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Species characteristics modulate tropical mammal responses to forest quality in Southeast Asia

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ABSTRACT

Anthropogenic activities such as forest loss and degradation threaten many species-rich tropical forests. However, how species respond to forest quality and the role of species characteristics (i.e., body mass, carnivory, and habitat breadth) in mediating such responses remain poorly understood. We assessed how the occupancy of 61 mammal species in tropical forests of Southeast Asia responded to forest cover, canopy height, and disturbance history. We used data from 627 camera trap sites across 11 landscapes in Southeast Asia and applied a customized Bayesian multi-species occupancy modelling framework. Higher forest quality was positively related to the occupancy of 77 % mammal species while 5 % showed a negative relationship. Species with limited habitat breadths (habitat specialists) showed the strongest positive relationships, such as the dusky monkey (*Trachypithecus obscurus*). Similarly, large-bodied species like the Asian elephant (*Elephas maximus*) also exhibited strong positive relationships. Our study highlights the critical need to maintain and restore forests with dense canopies and with old and tall trees, especially for large-bodied and habitat-dependent species. Despite recent suggestions that Asian wildlife may not always be negatively influenced by forest degradation, our study underscores the dependency of most mammal species on relatively undisturbed interior forests for long-term conservation.

1. Introduction

Tropical forests harbour more than 63 % of the world's mammal species (Pillay et al., 2022a). Large-scale plantations, cattle ranching, timber cutting or the expansion of roads, have dramatically transformed tropical forests in recent decades (Engert et al., 2024; Hansen et al., 2013; Laurance, 2015; Potapov et al., 2022; Syaufina and Ainuddin, 2011). Such activities have led to forest loss, fragmentation, and degradation, ultimately reshaping the structure and composition of these forests (Smith et al., 2023). Forest quality – as opposed to just forest cover – encompasses a spectrum of attributes and dynamics, including canopy height, cover, and disturbance histories (Deere et al., 2020a; Hansen et al., 2019). Hence, using forest quality when assessing human impacts on biodiversity enables more nuanced inferences and the development of targeted conservation strategies (Hansen et al., 2019; Pillay et al., 2022b).

Mammals are crucial to tropical forest ecosystems. They are integral to the structure and functioning of forest food webs and are ecosystem engineers, playing pivotal roles through predation, facilitation of plant dispersal, and contribution to nutrient cycling (Lacher et al., 2019). Because of these critical roles, the preservation of their habitat and its quality is essential for their survival and ecological functions. Mammals occupying structurally intact forests are at a lower risk of extinction compared to mammals occupying forests with good cover only (Pillay et al., 2022b). Deere et al. (2020a) found that maintaining and enhancing forest quality is crucial for more than half of the mammals in Borneo as they responded positively to forest quality characteristics such as canopy height and cover. Forest quality can thus affect the

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distribution and occupancy of mammals. However, the strength of the effect varies between species (Pardini et al., 2005; Puttker et al., 2008) and can sometimes be explained by species characteristics (Culhane et al., 2022; Hannibal et al., 2020; Meijaard et al., 2007).

Mammal species characteristics, such as body mass, dietary habits, and habitat breadth/specialization, can inform about community assemblages and species interactions with their environment (Nock et al., 2016; Semper-Pascual et al., 2022; Semper-Pascual et al., 2023). For instance, large-bodied mammals are more susceptible to hunting due to their size, which makes them more visible and valuable targets (Gallego-Zamorano et al., 2020). Larger mammals also often prefer relatively undisturbed forest areas over degraded ones to meet their higher overall energy demands and to find refuge from hunting pressures (Núñez-Regueiro et al., 2015; Regolin et al., 2017). Carnivorous species often rely on high quality habitats that offer structural features like woody debris for camouflage and hunting, along with sufficient prey availability and low human presence, making them particularly sensitive to habitat degradation (Duckworth et al., 2016; Jennings and Veron, 2011; Mathai et al., 2017; Phumanee et al., 2021; Salom-Perez et al., 2021; Sunarto et al., 2012). Furthermore, habitat specialists, due to their dependence on specific and very narrow ecological conditions, are generally more vulnerable to changes in forest attributes compared to generalists (Hannibal et al., 2019; Semper-Pascual et al., 2023). For example, Semper-Pascual et al. (2023) demonstrated that habitat generalist and specialist mammals across the tropics showed variable responses to forest cover. Hannibal et al. (2020) showed that different responses to forest quality among small mammals in a fragmented landscape in Brazil were explained by habitat specialization and feeding guild. Therefore, studies including species characteristics when assessing mammal responses to forest quality can help to better understand how species groups respond differently to changes in forest quality and can serve as a foundation for designing conservation efforts for species sharing similar characteristics (Rovero et al., 2019).

