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Species-specific effect of forest cover on the occupancy of tropical forest mammals of Southeast Asia

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Abstract

Tropical forests harbour more than half of the world's biodiversity and 63% of the world's terrestrial mammals. Today this biodiversity is under threat due to habitat loss and degradation by human activities. This makes tropical mammals vulnerable as mammals are very sensitive to changes in their habitat. In this regard, protected areas are critical for the conservation of tropical biodiversity including mammals because they are the core refuge and the best remaining habitats for many threatened mammals. Protected areas, however, are not unaffected by human activities and the forest cover within them is not uniform. How does forest cover relate to the occupancy of mammals in tropical protected areas? Do these relationships vary among species and/or groups of species? In this study, I analysed mammal occurrence and forest cover relations in tropical protected areas of Southeast Asia, and how these responses are modulated by species-specific functional traits.

I used systematic camera trap data of 2013/2014 from the TEAM (Tropical Ecology Assessment and Monitoring) Network. I analysed a total of 45,182 photographs of 37 mammal species captured through 4,178 trap days. First, I fitted single-season single-species occupancy models to assess the relationship between occupancy and forest cover. Second, I used the parameter estimates for forest cover and species' functional traits to understand how the occupancy-forest cover relations are governed by the species' functional traits.

The occupancy analysis resulted in 12 species whose results can be interpreted. I found a positive association between forest cover and occupancy. Although insignificant, there were variations in these associations across species and species groups and were defined by forest specialisation and the feeding guild of the species. Forest specialists and carnivores/omnivores had stronger and more positive associations than non-specialists and herbivores/insectivores. Because these forests are tropical protected areas, the lack of pronounced and clear effects suggests that there may not be enough variation in forest cover to observe differences in response. Furthermore, efforts to conserve biodiversity in these areas may still be effective. Using multiple years' data and following alternate statistical approaches of occupancy modelling and parameter estimation is recommended for future studies, to overcome the issues with sparse data.

***Keywords**: camera-traps, forest cover, functional trait, occupancy model, mammals, protected area, southeast Asia, tropical forest*

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1. Introduction

1.1 Background

Tropical forests are some of the richest biodiverse regions on Earth.(Muhammad Nawaz, 2018; Sodhi et al., 2004). Higher temperature (Brown, 2014), availability of diverse habitat and food resources, and safe sites to shelter and breed are considered important in supporting this high biodiversity (Muhammad Nawaz, 2018). All these factors have contributed to higher speciation rates (Rolland et al., 2014) making the tropical forests home to more than 50% of the planet's biodiversity (Lewis et al., 2015; Primack & Morrison, 2013) and almost two-thirds of the land species (Stork et al., 2009). A study by Pillay et al. (2022) found that a striking 63% of the global terrestrial mammal species live in these forests.

However, the tropical forests and their biodiversity are facing a severe threat from human activities (Morris, 2010) such as selective logging, commercial agriculture, cattle farming, palm-oil plantation, road expansion and increasing biofuel demand (Laurance, 2015). More than half of the tropical forest area is already lost (Wright, 2005), or degraded (Deere et al., 2020; Muhammad Nawaz, 2018). PAs (protected areas) are considered the most important tool in the conservation of biodiversity and habitat (Coetzee et al., 2014; Díaz et al., 2019; MacKinnon et al., 1986; Rodrigues et al., 2004). During the 2000s, the PA network across the tropics prevented 83,500 km^2 from being deforested (Kim & Anand, 2021). These PAs are core refuges or even the only suitable habitats for many threatened mammal species (Pacifici et al., 2020; Scullion et al., 2021). Additionally, since tropical forests harbour almost two-thirds of the terrestrial mammals (Pillay et al., 2022), protected areas of the tropics globally are critical for mammal conservation.

Unfortunately, most of the protected areas do not remain untouched or unaffected by human activities despite their protected status (Buckley et al., 2016; Palomo et al., 2014), leaving a mere few entirely pristine (Buckley et al., 2016). In fact, PAs including those in the tropical areas are facing the problem of deforestation and degradation due to human activities (Leisher et al., 2013; Zeng et al., 2005). Even the disturbance caused by low-intensity use over much longer times can significantly change their ecosystem (Josefsson et al., 2009). This results in a change in the quality of forests inside them. Further, climatic, geographical, and edaphic factors are also responsible for the variation in the quality of forests in the tropics (Corlett, 2014; Feeley et al., 2011; Wang, 2006). The variation in forest quality affects the occurrence and distribution of mammals (August, 1983; Haro-Carrión et al., 2021; Pardini et al., 2005; Püttker et al., 2008) at varying levels (Feng et al., 2021; Zungu et al., 2020). Forest quality is “the significance and value of all ecological, social and economic components of the forest landscape” (Dudley et al., 2012). Forest cover and canopy height are among the most important indicators of forest quality and are related to biodiversity (Dudley et al., 2012; Foley et al., 2005; Moiseev et al., 2002; Moles et al., 2009).

It is important to assess how the occupancy of tropical forest mammals is affected by forest quality as the tropical forests’ quality is changing at an increased rate (Feeley et al., 2011; Phillips, 1996; Wright, 2005). Occupancy is defined as “the proportion of an area occupied by a species or fraction of landscape units where the species is present” (MacKenzie et al., 2006). It is considered as an alternative and cost-effective method of studying the abundance of a species because intraspecific abundance and occupancy are positively related (Gaston et al., 2000; He et al., 2002). Occupancy models integrate the environmental factors as covariates (MacKenzie & Bailey, 2004) to assess how these factors affect the presence of species.

