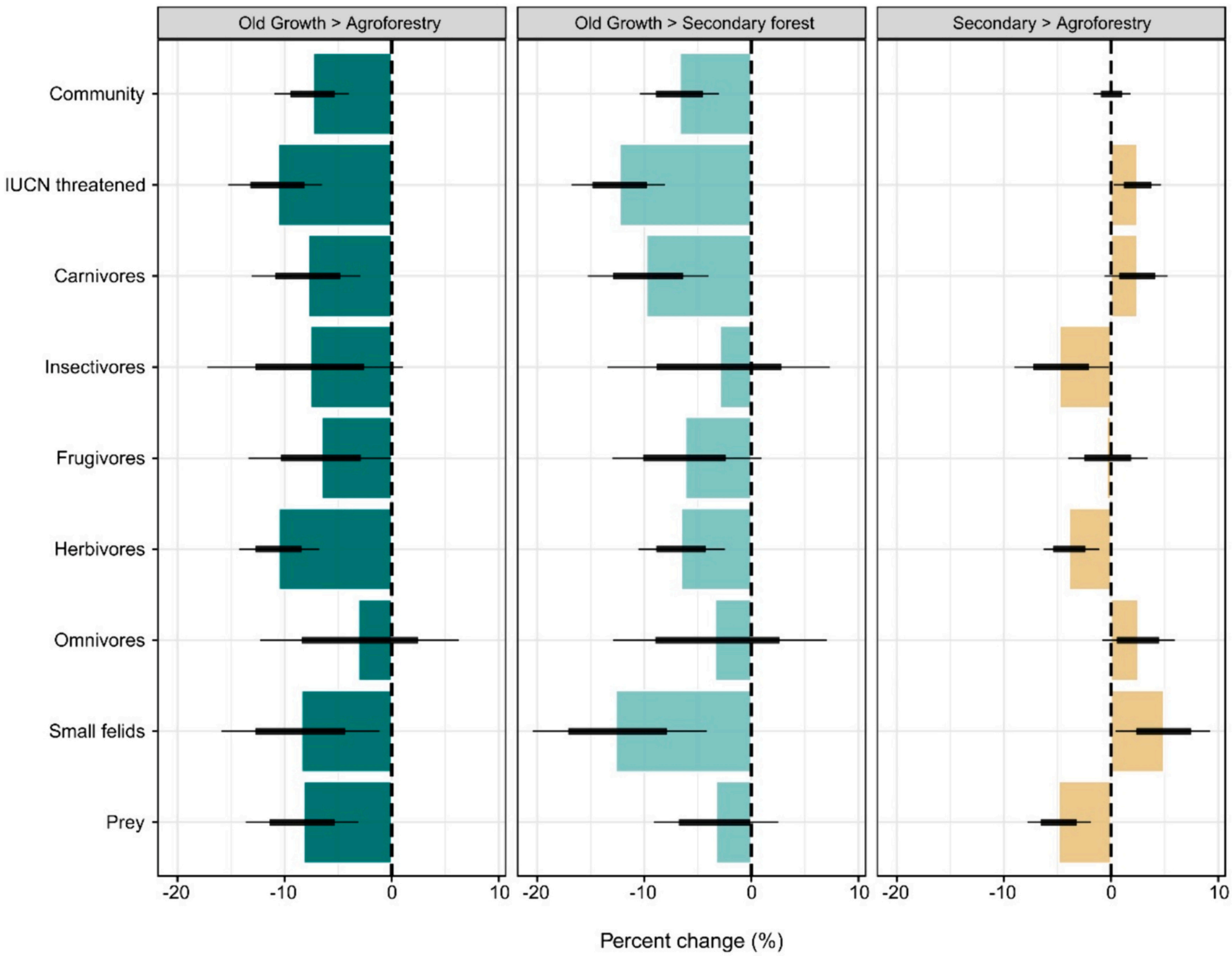

Fig. 5. Percent change in community- and guild-level mammal abundance relative to transitions in land-use. Population change was calculated by comparing the abundance of species clusters in habitat classes reflective of disturbance history, encompassing pristine (old growth forest), moderately perturbed (secondary forest) and heavily disturbed (agroforestry) land-use classes. Bars represent posterior means and uncertainty is denoted using both 75 % and 95 % Bayesian credible intervals (thick and thin horizontal lines respectively).

for, the model therefore perversely associates low patrol effort with high wildlife abundance. A dynamic approach to modelling, ideally incorporating a latent layer of poaching pressure, is likely better suited to uncovering the impact of patrolling (e.g. Moore et al., 2018) rather than the static approach we took.