Tropical forests of Southeast Asia sustain rich and unique biota (Sodhi et al., 2004) but land-use change poses a considerable threat, especially to mammals (Duckworth et al., 2012; Gaveau et al., 2022; Sodhi et al., 2009). Land-use changes are often associated with forest degradation, not only forest loss, and understanding how forest degradation impacts mammal occupancy is therefore critical for effective conservation. Yet the extent to which tropical mammals in Southeast Asia respond to variation in canopy height, cover, and disturbance histories (hereafter forest quality) remains poorly understood.

Recent work has suggested that some species in Asian rainforests, mostly habitat generalists, are indifferent or exhibit positive responses to forest degradation (Amir et al., 2022; Dehaudt et al., 2022; Luskin et al., 2023; Moore et al., 2023). However, these studies focused on a subset of species and their results may therefore obscure true community-wide trends. Further, they did not assess species-specific characteristics underpinning variable responses to degradation limiting our inferences about the connections between species ecology and conservation threats. Therefore, we aimed to determine how forest quality affects the entire communities of Southeast Asian mammals consisting of species with an average adult body mass greater than 1 kg, and the role of species characteristics in modulating the responses.

Here, we developed and applied a customized Bayesian occupancy modelling approach with camera trap data from 11 tropical landscapes in Southeast Asia to assess 1) how forest quality relates to the occupancy of 61 mammal species, and 2) how mammal species characteristics (body mass, carnivory and habitat breadth) influence species responses to forest quality. Contrary to recent studies, and consistent with global trends (Dirzo et al., 2014), we expected mammal occupancy to be positively associated with forest quality in general, albeit with variation among species in the direction and magnitude of this association (Zungu et al., 2020). Specifically, we hypothesized that large-bodied mammals will exhibit a stronger positive association with forest quality because they are more susceptible to hunting, and higher-quality forests provide better refuge from humans than degraded ones (Gallego-Zamorano et al., 2020; Harrison et al., 2016; Núñez-Regueiro et al., 2015; Peres, 2002). We further predicted that carnivores would exhibit a stronger positive association with forest quality because natural covers such as fallen logs, bushes, dense understory and canopy cover in higher quality forest provide better camouflage during predation (Phumanee et al., 2021; Sunarto et al., 2012) and predators are more acutely threatened by people (Krofel et al., 2015; Ripple et al., 2014). Finally, we predicted species having lower habitat breadth living in forest to be positively associated with forest quality, as they may have a reduced ability to adapt to or exploit a variable or changing landscape due to their strong reliance of forest habitats (Semper-Pascual et al., 2023).

2. Methods

2.1. Study area and camera trap data

We used wildlife photos collected with camera traps between November 2009 and January 2022 at 11 landscapes in Southeast Asia (Fig. 1 and Supplementary Information S1). In Sumatra we surveyed three landscapes including Bukit Barisan Selatan National Park (129 camera trap sites), Gunung Leuser National Park (56) and Kerinci Seblat National Park (52). In Borneo we surveyed Lambir Hills National Park (14) and Danum Valley Conservation Area (25). In continental Southeast Asia, we surveyed Nam Kading National Protected Area (60), Khao Ban That Wildlife Sanctuary (20), Ulu Muda Forest Reserve (132), Pasoh Forest Reserve and adjacent forest (112), and in Singapore the Central Catchment Nature and Palau Ubin (27) were treated as a single landscape (Lamperty et al., 2023). In total, we sampled 627 camera trap sites, however, not all sites were sampled every year, meaning that the number of sites per landscape may vary between years (Supplementary Information S2).

Our camera trap data were collected as part of two projects: the Tropical Ecology Assessment and Monitoring (TEAM) Network (232 camera trap sites) (Rovero and Ahumada, 2017) and the Ecological Cascades Lab (NECL, 395 camera trap sites) (Amir et al., 2022). Following the TEAM protocol, cameras were active for ~30 days annually. NECL cameras were active for 60–90 days annually. However, in both datasets, a small number of cameras were operational for fewer days due to damage or failure (Supplementary Information S3). On average, cameras used in this study (i.e., combination of both datasets) were active for 39.34 days (min = 7, max = 231) and the total sampling effort was 59,409 trap-days. In both datasets, 20–30 cameras were deployed across 2–3 arrays sequentially in multiple sampling bouts. On average, cameras were separated by 1013.33 m (SD = 819.20 m). In cases where more than one camera trap was placed at the same location and during the same year, we retained only data from the camera with the longest duration of operation. All cameras were affixed to trees at a height of 20–50 cm above the ground along natural trails without baits (Amir et al., 2022; Rovero and Ahumada, 2017). We restricted our analysis to wild mammal species with an average adult body mass > 1 kg, as camera traps tend to be less effective in capturing smaller mammal species (Dundas et al., 2019; Jumeau et al., 2017).