Most mammals are sensitive to habitat quality change because of their specialised niches (Crooks et al., 2011; Rocha et al., 2018), yet species may respond differently to changes in habitat quality. Intrinsic characteristics of mammals also known as the functional traits, such as body size, habitat specialization or feeding guild influence how they respond to changes in their environment (Nock et al., 2016). Functional traits are “morphological, biochemical, physiological, structural, phenological or behavioural characteristics of organisms that influence performance or fitness” (Nock et al., 2016). Trait characteristics and trait-based assemblages are considered more informative than the individual or species level characteristics (Pollard & Yuan, 2010). Studies based on the functional trait approach give information on how organisms interact with their environment and how communities assemble, interact and function (McGill et al., 2006; Nock et al., 2016). This is especially useful to describe the response of the animal community to environmental changes (Nock et al., 2016). For instance, large mammals are particularly vulnerable to threats from the change in habitat quality due to higher resource and energy demand, low population densities, and their susceptibility to hunting by humans (Cardillo et al., 2005). Forest specialists are found to be associated with high forest cover while generalists with low forest cover (Salom-Pérez et al., 2021), Similarly, carnivore species richness is found positively related to forest cover (Regolin et al., 2017). Such relations determine their sensitivity towards changes in habitat. The nature of functional traits can be different like categorical (e.g. feeding guild, habitat specialisation), continuous (body mass), count (niche breadth), ordinal or binary (Nock et al., 2016).

An assessment like I have done in this research is important because of the representation of the tropical forests which harbour major mammalian biodiversity. Further, findings of such a study inside a protected area network can be used as a baseline for other similar studies. Moreover, as the protected areas are considered as the safest and most suitable habitats, these types of studies can reveal whether the biodiversity is witnessing the "trouble in paradise" by reflecting on the state of wildlife there.

1.2 Hypotheses

In this study, I have assessed the species-specific effect of forest quality on mammals in tropical forests on two approaches: occupancy analysis and functional trait analysis. The occupancy analysis focuses on the response of mammals towards forest quality, while the functional trait analysis focuses on what species characteristics are associated with those responses. In particular, I tried to find answers to 1) How are occupancy of mammal species related to forest quality, here represented by forest cover, and 2) Are there any differences in these relationships among the species groups due to their functional traits?

To address these questions, I have tested the following hypotheses, with associated predictions:

H1: The occupancy of most of the mammal species is positively related to forest cover

- P1: The occupancy of mammals living in tropical forests is in general positively related to forest cover. However, there is between-species variation in the direction and magnitude of the effect of forest cover, as species react differently to forest cover.

H2: Relationships between occupancy and forest cover are determined by functional traits

- P1: Occupancy of forest-specialist species is more strongly and positively related to forest cover than that of the non-forest-specialists (Salom-Pérez et al., 2021).
- P2: Occupancy of carnivores and omnivores is positively associated with higher forest cover because of more prey availability and help in camouflage during predation (Lesmeister et al., 2015; Salom-Pérez et al., 2021).
- P3: Occupancy of the species with larger body mass is more associated with forest cover. Larger mammals are more prone to hunting (Gallego-Zamorano et al., 2020) and a large area of forest with high cover provides a refuge from hunting as well as from predation (Núñez-Regueiro et al., 2015; Peres, 2001).

P4: Species with higher habitat breadth will be less associated with forest cover. Species with higher habitat breadth tend to be more generalists, and thus are not confined only to the forests.

2. Methodology

2.1 Study area

The study was conducted in three tropical protected areas of Southeast Asia (Fig: 1). Bukit Barisan Selatan (BBS) National Park of Indonesia has an area of 3568 km^2 (Government of the Republic of Indonesia, 2004) and is the third-largest protected area of Sumatra (O'Brien & Kinnaird, 1996). It lies in the elevation range of 0-1964m asl (Pusparini et al., 2018). It supports diverse habitats for wildlife due to its large elevation range (Pusparini et al., 2018) and is a UNESCO world heritage site (Weiskopf et al., 2019). Nam Kading (NAK) National Protected Area lies in central Laos (Hallam & Hedemark, 2012). It is about 1685 km^2 in area and stretches from 160 m to 1600 m altitude, most of which is rugged and inaccessible (Chanthavong et al., 2021). Four rivers including the Nam Kading River, a major tributary of the Mekong River, pass through the protected area (Hallam & Hedemark, 2012), providing habitat to many flora and fauna (Chanthavong et al., 2021). Pasoh Forest Reserve (PSH) lies 140 km southeast of Kuala Lumpur, Malaysia (Fletcher et al., 2012; Peters, 2001). It has an area of 139 km^2 and has a maximum altitude of 600 m and has oil palm plantations on three sides (Fletcher et al., 2012).