Measuring population parameters at species, guild, and community levels provides more information to increase PA management effectiveness than other approaches based on species presence information, i.e. species distribution modelling. Raymond et al. (2020) used species distribution modelling and value of information analyses for both single and multiple species scenarios to identify optimal spatial resource allocations for guiding conservation interventions. Although our study was different to that of Raymond et al. (2020) in terms of species, method, area, and resources, we consider our approach for defining high-guild overlap and priority areas to be the best available for PA and wildlife managers in Sumatra, where resources and long-term robust data are scarce, as in other developing tropical countries (Natusch et al., 2019). This would be useful in designating areas of High Conservation Value, which are often hindered by gaps in knowledge on species richness (Senior et al., 2015).

Optimistically, multi-species and multi-taxa conservation interventions should be implemented in most Indonesian PAs, with more cost-efficient ways sought to enable this where available funding for wildlife population monitoring is limited (KKH, 2020). When efforts to improve PA management effectiveness are strategically permitted, this could create opportunities to obtain various technical and financial support from international networks. Geldmann et al. (2015) provided global analyses of changes in PA management effectiveness, where questions were set for global measures. Additionally, the Management Effectiveness Tracking Tool (METT) is being repeatedly applied at scale across Indonesia's PA network and through our approach we propose multi-species population monitoring to be included in one PA-specific question that should supplement the METT questions on resource inventory (Q9), research (Q10), and resource management (Q11).

Our study represents the first multi-guild analysis in Indonesia. Our methods and results can be used by both PA managers in the field and policy makers in the Indonesian MoEF to assess priority areas for further conservation interventions, as well as spatial planners to incorporate environmental concerns into infrastructure development outside of PAs (Setyawati et al., 2020). From a strategic conservation perspective, we appeal for PA managers in the tropics to maximize existing wildlife population monitoring efforts (and available datasets) through multi-species (guilds) analyses. We believe this is critical in guiding conservation efforts and applying spatial prioritization within landscapes to