2.2. Spatial covariates

We used Elevation (meters) and Slope (degrees) as detection covariates, extracted at the camera trap site from the 30 m resolution raster SRTM DEMs (Farr et al., 2007). We included elevation and slope as covariates on detection probability because both are known to influence camera trap performance and animal space use. Steeper slopes reduce detectability of animals that prefer gentler slopes and flatter terrain and can obstruct camera views (Moll et al., 2020; Sultaire et al., 2022). Elevation affects vegetation density through microclimatic changes, influencing detection rates (Sultaire et al., 2022; Theobald et al., 2015). While other factors may also play a role, we selected these covariates for

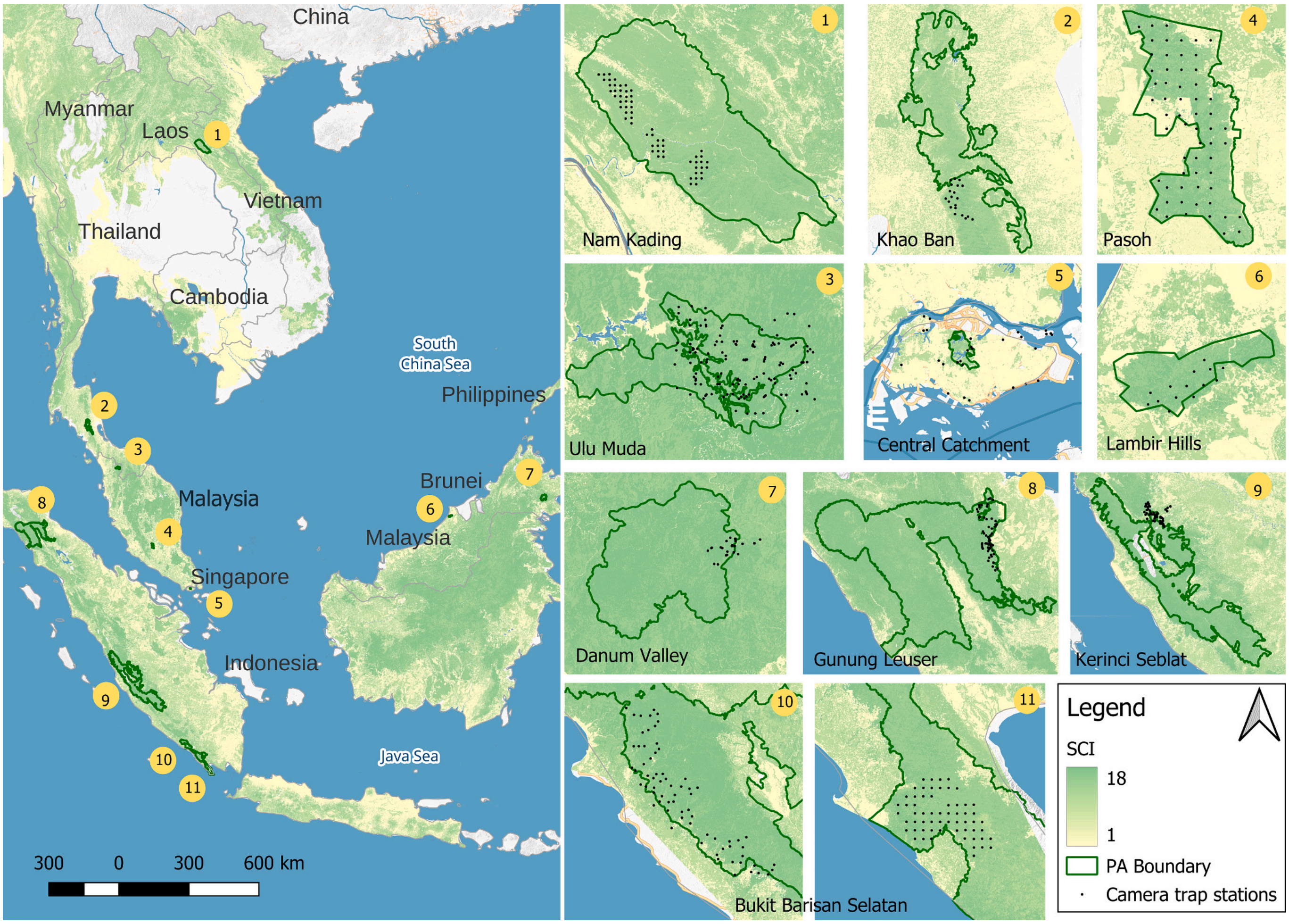

Fig. 1. Distribution of the 11 landscapes in southeast Asia (left map). The panels on the right show the study landscapes, including the location of the camera trap sites (black dots). The basemap used is the Forest Structural Conditional Index (SCI) raster (Hansen et al., 2019) (see Spatial covariates section).