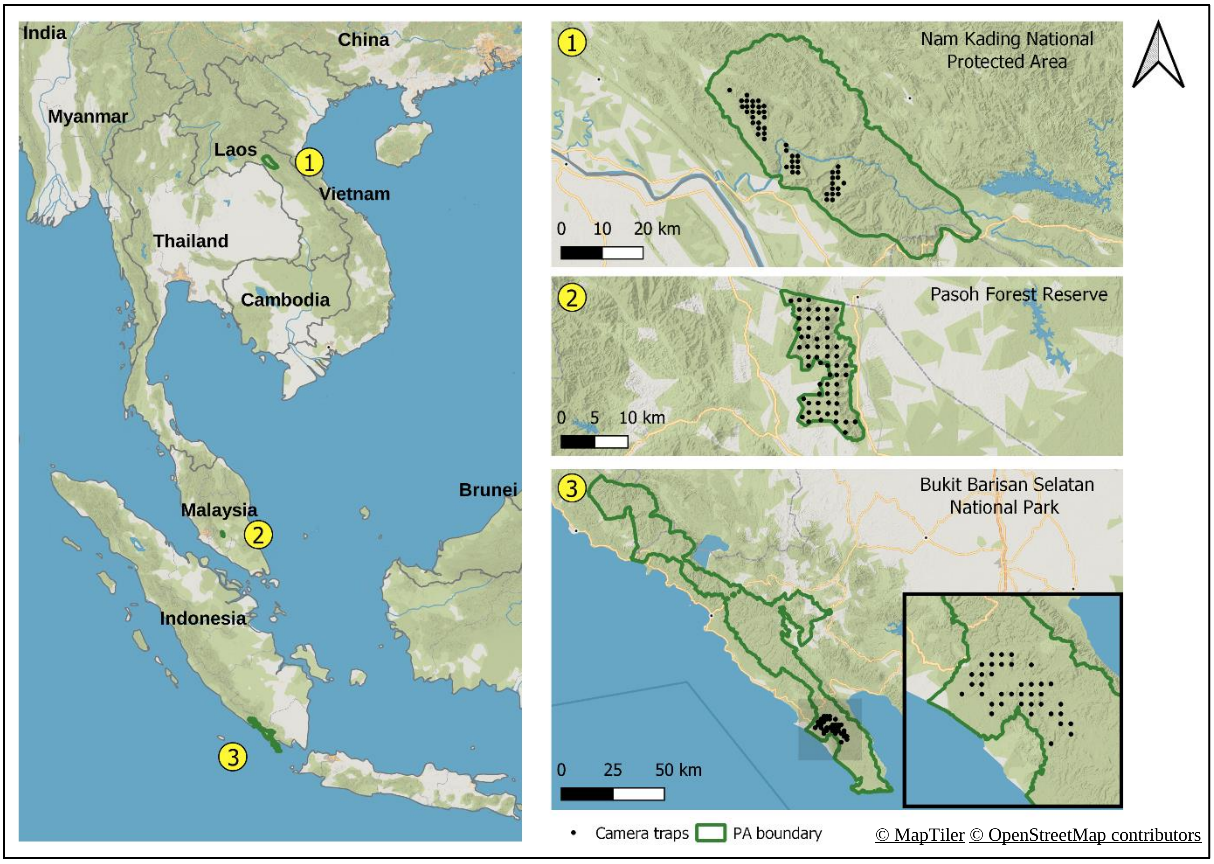

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Fig 1: Map showing the locations of the three protected areas (dark green boundary) and camera trap deployment design (shown as black dots in the maps of the right column)

2.2 Data and sampling design

The data used in this study was obtained from the Tropical Ecology Assessment and Monitoring (TEAM) Network. The TEAM Network is a partnership between Conservation International, the Smithsonian, and the Wildlife Conservation Society, and uses standardised methods for monitoring terrestrial mammals and birds in 17 tropical protected areas across Africa, Asia, and Latin America (Beaudrot et al., 2016) including the protected areas included in this study. Camera traps deployment followed the standardised protocol developed by the TEAM network. Camera traps were placed at 38, 49 and 58 points in BBS, NAK and PSH respectively, each within a grid of 1.4 km inter-spacing. The deployment was divided into two or three sampling arrays with 20 -30 camera points each to allow sequential sampling (TEAM Network, 2011). At each point, a camera trap was deployed for at least 30 days (Jansen et al., 2014; TEAM Network, 2011). The camera traps were installed close to wildlife trails at 30-50 cm above and parallel to the ground (Rovero & Ahumada, 2017; TEAM Network, 2011). Photo management including tagging and species identification was done by site technicians of the TEAM (TEAM Network, 2011). Information including species ID (order, family, genus, species), coordinates, sampling unit, sampling period, date and time information, serial number and model of camera used, etc., was then exported to a standardised format ready to be analysed (TEAM Network, 2011).

I used camera trap data from a single sampling season during 2013/2014 (table 1). I excluded the images of humans and dogs during data analysis. Further, I only included species with an average body mass of more than 1 kg in the analysis because camera traps are less efficient in capturing small mammals as compared to medium and large-sized ones (Dundas et al., 2019).

Table 1: Camera trapping dates, number of days and number of trap points

Site	Start date	End date	No. of trap locations	Average no of days
BBS	2014-04-04	2014-07-21	38	24.63
NAK	2013-11-07	2014-02-28	49	32.22
PSH	2013-05-29	2014-02-12	58	28.67

2.3 Occupancy analysis

I followed the single-season single-species model, also called the static model approach for occupancy modelling using package “unmarked” (Fiske & Chandler, 2011) in R (R Core Team, 2021) through R Studio (RStudio Team, 2012). Unmarked follows hierarchical occupancy modelling given in MacKenzie et al. (2002) and takes into account the imperfect detections that occur when the species is present but is not detected, and estimates the probability of occurrence of that species at that site. Thus, it includes both: i) state process – which deals with the species occurrence, and ii) observation process – which deals with the species detection (Kéry & Royle, 2016). The state process is the true occupancy status or the presence/absence status of the species at a site (1,0; if site is occupied or not, respectively). It is represented as a latent variable z_i, and is expressed as:

$$z_i \sim Bernoulli(\psi_i)$$

Where, ψ_i is the expected probability of occurrence or the occupancy probability at site *i*. The observation process is expressed as:

$$y_{ij}|z_i \sim Bernoulli(z_i * p_{ij})$$

where y_{ij} is the observed occurrence at site *i* during survey *j*, and p_{ij} is the detection probability of the species at site *i* during survey *j*. The term $y_{ij}|z_i$ indicates that y_{ij} depends on the conditions of z_i (Kéry & Royle, 2016).