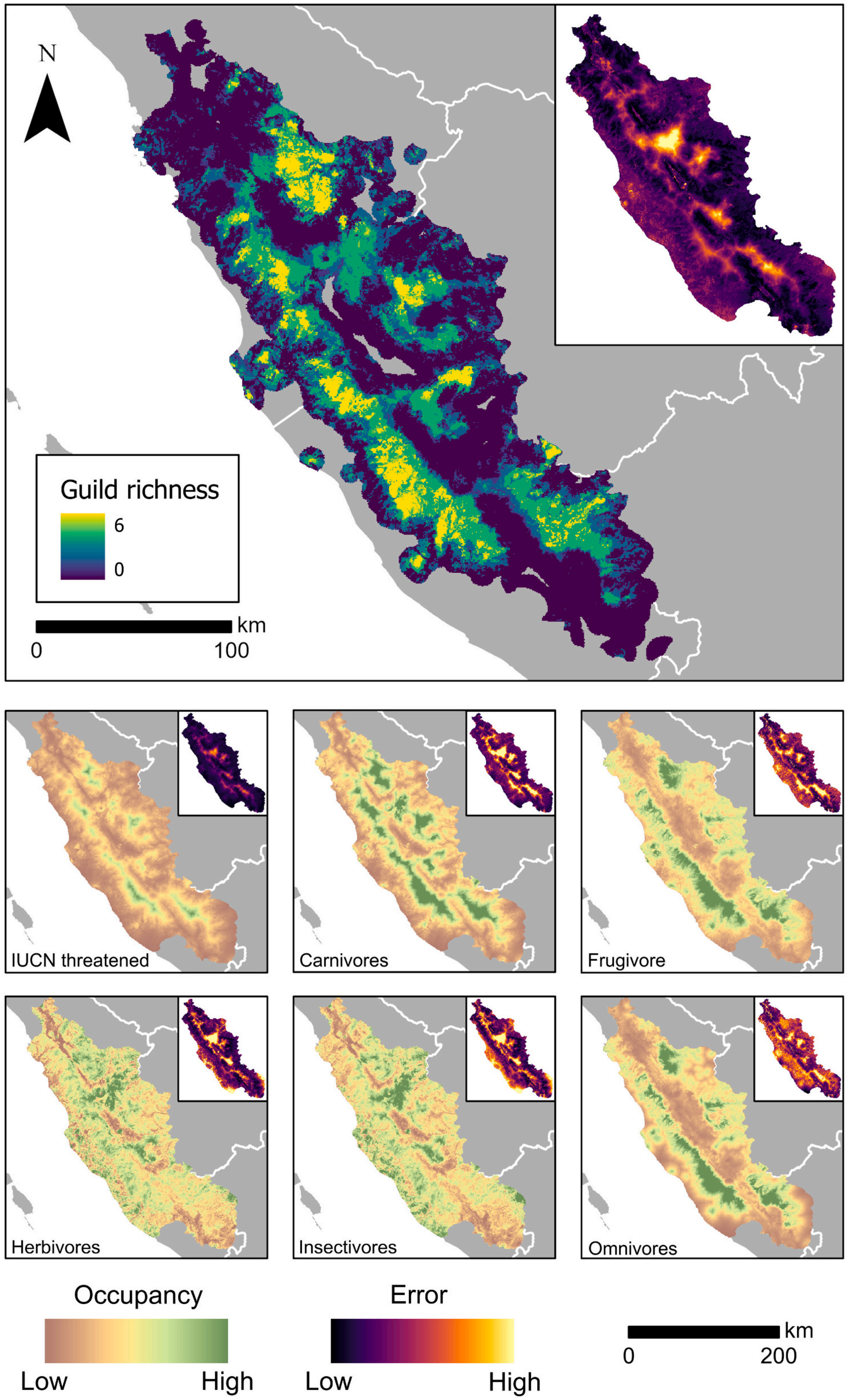

Fig. 6. Areas within the Kerinci Seblat landscape demonstrating the highest multi-guild overlap (main panel). We extrapolate spatial predictions to forested areas in the landscape plus a 5 km buffer to account for sampling beyond the forest extent. Predictions were derived from guild-specific occurrence maps based on associations with prominent environmental and anthropogenic covariates (lower panels). Probability of habitat use is expressed as the median value obtained from 3000 spatial predictions drawn from the posterior distribution. Throughout, insets denote spatial uncertainty, calculated as the standard deviation across all posterior predictions.