their influence revealed in previous studies (Moll et al., 2020; Sultaire et al., 2022; Theobald et al., 2015). We used forest quality as the only covariate on occupancy. We derived forest quality from the Forest Structural Conditional Index (SCI, Fig. 1) maps (Hansen et al., 2019). The SCI integrates Information on tree cover, canopy height and time since last major disturbance, and ranges from 1 (short, open canopy forest with recent disturbance history) to 18 (tall, old, and closed canopy forest). We reclassified the SCI raster map into "high quality" and "low quality" pixels using a cut-off value of 14. Thus, pixels with values higher or equal to 14 were classified as "high quality" forest and pixels with values lower than 14 as "low quality" forests. We used 14 as a cut-off value following Pillay et al. (2022b) and because it represented the median value (Supplementary Information S4). This threshold defines high quality forests as forests with canopy cover >75 %, forest height > 15 m, and where the 30 m pixel area has had no stand-replacement disturbance or complete canopy removal since 2000 (Hansen et al., 2019). Then we calculated the proportion of "high quality" pixels within a circular buffer around each camera trap site. We selected three different buffer sizes based on the home range sizes of the species detected (300 m, 900 m, and 3000 m radius) and we assigned each species to one buffer size depending on its home range size (see Supplementary Information S5 and S6).

2.3. Species covariates

We used average adult body mass, habitat breadth (as a proxy of habitat specialization), and carnivory as species characteristics. We used data on body mass (average adult body mass) and carnivory (proportion of vertebrates in the diet of each species) from Faurby et al. (2018). We used habitat breadth (number of IUCN habitats listed as suitable) data from Cooke et al. (2019). All species covariates were log-transformed, to address the skewedness of the distributions and to provide a more linear relationship with the response variable (the forest quality parameter). Species covariates were standardised to improve the interpretability and comparability of the estimates (Schielzeth, 2010).

2.4. Multi-species occupancy model

We used a multi-species occupancy model (Dorazio and Royle, 2005) to answer our first research question, i.e., how each species' occupancy responds to forest quality (Dorazio and Royle, 2005). Occupancy models are hierarchical models estimating the probability of a predetermined area (e.g., a grid cell or habitat patch, hereafter "site") being occupied by a species, while accounting for imperfect detection. Occupancy and detection probabilities are modelled jointly, and their respective submodels can accommodate explanatory variables. Estimating detection probability requires detection/non-detection data from repeated surveys/visits (hereafter referred to as 'occasions'). Therefore, a sampling site is surveyed on multiple occasions within a defined study period, during which the site is assumed to be closed to changes in occupancy, meaning no site-level species extinction or colonization (MacKenzie et al., 2002). We defined a detection as at least one photographic capture of a species at one camera trap during a sampling occasion, and a sampling occasion as one camera trap week. We discarded occasions with incomplete weeks (e.g., from Monday to Wednesday) to avoid bias caused by different sampling effort. We obtained data from a maximum of 33 sampling occasions (range: 1–33; mean: 5.62, Supplementary Information S2 and S3) at a camera trap site during any given survey period. We consider the closure assumption to be met during this period.

Multi-species occupancy models expand the single-species approach by utilizing the detections of multiple species within a community to estimate both species-specific and community-level parameters. Thus, species-specific parameters can be treated as random effects which are drawn from community-level hyper-parameters (Dorazio and Royle, 2005). Here, we used the model described in Semper-Pascual et al. (2022) which incorporates data from multiple areas and years (survey periods).

We organized the detection/non-detection data in a 6-dimensional array with the following dimensions: site (i) × occasion (j) × year (t) × species (k) × area (a) × landmass (l). Landmasses included Borneo, Sumatra, and continental Asia (see Fig. 1 and Supplementary Information S1). Our hierarchical model had two sub-models. The first sub-model is an ecological process model which estimates the latent occupancy state, i.e., the true occurrence (z) and which is the outcome of a Bernoulli process:

$$z_{i,t,k,a,l} \sim Bernoulli\left(\Psi_{i,t,k,a,l}\right) \tag{1}$$

where Ψ represents the occupancy probability.

The second sub-model is an observation process model which estimates the observed (apparent) occupancy state (y) as a Bernoulli process of the product of the true occurrence and detection probability (p):

$$y_{i,j,t,k,a,l} \sim Bernoulli\left(z_{i,t,k,a,l} \times p_{i,t,k,a,l}\right) \tag{2}$$

We modelled detection probability as a linear function of *Slope* and *Elevation* which we calculated for each camera trap site:

$$logit\left(p_{i,t,k,a,l}\right) = \alpha p_k + \beta p_1 \times Slope_{i,a,l} + \beta p_2 \times Elevation_{i,a,l} \tag{3}$$

where αp_k represents the species-specific intercept and βp_1 and βp_2 the species-specific coefficients.

In the linear regression of the submodel for occupancy, we included *ForestQuality*:

$$logit\left(\Psi_{i,t,k,a,l}\right) = \alpha\Psi_k + \beta\Psi_{ForestQuality_k} \times ForestQuality_{i,a,l} \tag{4}$$

where $\alpha\Psi_k$ represents the species-specific intercept and $\beta\Psi$ the species-specific coefficient.