I initially selected forest cover and canopy height as site covariates and as measures of forest quality. I later excluded canopy height from the covariates because it was highly correlated with forest cover ($r \geq 0.7$). I retained forest cover because it is more important to the occurrence of species (Regolin et al., 2017) than canopy height (Roll et al., 2015). Additionally, I used elevation and protected area (PA) as site covariates affecting occupancy and, slope and the camera trap model as covariates affecting detection. The covariates are included in the model through a logit-link function at PA *i* as:

$$logit(\psi_i) = \beta_0 + \beta_1 * Forest\ cover_i + \beta_2 * Elevation_i + \beta_3 * PA_i$$

$$logit(p_i) = \alpha_0 + \alpha_1 * Slope_i + \alpha_2 * Camera\ model_i$$

2.4 Covariates

Forest cover in 2013 was calculated using the global forest cover change dataset mapped by Hansen et al. (2013), defining forest pixels as those with tree canopy cover > 75% (Beaudrot et al., 2016). I used the Digital Elevation Model (DEM) from the Shuttle Radar Topography Mission (SRTM) (Farr et al., 2007) version 3 at 1 arc-second (approx. 30m) as the elevation data. I downloaded this elevation dataset from the United States Geological Survey's

Earthexplorer website provided by NASA’s Jet Propulsion Laboratory (NASA JPL, 2013). I used mean values for forest cover and elevation for all species at their respective home range sizes. For this, I calculated a radius size for a circular buffer from the home range information, rounded it to the nearest hundreds and used this buffer size to extract the means for the covariates around all camera trap points for all species. I used home range information from multiple sources as listed in annex 2. I included elevation as a site covariate because it is an important parameter influencing the abundance and distribution of species (Bateman et al., 2010; Campera et al., 2020; Feng et al., 2021; Ramírez-Bautista & Williams, 2019). I included ‘PA’ as a site covariate to capture the variance otherwise not captured by the other three covariates, that could arise due to the differences in PA characteristics such as disturbance, latitude, management practices of the PAs, water availability, etc. I calculated the slope at the original 30m resolution from the same SRTM DEM used for elevation. Camera model information was available in the exported camera trap database (table 2).

Table 2: Covariates used in occupancy analysis

Covariate	**Notation used**	**Category**	**Description**
Forest cover	Forest_Cover	Site covariate	The proportion of forest cover
Elevation	Elevation	Site covariate	Meters above sea level
Protected area	PA	Site covariate	The three protected areas used in this study (i.e., BBS, NAK, PSH)
Slope	Slope	Observation covariate	Slope in degrees at camera trap points
Camera model	Cam_model	Observation covariate	Different camera trap models used at the three sites: PC900 Professional, RM45 Rapidfire and HC500 Hyperfire

I standardised the continuous covariates before inclusion in the models. Standardising covariates helps in model convergence, prevents numerical problems, and enables comparison of the estimates (Kéry & Royle, 2016; Schielzeth, 2010). Since some of the species were present at a single PA or some of the PAs used only one camera model, I included covariate *PA* only when species were present at more than one PA. Similarly, I included the covariate *Camera model* only when more than one camera model was used in the PA where the species was present (Table 3). I included forest cover in every model as this was the covariate of interest. After model fitting and running occupancy analysis for a species, I chose the model that has the lowest Akaike Information Criterion (AIC) (Akaike, 1998) value as the best-fitted occupancy model. Finally, among the best fit models, only the models with no convergence issue or Hessian singular error were included in the analysis.

Table 3: Candidate models for the occupancy analysis. p() represents observation covariates and ψ() represents site covariates. Models with PA and Cam_model were only included for species that were found at more than one PA and/or more than one camera trap model

SN	Candidate models
1	p(.)ψ(Forest_Cover)
2	p(.)ψ(Forest_Cover + PA)
3	p(.)ψ(Forest_Cover + Elevation)
4	p(.)ψ(Forest_Cover + Elevation + PA)
5	p(Slope)ψ(Forest_Cover)
6	p(Slope)ψ(Forest_Cover + PA)
7	p(Slope)ψ(Forest_Cover + Elevation)
8	p(Slope)ψ(Forest_Cover + Elevation + PA)
9	p(Cam_model)ψ(Forest_Cover)
10	p(Cam_model)ψ(Forest_Cover + PA)
11	p(Cam_model)ψ(Forest_Cover + Elevation)
12	p(Cam_model)ψ(Forest_Cover + Elevation + PA)
13	p(Cam_model + Slope)ψ(Forest_Cover)
14	p(Cam_model + Slope)ψ(Forest_Cover + PA)
15	p(Cam_model + Slope)ψ(Forest_Cover + Elevation)
16	p(Cam_model + Slope)ψ(Forest_Cover + Elevation + PA)

2.5 Functional trait analysis

I used species body mass, feeding guild, habitat breadth and information on whether the species is a forest specialist or not, in the functional trait analysis (Table 4). I used body mass and feeding guild information from Faurby et al. (2018) and habitat breadth information from Cooke et al. (2019). To determine whether a species is a forest specialist or not, I used the information from the 'Habitat and Ecology in detail' section of the IUCN red list for each species (www.iucnredlist.org). I categorised a species as a forest specialist when only the forest habitat types were listed as suitable for that species. To match the hypothesis, I combined carnivores and omnivores into one group and herbivores and insectivores into another.