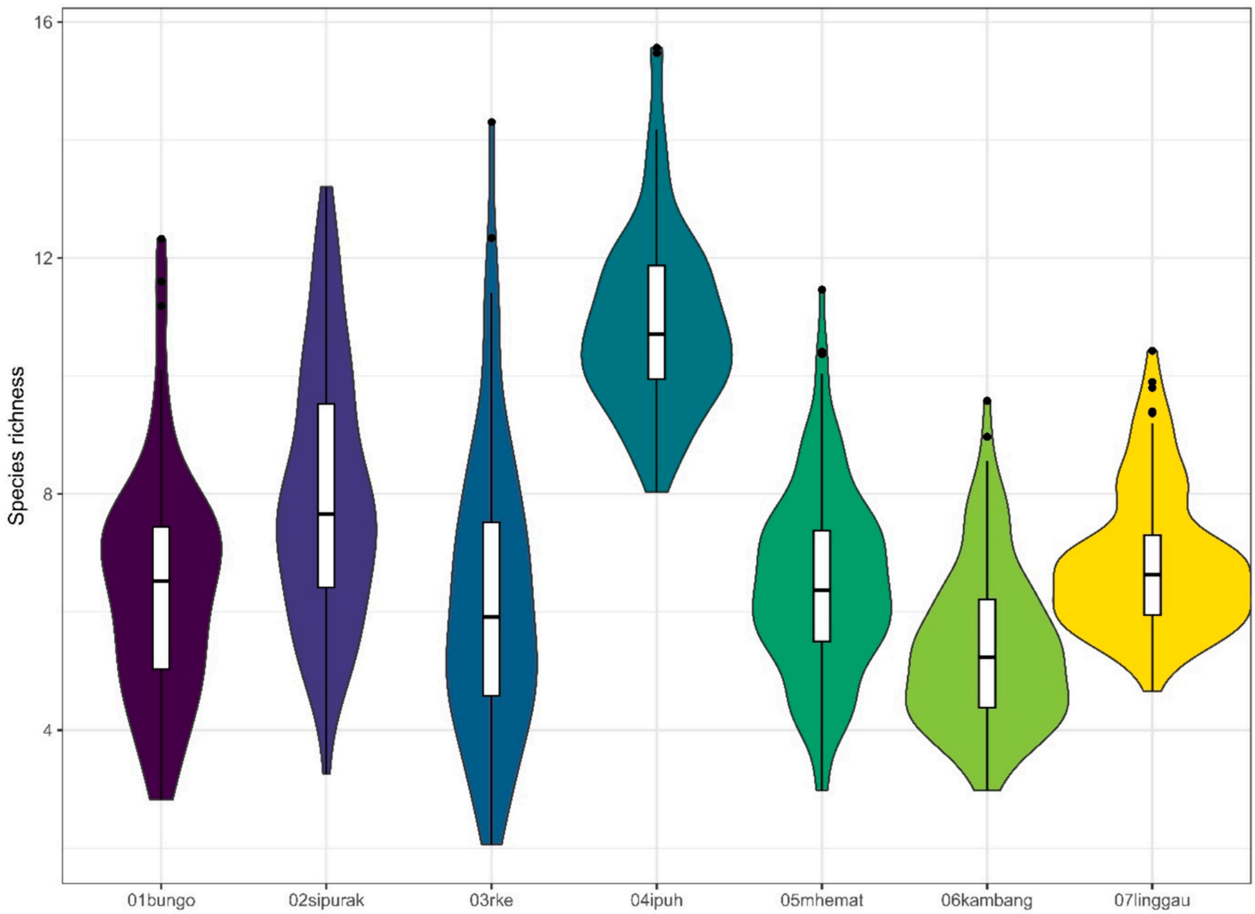

Fig. 7. Species richness across our seven study areas in the Kerinci Seblat landscape.

improve the effectiveness of PA management, research, resource inventory, and, more importantly, budget allocations.

CRediT authorship contribution statement

Iding A. Haidir: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Oliver R. Wearn:** Writing – review & editing, Supervision, Resources, Methodology. **Nicolas J. Deere:** Writing – review & editing, Visualization, Methodology. **Matthew J. Struebig:** Writing – review & editing, Supervision. **Alue Dohong:** Writing – review & editing, Project administration. **David W. Macdonald:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Matthew Linkie:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank Mr. Wiratno, former Director General of Natural Resources and Ecosystem Conservation of the Indonesian Ministry of Environment and Forestry, Mrs. Indra Exploitasia, Director of Biodiversity Conservation, and Mr. Tamen Sitorus, Head of Kerinci Seblat National Park for granting us permission to conduct this research and use of field facilities. We thank the World Animal Protection, Robertson Foundation, Rufford Foundation, and Dr. Holly Reed Conservation Fund for funding this project and Panthera for providing field equipment and camera trap units. NJD and MJS were funded by a Leverhulme Trust Research Leadership Award to contribute towards the analyses of the wildlife monitoring data. We thank Sabirudin, Kariyanto, Yosse Hendra, Ridwan, and Redhi for their assistance with field data collection and data processing.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110795.

References

Albert, C., Luque, G.M., Courchamp, F., 2018. The twenty most charismatic species. PloS One 13, e0199149.

Ardiantiono, Deere N.J., Ramadiyanta, E., Sibarani, M.C., Hadi, A.N., Andayani, N., Ginting, Y., Bull, J.W., Struebig, M.J., 2024. Selecting Umbrella Species as Mammal Biodiversity Indicators in Tropical Forest. Biol. Conserv. 292, 110511.

Atkinson, J., Brudvig, L.A., Mallen-Cooper, M., Nakagawa, S., Moles, A.T., Bonser, S.P., 2022. Terrestrial ecosystem restoration increases biodiversity and reduces its variability, but not to reference levels: A global meta-analysis. Ecology Letter July 25 (7), 1725–1737. https://doi.org/10.1111/ele.14025.

Balmford, A., Whitten, T., 2003. Who should pay for tropical conservation, and how could the costs be met? Oryx 37, 238–250.