Species-specific intercepts, both for occupancy and detection, are random effects drawn from a normal distribution with a common mean μ and variance σ^2:

$$\alpha\Psi_k \sim\sim Normal\left(\mu_\Psi, \sigma_\Psi^2\right) \tag{5}$$

$$\alpha p_k \sim Normal\left(\mu_p, \sigma_p^2\right) \tag{6}$$

To answer our second research question, i.e., how species characteristics influence species responses to forest quality, we extended the hierarchical model described above with an additional regression. The response variable was the species-specific posteriors of the coefficient of our occupancy model (i.e., $\beta\Psi_{ForestQualityk}$), and the predictors the species characteristics, i.e., body mass (*Mass*), carnivory (*Carn*) and habitat breadth (*HabBreadth*):

$$\beta\Psi_{ForestQuality_k} = \alpha + \beta_{Mass} \times Mass_k + \beta_{Carn} \times Carn_k + \beta_{HabBreadth} \times HabBreadth_k \tag{7}$$

Model code is provided in Supplementary Information S7. The diagrammatic representation of this model is given in Fig. 2. Note that all parameters, including $\beta\Psi_{ForestQualityk}$ and the species trait-specific coefficients, were estimated jointly as all three regressions (occupancy, detection, and forest quality effect) were integrated into the same Bayesian model. This approach also ensured that uncertainty in any of the sub-models and constituent regressions was propagated to the uncertainty around the final parameter estimates.

2.5. Model fitting

We fitted the models using Markov chain Monte Carlo (MCMC) methods using R package nimble (version 1.0.0) in R (de Valpine et al., 2017). For each model, we used uninformative or weakly informative priors for all parameters (see model code in Supplementary Information S7) and 160,000 MCMC iterations of 4 model chains. We estimated parameters after discarding the first 20,000 iterations as burn-in and thinning by 10. We evaluated MCMC convergence and mixing using trace plots and the Gelman–Rubin statistic for each parameter, where values <1.1 indicated convergence (Gelman et al., 2013). We used the mean of the posterior distribution and the associated 95 % Bayesian credible intervals (95 % BCI) of each coefficient to assess the effect of the corresponding covariate on detection and occupancy probability, as well as the effect of species characteristics on the occupancy coefficients.

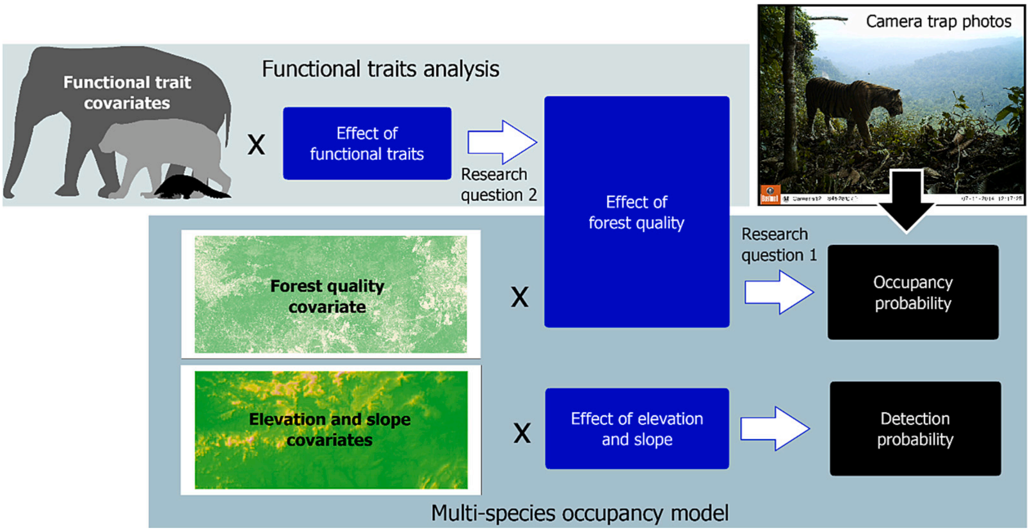

Fig. 2. Schematic diagram representing covariates, their sources, and the flow of statistical analyses targeting the research questions. Species silhouettes credit: Phylopic (*Manis culionensis* and *Helarctos malayanus* under Universal Public Domain Dedication license; *Elephas maximus* by T. Michael Keesey).

3. Results

We detected 61 mammal species >1 kg with the total number of species per landscape ranging from 8 (Singapore) to 32 (Bukit Barisan Selatan) and a median of 24 species per landscape. Body mass ranged from 1.4 kg (Palawan stink badger; *Mydaus marchei*) to 3160 kg (Asian elephant; *Elephas maximus*). The species habitat breadth ranged from 1 (Sumatran Mountain muntjac; *Muntiacus montanus* and Thick-spined porcupine; *Hystrix crassispinis*) to 25 (wild boar; *Sus scrofa*). Southern pig-tailed macaque (*Macaca nemestrina)* and wild boar collectively accounted for almost half of all weekly detections, contributing 23.92 % and 20.76 %, respectively (Supplementary Information S8 and S9).