Table 4: Functional traits used and their properties

Functional trait	**Type**	**Values/Range**	**Description**
Forest specialisation	Categorical	Specialist Non-specialist	Whether a species is a forest specialist or not
Feeding guild	Categorical	Carnivore Omnivore Insectivore Herbivore	Group of species feeding on similar resources
Habitat breadth	Count	1 - 25	Different IUCN habitat types the species occupies
Body mass	Continuous	1842.5 gm – 3160000 gm	The average adult body mass of a species

To assess how the relationship between occupancy and forest cover is associated with species' functional traits, I extracted the estimated values (β) of the forest cover covariate from the best-fitted occupancy models and fitted linear models with individual functional traits as the predictor variables (fig 2). The uncertainty of estimation for forest cover was accounted for by weighting the linear models as $\omega = \frac{1}{SE\ (\beta\_forest\ cover)}$, where SE is the standard error of the estimate. I fitted a model for each functional trait as:

$$\beta_{Forest\ cover} = \alpha + \beta_1 * Forest\ specialisation$$

$$\beta_{Forest\ cover} = \alpha + \beta_2 * Feeding\ guild$$

$$\beta_{Forest\ cover} = \alpha + \beta_3 * Habitat\ breadth$$

$$\beta_{Forest\ cover} = \alpha + \beta_4 * \log Body\ mass$$

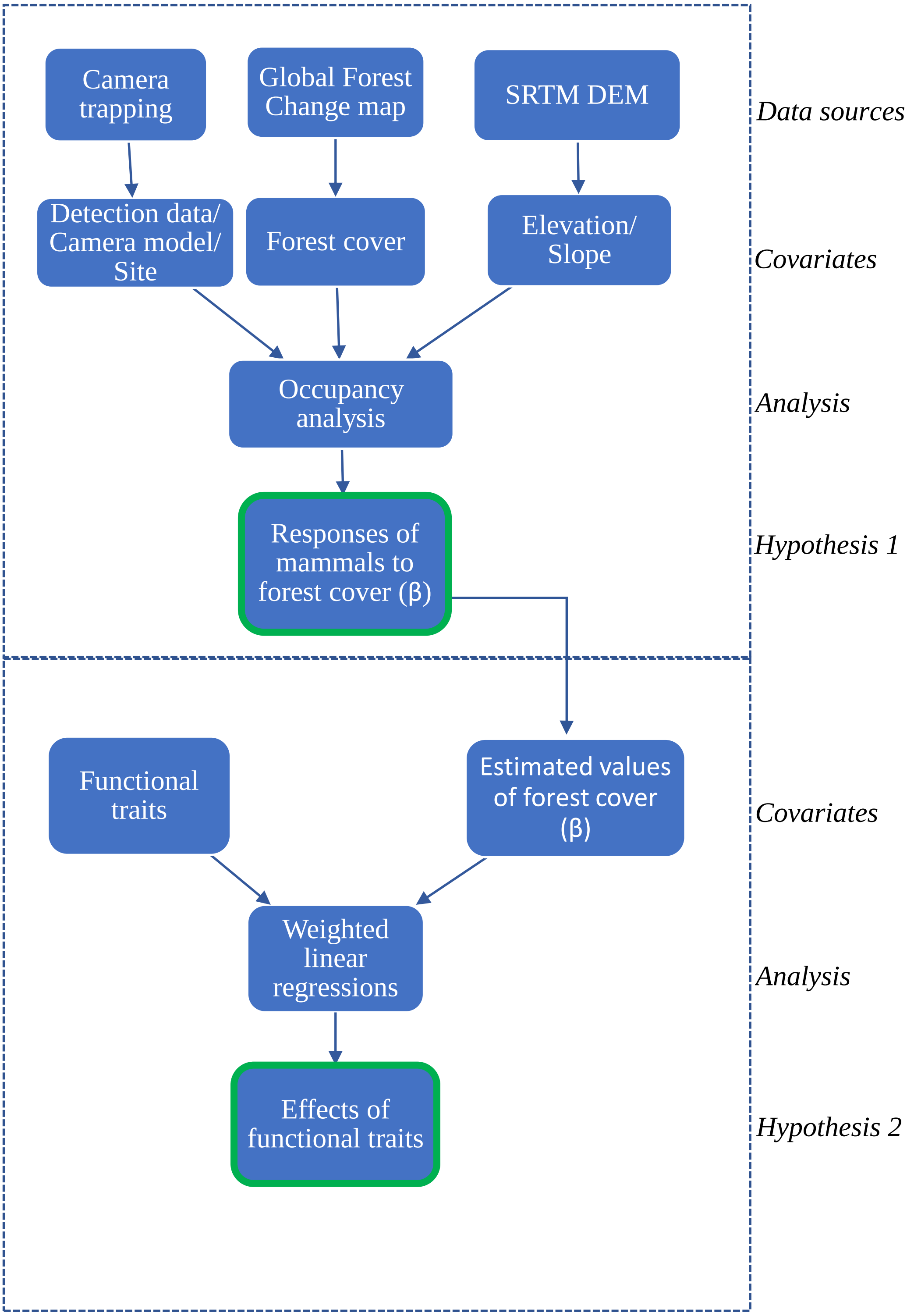

Fig 2: Flowchart representing statistical analysis

3. Results

The camera trap sampling period included an effort equivalent to 4,178 trap days (936 in BBS, 1579 in NAK, and 1663 in PSH) and 45,182 photographs of 37 mammal species (6,667 in BBS, 3,666 in NAK, and 36,487 in PSH) were included in the analysis. The number of mammal species captured was 20, 14 and 24 in BBS, NAK and PSH respectively. Out of the 37 species, 22 (59%) were captured at a single site, 9 (24%) were captured at any two of the sites and only 6 (16%) were captured at all three sites (Annex 1). Body mass ranged from 1.84 kg to 3,160 kg with a median weight of 6,750 kg (Annex 2). Out of the 37 species, 12 were forest specialists while 25 were not forest specialists (Annex 2). Similarly, 8 species were omnivores, 9 carnivores, 18 herbivores and 2 insectivores (Annex 2). The habitat breadth ranged from 1 to 25 with a median breadth of 5 (Annex 2).

In the occupancy analysis, only the best models for 12 species out of 37 converged. The other 24 species for which the best models did not converge, had low detections with naïve occupancy ranging from 0.0045 to 0.053. The best model for one species converged but produced boundary estimates for occupancy and detection with large estimates and SE for forest cover. Out of the 12 species for which the models converged, the detection of 5 species was affected by the camera model and that of 3 species was affected by the slope. The detection of 4 species, however, was neither affected by the camera model nor by the slope. The effect of elevation on occupancy was observed only on three species, while the effect of the PA was seen on five species.