Barlow, J., França, F., Gardner, T.A., Hicks, C.C., Lennox, G.D., Berenguer, E., Castello, L., Economo, E.P., Ferreira, J., Guénard, B., Gontijo Leal, C., 2018. The future of hyperdiverse tropical ecosystems. Nature 559, 517–526.

Benítez-López, A., Alkemade, R., Schipper, A.M., Ingram, D.J., Verweij, P.A., Eikelboom, J.A.J., Huijbregts, M.A.J., 2017. The impact of hunting on tropical mammal and bird populations. Science 356, 180–183. https://doi.org/10.1126/science.aaj1891.

Berry, N.J., Phillips, O.L., Lewis, S.L., Hill, J.K., Edwards, D.P., Tawatao, N.B., Ahmad, N., Magintan, D., Khen, C.V., Maryati, M., Ong, R.C., 2010. The high value of logged tropical forests: lessons from northern Borneo. Biodivers. Conserv. 19, 985–997.

Bhagabati, N.K., Ricketts, T., Sulistyawan, T.B., Conte, M., Ennaanay, D., Hadian, O., McKenzie, E., Olwero, N., Rosenthal, A., Tallis, H., Wolny, S., 2014. Ecosystem services reinforce Sumatran tiger conservation in land use plans. Biol. Conserv. 169, 147–156.

Bhatia, U., Dubey, S., Gouhier, T.C., Ganguly, A.R., 2023. Network-based restoration strategies maximize ecosystem recovery. Communications Biology 6, 1256. https://doi.org/10.1038/s42003-023-05622-3.

Bladon, A., Mohammed, E., Milner-Gulland, E., 2014. A Review of Conservation Trust Funds for Sustainable Marine Resources Management: Conditions for Success. www.iied.org/sites/default/files/pdfs/migrate/16574IIED.pdf.

Boyd, C., Brooks, T.M., Butchart, S.H., Edgar, G.J., Da Fonseca, G.A., Hawkins, F., Hoffmann, M., Sechrest, W., Stuart, S.N., Van Dijk, P.P., 2008. Spatial scale and the conservation of threatened species. Conserv. Lett. 1, 37–43.

Brodie, J.F., Mohd-Azlan, J., Chen, C., Wearn, O.R., Deith, M.C.M., Ball, J.G.C., Slade, E. M., Burslem, D.F.R.P., Teoh, S.W., Williams, P.J., Nguyen, A., Moore, J.H., Goetz, S. J., Burns, P., Jantz, P., Hakkenberg, C.R., Kaszta, Z.M., Cushman, S., Coomes, D., Helmy, O.E., Reynolds, G., Rodríguez, J.P., Jetz, W., Luskin, M.S., 2023. Landscape-scale benefits of protected areas for tropical biodiversity. Nature 620, 807–812. https://doi.org/10.1038/s41586-023-06410-z.

Chadès, I., McDonald-Madden, E., McCarthy, M.A., Wintle, B., Linkie, M., Possingham, H.P., 2008. When to stop managing or surveying cryptic threatened species. Proc. Natl. Acad. Sci. 105, 13936–13940.

Chiaverini, L., Macdonald, D.W., Bothwell, H.M., Hearn, A.J., Cheyne, S.M., Haidir, I., Hunter, L.T.B., Kaszta, Ż., Macdonald, E.A., Ross, J., Cushman, S.A., 2022. Multi-scale, multivariate community models improve designation of biodiversity hotspots in the Sunda Islands. Animal Conservation 25, 660–679.

Coad, L., Leverington, F., Knights, K., Geldmann, J., Eassom, A., Kapos, V., Kingston, N., de Lima, M., Zamora, C., Cuardros, I., Nolte, C., 2015. Measuring impact of protected area management interventions: current and future use of the Global Database of Protected Area Management Effectiveness. Philos. Trans. R. Soc., B 370, 20140281.

Dancer, A., Keane, A., Beale, C.M., Dobson, A.D., Amin, R., Freeman, R., Imong, I., Jones, K., Linkie, M., Long, B., Okeke, F.O., 2022. Evidence of deterrence from patrol data: Trialling application of a differenced-CPUE metric. Conservation Science and Practice 4, e12746.

Deere, N.J., Guillera-Arroita, G., Platts, P.J., Mitchell, S.L., Baking, E.L., Bernard, H., Haysom, J.K., Reynolds, G., Seaman, D.J., Davies, Z.G., Struebig, M.J., 2020. Implications of zero-deforestation commitments: Forest quality and hunting pressure limit mammal persistence in fragmented tropical landscapes. Conserv. Lett. 13, e12701.