Detection probability was negatively associated with elevation (β = −0.045, 95 % BCI: −0.07 to −0.015) and positively associated with slope (β = 0.08, 95 % BCI = 0.06 to 0.11).

3.1. Forest quality and mammal occupancy relationship

Forty-seven (77 %) of the 61 species, exhibited a significant positive relationship between occupancy and forest quality, with β values ranging from 0.1 (*n* = 28 weekly detections, 95 % BCI: 0.004–0.193) for the Palawan stink badger, to 0.91 (n = 2, 95 % BCI: 0.72–1.09) for the Sumatran muntjac (Figs. 3 and S8).

Other species with a strong positive relationship between occupancy and forest quality include the dusky monkey (*Trachypithecus obscurus*) (*n* = 14, β = 0.84, 95 % BCI = 0.67–1.01), the thick-spined porcupine (*n* = 121, β = 0.82, 95 % BCI = 0.66–0.99), the banteng (*Bos javanicus*) (n = 1, β = 0.78, 95 % BCI = 0.59–0.98), and the long-tailed porcupine (*Trichys fasciculata*) (*n* = 62, β = 0.74, 95 % BCI = 0.58–0.90). Only three species (5 %) showed a significant negative relationship between occupancy and forest quality, including the Asian small-clawed otter (*Aonyx cinereus*) (n = 1, β = −0.34, 95 % BCI = −0.48 to −0.19), Eurasian otter (*Lutra lutra*) (n = 1, β = −0.13, 95 % BCI = −0.24 to −0.02), and wild boar (*n* = 2755, β = −0.11, 95 % BCI = −0.22 to −0.01) (Figs. 3 and S8).

Eleven species (18%) showed no effect of forest quality on occupancy, such as the large Indian civet (*Viverra zibetha*), dhole (Cuon alpinus), yellow-throated marten (*Martes flavigula*), and leopard (*Panthera pardus*) (Fig. 3 and S8).

3.2. Effect of species characteristics on the occupancy-forest quality relationship

Habitat breadth had a significant negative relationship with the occupancy-forest quality association (β = −0.26, 95 % BCI = −0.33 to −0.20) indicating that specialists respond more positively to forest quality (Fig. 4). Body mass had a significant positive effect on the occupancy-forest quality relationship (β = 0.12, 95 % BCI = 0.06 to 0.17), indicating that large mammals respond more positively and strongly to forest quality (Fig. 4). The effect of carnivory on the occupancy-forest quality relationship was not significant (β = −0.02, 95 % BCI = −0.07 to 0.04) (Fig. 4).

4. Discussion

Our study revealed that the occupancy of tropical Southeast Asian mammals is positively associated with denser, taller and old forests. Only three species, the Asian small-clawed otter, Eurasian otter and wild boar, preferred a less intact forest structure. We found that habitat specialists and large-bodied species are particularly dependent on high-quality forests, likely due to their large home range requirements, greater susceptibility to hunting, and reliance on specific habitat features. These findings support the idea that species traits such as body mass and habitat specialization mediate species' responses to habitat change and provide strong evidence that forest degradation, which is rampant throughout Southeast Asia and elsewhere (Grantham et al., 2020; Venter et al., 2016), has a negative impact on mammal communities across the Asian tropics.