3.1 Species response to forest cover

The occupancy of 8 (67%) species was positively related to forest cover with β values from 0.053 for barking deer (*Muntiacus muntjac*) to 6.63 for sambar (*Rusa unicolor*). Other species positively related to forest cover are wild boar (*Sus scrofa*), lesser mouse-deer (*Tragulus kanchil*), tiger (*Panthera tigris*), banded palm civet (*Hemigalus derbyanus*), short-tailed mongoose (*Herpestes brachyurus*), and marbled cat (*Pardofelis marmorata*). On the other hand, the occupancy of 4 (33%) species was negatively related to forest cover with β values from -0.002 for crab-eating macaque (*Macaca fascicularis*) to -1.31 for Malayan porcupine (*Hystrix brachyura*). Additionally, southern pig-tailed macaque (*Macaca nemestrina*) and Asiatic brush-tailed porcupine (*Atherurus macrourus*) were also negatively associated with forest cover (annex 3). But no significance was observed in this relation as the confidence intervals for all species overlap zero (Fig: 3).

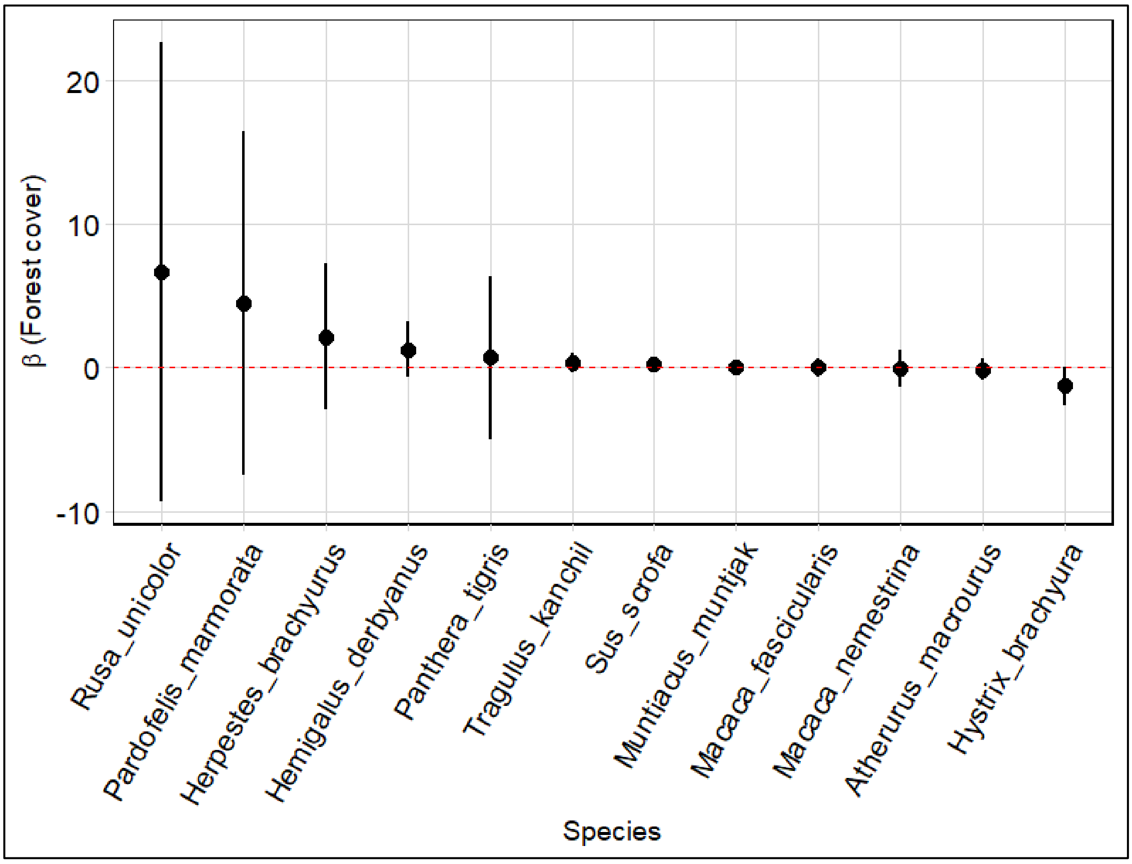

Fig 3: β-estimates of forest cover for species with standard error. The estimates are considered significant when the confident intervals do not overlap zero.

3.2 Effect of functional traits

On average, forest specialists had higher association with forest cover (β = 0.574 ± 1.12) than non-specialists (β = 0.059 ± 0.55) as predicted. Similarly, carnivores/omnivores were more related to forest cover than herbivores/insectivores with β = 0.464 ± 1.20 compared to β = 0.095 ± 0.55. Body mass and habitat breadth did not show any noticeable associations (Fig 4). I did not find any statistical significance in these associations of functional traits with forest cover ($p > 0.05$).