Deith, M.C.M., Brodie, J.F., 2020. Predicting defaunation: accurately mapping bushmeat hunting pressure over large areas. Proc. R. Soc. B Biol. Sci. 287, 20192677. https://doi.org/10.1098/rspb.2019.2677.

Devarajan, K., Morelli, T.L., Tenan, S., 2020. Multi-species occupancy models: review, roadmap, and recommendations. Ecography 43, 1612–1624.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Ducarme, F., Luque, G., Courchamp, F., 2013. What are "charismatic species" for conservation biologists? BioSciences Master Reviews 1, 1–8.

Dunn, J.C., Buchanan, G.M., Stein, R.W., Whittingham, M.J., McGowan, P.J.K., 2016. Optimising different types of biodiversity coverage of protected areas with a case study using Himalayan Galliformes. Biol. Conserv. 196, 22–30.

Finke, D.L., Snyder, W.E., 2010. Conserving the benefits of predator biodiversity. Biol. Conserv. 143, 2260–2269.

Geldmann, J., Coad, L., Barnes, M., Craigie, I.D., Hockings, M., Knights, K., Leverington, F., Cuadros, I.C., Zamora, C., Woodley, S., Burgess, N.D., 2015. Changes in protected area management effectiveness over time: A global analysis. Biol. Conserv. 191, 692–699.

Guillera-Arroita, G., 2017. Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. Ecography 40, 281–295.

Gülgen, F., 2017. A stream ordering approach based on network analysis operations. Geocarto Int. 32, 322–333.

Haidir, I.A., Macdonald, D.W., Linkie, M., 2018. Assessing the spatiotemporal interactions of mesopredators in Sumatra's tropical rainforest. PloS One 13, e0202876.

Haidir, I.A., Kaszta, Ż., Sousa, L.L., Lubis, M.I., Macdonald, D.W., Linkie, M., 2020a. Felids, forest and farmland: identifying high priority conservation areas in Sumatra. Landsc. Ecol. 36, 475–495.

Haidir, I., Macdonald, D.W., Linkie, M., 2020b. Sunda clouded leopard *Neofelis diardi* densities and human activities in the humid evergreen rainforests of Sumatra. Oryx 55, 1–8.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., 2013. High-Resolution global maps of 21st-century forest cover change. Science 342, 850–853.

Hull, V., Xu, W., Liu, W., Zhou, S., Viña, A., Zhang, J., Tuanmu, M.N., Huang, J., Linderman, M., Chen, X., Huang, Y., 2011. Evaluating the efficacy of zoning designations for protected area management. Biol. Conserv. 144, 3028–3037.

IUCN, 2004. World Heritage Nomination - IUCN Technical Evaluation Tropical Rainforest Heritage of Sumatra (Indonesia) ID N°1167. IUCN.

Kéry M, JA Royle (2015) Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS*: Volume 1: Prelude and Static Models,* Academic Press.

Kéry M, Royle JA (2016) Applied hierarchical modeling in ecology. Volume 1, Prelude and static models: analysis of distribution, abundance and species richness in R and BUGS. Prelude and static models. Elsevier, Amsterdam.

Kiffner, C., Binzen, G., Cunningham, L., Jones, M., Spruiell, F., Kioko, J., 2020. Wildlife population trends as indicators of protected area effectiveness in northern Tanzania. Ecol. Indic. 110, 105903.

KKH, 2020. Anggaran Direktorat KKH. Ditjen KSDAE Kementerian Lingkungan Hidup dan Kehutanan, Directorate of Biodiversity Conservation, Jakarta.

Laurance, W.F., Clements, G.R., Sloan, S., O'Connell, C.S., Mueller, N.D., Goosem, M., Venter, O., Edwards, D.P., Phalan, B., Balmford, A., Van Der Ree, R., 2014. A global strategy for road building. Nature 513, 229–232.

Linkie, M., Haidir, I.A., Nugroho, A., Dinata, Y., 2008. Conserving tigers *Panthera tigris* in selectively logged Sumatran forests. Biol. Conserv. 141, 2410–2415.