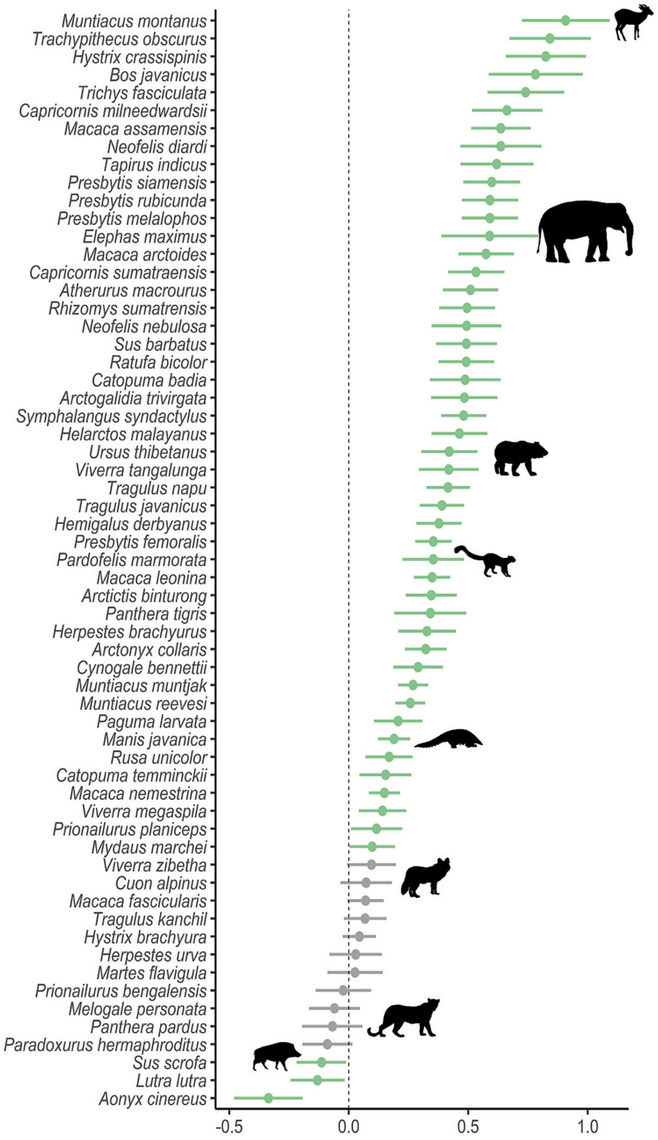

Fig. 3. Effect of forest quality on the occupancy of 61 Southeast Asian tropical mammal species. Shown are the mean standardised β coefficients (points) and associated 95 % BCI (horizontal bars). Estimates were considered significant (green color) when the 95 % BCI did not overlap zero (vertical dotted line). Species silhouettes credit: Phylopic (*Sus scrofa*, *Manis culionensis*, *Panthera pardus*, *Helarctos malayanus*, *Elephas maximus*, and *Ursus thibetanus* under Universal Public Domain Dedication license; *Cuon alpinus* by Renata F. Martins), *Muntiacus* sp. and *Pardofelis marmorata* by Andrea F. Vallejo-Vargas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.1. Understanding forest quality impacts on mammals

Our results showed that occupancy of most mammal species was positively related to forest quality in tropical forests of Southeast Asia. Habitat quality has also been identified as an important predictor of mammal occupancy in tropical forests of Brazil (Cerqueira et al., 2016; Regolin et al., 2021; Zimbres et al., 2018). This is reasonable as forests with high structural complexity – an attribute associated with high quality forests (Cerqueira et al., 2016; Franklin and Van Pelt, 2004) – provide a higher variety of food resources, refuge from predators and hunters, and protect mammals from high tropical temperatures (Deere

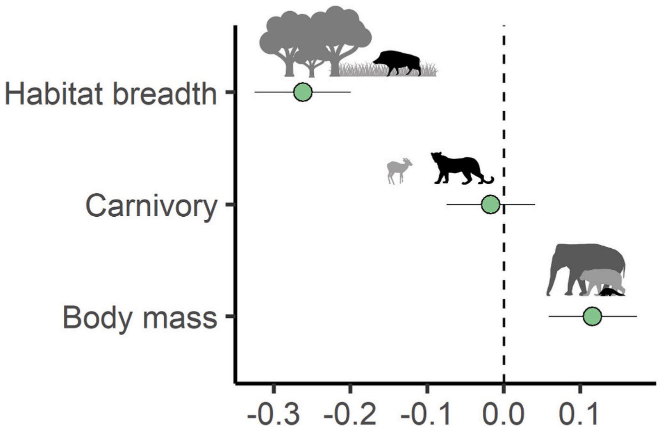

Fig. 4. Effect of species characteristics on the forest quality-occupancy relationship. The plot includes the mean standardised β coefficients (points) and 95 % BCI (horizontal bars). The estimates were considered significant when the 95 % BCI did not overlap zero (vertical dotted line). Species silhouettes credit: Phylopic (*Sus scrofa*, *Manis culionensis*, *Panthera pardus*, and *Helarctos malayanus* under Universal Public Domain Dedication license; *Elephas maximus* by T. Michael Keesey); *Muntiacus* sp. by Andrea F. Vallejo-Vargas.

et al., 2020b; Price et al., 2010). However, the level of dependence on such resources may differ among the species (Price et al., 2010). This is evidenced by our findings, as some species responded more strongly than others to forest quality.

4.2. *Species characteristics mediate mammalian responses*

We found that differences in species responses to forest quality can be explained by species characteristics such as habitat breadth and body size. Habitat specialists such as the Sumatran mountain-muntjac, the dusky monkey, and the thick-spined porcupine were found to be more positively associated with forest quality than generalists. On the other hand, habitat generalists viz. the Asian small-clawed otter, Eurasian otter, and wild boar were negatively associated with the forest quality. Similar results were reported from several tropical forests, where habitat specialists were more positively associated with sites characterized by high forest cover and quality than habitat generalists (Hannibal et al., 2020; Semper-Pascual et al., 2023). Using simulations, Ramiadantsoa et al. (2018) also demonstrated that specialists can be expected to thrive well in high-quality habitats as they provide stable and resource-rich environments favouring specialized adaptations and ecological requirements of specialists.