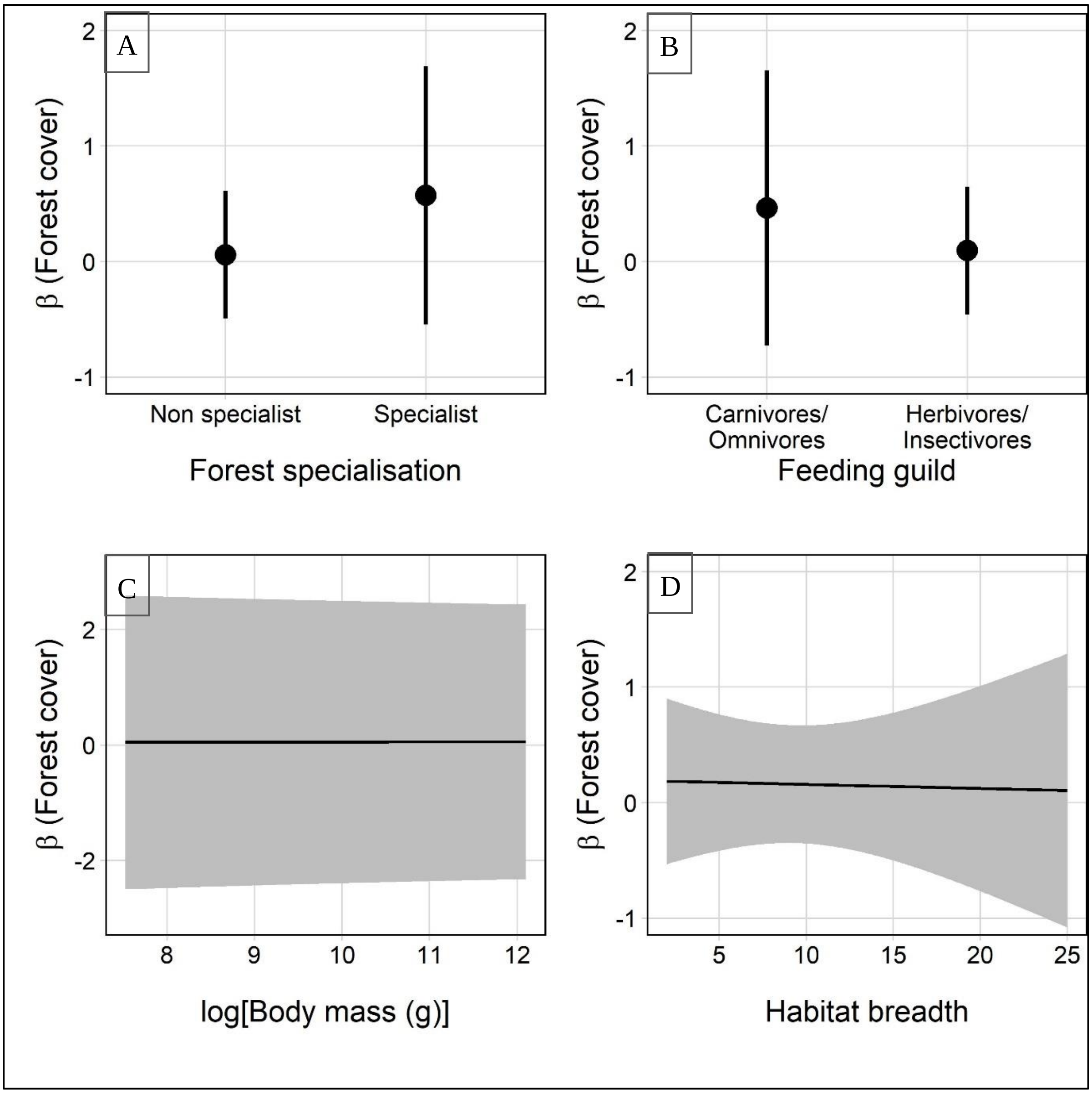

Fig 4: Plots between functional traits and forest cover parameter. The bars in plots A and B, and the grey areas in C and D are the 95% confidence intervals. The scale of the y-axis in C is different from other plots.

4. Discussion

In this study, I have found that while the occupancy of 67% of the species was positively related to forest cover, that of the other 33% was negatively related. In the functional trait analysis, forest specialists and carnivores/omnivores were more associated with forest cover than other assemblage groups. Body mass and habitat breadth did not show any strong direction or magnitude of the relationship. These associations were however not statistically significant.

4.1 Species response to forest cover

As hypothesised (H1), mammal species have varying associations between occupancy and forest cover given by the β values for forest cover which were distributed across a wide range. I found that two-thirds of the species were positively associated with forest cover while a third were negatively associated. In a similar study, Salom-Pérez et al. (2021) assessed the occupancy of mammals in a semi-protected strip including two protected areas and a corridor between them. They found that forest cover was the most important factor determining the occupancy of mammals but with different effects at the species level. Similarly, forest cover as an important factor associated with mammalian occupancy was also observed in protected areas of China (Feng et al., 2021) and South Africa (Zungu et al., 2020). Both studies again found that the response varied among species. Again, in another study conducted in Brazilian forests, Regolin et al. (2017) also observed varying degrees of association of mammals with forest cover. This shows that the occupancy of the majority of the mammal species is positively related to the forest cover, however, the direction and magnitude of the effect of forest cover vary between species.

The species with the highest positive association with forest cover was Sambar (*Rusa unicolor)*. Other studies also have found its preference for areas with high forest cover (Haleem & Ilyas, 2022; Kushwaha et al., 2004) because of its shy disposition and preference for dense forests (Haleem & Ilyas, 2022). It faces threats from poaching because of its large size (Widodo et al., 2022) and thus may have chosen areas with higher forest cover as a refuge (Gallego-Zamorano et al., 2020). Similarly, the marbled cat (*Pardofelis marmorata*), short-tailed mongoose (*Herpestes brachyurus*), the banded palm civet (*Hemigalus derbyanus*), and tiger (*Panthera tigris*) also have higher and positive relations with forest cover. Studies of marbled cats have found their preference for forested habitats (Nowell & Jackson, 1996; Rustam et al., 2016). The short-tailed mongoose (Jennings et al., 2010; Jennings & Veron, 2011), the banded palm civet (Dunn et al., 2022) and the tiger (Sunarto et al., 2012) are also reported to be positively associated with forest cover. The barking deer (*Muntiacus muntjac*) showed a faint positive association, as it has been reported to prefer medium tree cover of 19% (Hameed & Mian, 2009) at which it can move easily and escape from predators (Habiba et al., 2021).