Linkie, M., Guillera-Arroita, G., Smith, J., Ario, A., Bertagnolio, G., Cheong, F., Clements, G.R., Dinata, Y., Duangchantrasiri, S., Fredriksson, G., Gumal, M.T., 2013. Cryptic mammals caught on camera: assessing the utility of range wide camera trap data for conserving the endangered Asian tapir. Biol. Conserv. 162, 107–115.

Linkie, M., Martyr, D.J., Harihar, A., Risdianto, D., Nugraha, R.T., Leader-Williams, N., Wong, W.M., 2015. Safeguarding Sumatran tigers: evaluating effectiveness of law enforcement patrols and local informant networks. J. Appl. Ecol. 52, 851–860.

Linkie, M., Martyr, D., Harihar, A., Mardiah, S., Hodgetts, T., Risdianto, D., Subchaan, M., Macdonald, D., 2018. Asia's economic growth and its impact on Indonesia's tigers. Biol. Conserv. 219, 105–109.

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

Macdonald, D.W., Chiaverini, L., Bothwell, J.M., Kaszta, Z., Ash, E., Bolongon, G., Can, Ö.E., Campos-Arceiz, A., Channa, P., Clements, G.R., Hearn, A.J., Hedges, L., Htun, S., Kamler, J.F., Macdonald, E.A., Moore, J., Naing, H., Onuma, H., Rasphone, A., Rayan, D.M., Ross, J., Singh, P., Tan, C.K.W., Wadey, J., Yadav, B.P., Cushman, S.A., 2020. Predicting biodiversity richness in rapidly changing landscapes: climate, low human pressure or protection as salvation? Biodivers. Conserv. 29, 4035–4057.

Mackenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. 42, 1105–1114.

McCarthy, J.L., 2013. Conservation and ecology of four sympatric felid species in Bukit Barisan National Park. Indonesia University of Massachusetts, Sumatra.

Moore, J.F., Mulindahabi, F., Masozera, M.K., Nichols, J.D., Hines, J.E., Turikunkiko, E., Oli, M.K., 2018. Are ranger patrols effective in reducing poaching-related threats within protected areas? J. Appl. Ecol. 55, 99–107.

MoPWH, 2017. Peraturan Pemerintah No. 13 tahun 2017 tentang Perubahan atas Peraturan Pemerintah No. 26 tahun 2008 tentang Rencana Tata Ruang Wilayah Nasional (Jakarta).

Natusch, D.J.D., Lyons, J.A., Riyanto, A., Mumpuni, Khadiejah S., Shine, R., 2019. Detailed biological data are informative, but robust trends are needed for informing sustainability of wildlife harvesting: A case study of reptile offtake in Southeast Asia. Biol. Conserv. 233, 83–92.

Pacifici, K., Zipkin, E.F., Collazo, J.A., Irizarry, J.I., DeWan, A., 2014. Guidelines for a priori grouping of species in hierarchical community models. Ecol. Evol. 4, 877–888.

Rabus, B., Eineder, M., Roth, A., Bamler, R., 2003. The shuttle radar topography mission—a new class of digital elevation models acquired by spaceborne radar. ISPRS J. Photogramm. Remote Sens. 57, 241–262.

Rayan, D.M., Linkie, M., 2016. Managing conservation flagship species in competition: Tiger, leopard and dhole in Malaysia. Biol. Conserv. 204, 360–366.

Raymond, C.V., McCune, J.L., RosnerвЂђKatz, H., ChadГËs, I., Schuster, R., Gilbert, B., Bennett, J.R., 2020. Combining species distribution models and value of information analysis for spatial allocation of conservation resources. J. Appl. Ecol. 57, 819–830.

Risdianto, D., Martyr, D.J., Nugraha, R.T., Harihar, A., Wibisono, H.T., Haidir, I.A., Macdonald, D.W., D'Cruze, N., Linkie, M., 2016. Examining the shifting patterns of poaching from a long-term law enforcement intervention in Sumatra. Biol. Conserv. 204, 306–312.

Roberge, J.-M., Angelstam, P., 2004. Usefulness of the Umbrella Species Concept as a Conservation Tool. Conserv. Biol. 18, 76–85.

Royle, J.A., Dorazio, R.M., 2009. 3- Modeling occupancy and occurence probability. In: Royle, J.A., Dorazio, R.M (Eds.), Hierarchical Modeling and Inference in Ecology. Academic Press, San Diogo, pp. 83–125. https://doi.org/10.1016/B978-0-12-2374097-7.00005-3.