Regarding body mass, larger species like the banteng, the Malay tapir (*Tapirus indicus*), or the Asian elephant, showed stronger positive associations with forest quality than smaller species. Similar results were also observed by Salom-Perez et al. (2021) and can be explained by the fact that large mammals are highly susceptible to hunting (Gallego-Zamorano et al., 2020; Jerozolimski and Peres, 2003), and high-quality forests are often more remote and provide better refuge from hunters than low-quality forests (Deere et al., 2020b; Núñez-Regueiro et al., 2015; Peres, 2002; Price et al., 2010).

While our study provides insights into how tropical mammal occupancy responds to forest quality, some limitations should be considered. First, our camera trap design, though effective for terrestrial mammals, may underrepresent riparian or semi-aquatic species like otters, which rely on waterways. Since our cameras were not specifically placed along riparian corridors, the observed negative association for otters with forest quality may reflect a methodological bias rather than an ecological signal. Second, we used the Structural Condition Index (SCI) to represent forest quality, which is based on data centered on 2013 (Hansen et al., 2019), whereas our camera trap data span from 2009 to 2022. This temporal mismatch could affect how well SCI reflects forest conditions during the entire sampling period. However, many of our study sites are protected areas that have experienced relatively limited change in forest cover during the study period. Although changes in forest quality cannot be ruled out entirely, especially from selective logging or understory disturbance, we believe the SCI still offers a reliable proxy for large-scale habitat structure across sites. Future studies could benefit from integrating dynamic forest data to better align habitat metrics with long-term ecological monitoring data.

4.3. *Conclusions and conservation implications*

Our study provides persuasive evidence that forest quality influences mammal occupancy in Southeast Asia, with most species exhibiting a strong positive response to forest quality. Although recent studies have suggested that some Asian wildlife might not be negatively affected by forest degradation (Amir et al., 2022; Dehaudt et al., 2022; Luskin et al., 2023; Moore et al., 2023), our findings align with global patterns observed in other tropical forests, where large-bodied and habitat-specialist mammals are disproportionately affected by anthropogenic threats including forest loss and degradation (Gallego-Zamorano et al., 2020; Semper-Pascual et al., 2023). This consistency across diverse tropical regions underscores the broad applicability of our results and highlights the universal challenges faced by many large and habitat specialist species.

As tropical deforestation and degradation continue worldwide, conserving forest quality, not just forest extent, is critical for maintaining mammalian biodiversity and ecological function. Thus, our study strengthens the growing recognition that conservation policies must prioritize structural and functional integrity of forests as a key element of biodiversity protection. (Amir et al., 2022; Arroyo-Rodriguez et al., 2020). Our work has two main implications for the conservation of tropical mammals in Southeast Asia and other deforestation hotspots. First, conservation strategies must prioritize the preservation of high-quality forests, characterized by older trees, taller canopies, and denser coverage. This includes not only protecting existing forest interiors but also actively restoring degraded areas to enhance structural complexity. Nevertheless, we caution against disregarding the conservation value of more degraded forests. In fact, some species may persist in such landscapes (Amir et al., 2022), and these forests may eventually attain the ecological value of primary forests through natural regeneration or assisted restoration (Romanelli et al., 2025). In addition, even degraded forests can serve as critical corridors, facilitating species movement across fragmented landscapes (Arroyo-Rodriguez et al., 2020). Second, integrating trait-based approaches into conservation planning is crucial. By linking mammalian occupancy patterns to measurable forest quality attributes and species traits, our study provides a practical framework that can be used to guide both research and management efforts aimed at mitigating biodiversity loss in tropical forest landscapes. Our framework therefore enables the effective identification of at-risk species, thereby allowing conservation efforts to be directed towards the most vulnerable species' groups.

CRediT authorship contribution statement

Pradeep Raj Joshi: Conceptualization, Writing – original draft, Formal analysis, Methodology. **Asunción Semper-Pascual:** Writing – review & editing, Methodology, Conceptualization, Validation, Supervision, Formal analysis. **Andrea F. Vallejo-Vargas:** Writing – review & editing, Conceptualization. **Douglas Sheil:** Data curation, Writing – review & editing, Funding acquisition. **Matthew S. Luskin:** Writing – review & editing, Data curation, Funding acquisition. **Jonathan Moore:** Writing – review & editing, Data curation. **Richard Bischof:** Project administration, Funding acquisition, Supervision, Conceptualization, Writing – review & editing, Methodology, Formal analysis.

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Declaration of competing interest

All the authors declare to have no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111388.

Data availability

Data and script used to run the multi-species occupancy model in NIMBLE have been archived in Zenodo at doi: https://doi.org/10.5281/zenodo.15576904.

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