Royle, J.A., Nichols, J.D., 2003. Estimating Abundance from Repeated Presence-Absence Data or Point Counts. Ecology 84, 777–790.

RStudio (2015) RStudio Team. RStudio, Inc., Boston, MA.

Sanderson, E.W., Miquelle, D.G., Fisher, K., Harihar, A., Clark, C., Moy, J., Potapov, P., Robinson, N., Royte, L., Sampson, D., Sanderlin, J., Yackulic, C.B., Belecky, M., Breitenmoser, U., Breitenmoser-Würsten, C., Chanchani, P., Chapman, S., Deomurari, A., Duangchantrasiri, S., Facchini, E., Gray, T.N.E., Goodrich, J., Hunter, L., Linkie, M., Marthy, W., Rasphone, A., Roy, S., Sittibal, D., Tempa, T., Umponjan, M., Wood, K., 2023. Range-wide trends in tiger conservation landscapes, 2001–2020. Frontiers in Conservation Science 4.

Sauer, J.R., Blank, P.J., Zipkin, E.F., Fallon, J.E., Fallon, F.W., 2013. Using Multi-Species Occupancy Models in Structured Decision Making on Managed Lands. J. Wildl. Manag. 77, 117–127.

Senior, M.J., Brown, E., Villalpando, P., Hill, J.K., 2015. Increasing the scientific evidence base in the "high conservation value" (HCV) approach for biodiversity conservation in managed tropical landscapes. Conserv. Lett. 8, 361–367.

Setyawati, T., Nando, S., Marthy, W., Andayani, N., Linkie, M., 2020. Planning to remove UNESCO World Heritage Sites in Sumatra from being 'In Danger'. Animal Conservation 24, 149–152.

Tobler, M.W., Hartley, A.Z., Carrillo-Percastegui, S.E., Powell, G.V.N., 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. J. Appl. Ecol. 52, 413–421.

UNEP-WCMC, IUCN, 2016. Protected Planet Report 2016. UNEP-WCMC & IUCN Cambridge UK and Gland, Switzerland.

Waldron, A., Mooers, A.O., Miller, D.C., Nibbelink, N., Redding, D., Kuhn, T.S., Roberts, J.T., Gittleman, J.L., 2013. Targeting global conservation funding to limit immediate biodiversity declines. Proc. Natl. Acad. Sci. 110, 12144.

Wearn, O.R., Rowcliffe, J.M., Carbone, C., Pfeifer, M., Bernard, H., Ewers, R.M., 2017. Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. Biol. Conserv. 212, 162–171.

Wibisono, H.T, Linkie, M., Guillera-Arroita, G., Smith, J.A, Sunarto, Pusparini W., Asriadi, Baroto P., Brickle, N., Dinata, Y., Gemita, E., Gunaryadi, D., Haidir, I.A., Herwansyah, Karina I., Kiswayadi, D., Kristiantono, D., Kurniawan, H., Lahoz-Monfort, J.J., Leader-Williams, N., Maddox, T., Martyr, D.J., Maryati, Nugroho A., Parakkasi, K., Priatna, D., Ramadiyanta, E., Ramono, W.S., Reddy, G.V., Rood, E.J.J., Saputra, D.Y., Sarimudi, A., Salampessy, A., Septayuda, E., Suhartono, T., Sumantri, A., Susilo, Tanjung I., Tarmizi, Yulianto K., Yunus, M., Zulfahmi, 2011. Population Status of a Cryptic Top Predator: An Island-Wide Assessment of Tigers in Sumatran Rainforests. PloS One 6, e25931.

Williams, H., Bartholomew, D., Amakobe, B., Githiru, M., 2017. Environmental factors affecting the distribution of African elephants in the Kasigau wildlife corridor. SE Kenya. African Journal of Ecology 56. https://doi.org/10.1111/aje.12442.

Wong, W.-M., Leader-Williams, N., Linkie, M., 2013. Quantifying changes in sun bear distribution and their forest habitat in Sumatra. Anim. Conserv. 16, 216–223.

Zuur, A.F., 2012. A beginner's guide to generalized additive models with R. Highland Statistics Limited, Newburgh, pp. 1–206.