The species most negatively related to the forest cover were Malayan porcupine (*Hystrix brachyura*) and Asiatic brush-tailed porcupine (*Atherurus macrourus*). The Malayan porcupine has been found associated with varieties of habitats ((Lunde et al., 2016; Talukdar et al., 2019) implying that forest cover may not be essential for it. However, the rarest of the porcupines, the Asiatic brush-tailed porcupine has been reported to be associated with forest cover and found in places with plenty of undergrowth (Molur et al., 2005; Talukdar et al., 2019), but this study suggests that it may as well occupy other habitat types. The two macaques, the southern pig-tailed macaque (*Macaca nemestrina*) and the crab-eating macaque (*Macaca fascicularis*) showed weak negative associations. These macaques are widely distributed and highly adaptable species (Hansen et al., 2021) and can use diverse types of habitats including artificial forests outside the PAs (Ang et al., 2020). This explains their weak association with forest cover.

4.2 Effect of functional traits

As predicted, the relationship between occupancy and forest cover in this study was stronger for the forest specialist than for the non-specialists. This is consistent with other studies where forest specialists are found to be more related to the amount of forest cover available (Beca et al., 2017; Bedoya-Durán et al., 2021; Salom-Pérez et al., 2021) than the generalists. This can be explained by the fact that more forest cover means more habitat available for forest specialists, and habitat amount is highly correlated with a species' occurrence (Fahrig, 2013). Non-specialists, on the other hand, were nominally associated with forest cover. In a study, Regolin et al. (2017) observed that the occurrence of generalists was not associated with forest cover. In another study, (Salom-Pérez et al., 2021) found that generalists were associated with lower forest cover. This can be explained as generalists are adapted to various habitat types (Schlinkert et al., 2016).

Considering the feeding guild, the carnivores-omnivores showed a higher association with forest cover than the herbivore-insectivores as predicted. Carnivores are positively related to forest cover as found by other studies (Regolin et al., 2017; Srivathsa et al., 2019). Higher prey availability, help in camouflage and reducing hunting pressure from humans (especially for large carnivores) are generally associated with this relation (Gallego-Zamorano et al., 2020; Phumanee et al., 2021; Salom-Pérez et al., 2021; Sunarto et al., 2012). Moreover, the availability of small prey species especially due to the presence of woody debris (Duckworth et al., 2016; Jennings & Veron, 2011; Mathai et al., 2017) explains the higher association of both carnivores and omnivores with forest cover.

Body mass and habitat breadth did not have any association with forest cover. But studies have shown that large mammals are often found to prefer intact forest areas to fragmented forests to meet the habitat amount requirement and to find refuge from hunting (Núñez-Regueiro et al., 2015; Regolin et al., 2017) as they are more susceptible to hunting because of their sizes (Gallego-Zamorano et al., 2020; Peres, 2001). Habitat breadth also did not explain the relationship between occupancy and forest cover. A species with lower habitat breadth can be arbitrarily related to any particular type of habitat, and one wth higher habitat breadth (the generalist) can be associated with multiple types of habitats, and both may not necessarily show any strong relation with forest cover (Gallego-Zamorano et al., 2020; Salom-Pérez et al., 2021; Sunarto et al., 2012). This uncertainty of association of habitat breadth with forest cover might explain the findings of this study.

The lack of pronounced and clear effects can be attributed to some factors. This research is conducted in tropical protected areas where forest cover is often high. But there may still be places, for example, along the edges where forest cover is low. Still, I did not find pronounced and clear effects of forest cover on species occupancy which suggests that there may not be enough variation in forest cover to observe significant differences. In other words, the proportion of the forest cover in these sites may be above the threshold to observe differences in responses (Pardo Vargas et al., 2016; Regolin et al., 2017). Moreover, the findings can be interpreted as an indication that protection in these areas is still effective, although the absence of evidence of an effect is not evidence of absence. During the occupancy analysis, I observed problems of model convergence, getting boundary solutions for $\boldsymbol{\psi}$ and p, and large uncertainties in the estimates. These have been reported as the limitations of the likelihood approach of parameter estimation when maximizing full likelihood is involved (Karavarsamis, 2019; Welsh et al., 2013). This happens when data is sparse (Guillera-Arroita et al., 2010;

Welsh et al., 2013) or when the species are elusive, and the model does not have enough information to distinguish whether a site is truly unoccupied by a species or it is just a case of non-detection (MacKenzie et al., 2002). This suggests using more data from multiple years as well as other statistical approaches like Bayesian multi-species occupancy modelling, penalised likelihood method (Hutchinson et al., 2015), and the two-stage approach of occupancy modelling (Karavarsamis, 2019).

5. Conclusion

The occupancy of most mammals was positively related to forest cover and there were variations in this relationship across species and species groups. The functional traits of the species helped to understand these variations. It was observed that the occupancy-forest cover relations are defined by forest specialisation and the feeding guild of the species. Forest specialists and carnivores/omnivores had stronger and more positive associations than non-specialists and herbivores/insectivores. However, the lack of pronounced effects suggests that the protected areas considered in this study might not have enough variation in forest cover to find differences in responses or it can also be said that these areas are effective in protection. Finally, issues with spare data were observed. Hence, I recommend future research include data from multiple years and follow alternate statistical approaches of occupancy modelling and parameter estimation.

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Annex

Annex 1: Home ranges & references for the species

Species	**Site the species is detected at**	**Home range (km^2)**	**Reference species for home range***	**Reference for home range**
Arctictis binturong	NAK	6.2	*Arctictis binturong*	(Grassman, L. I. et al., 2005)
Atherurus macrourus	NAK, PSH	15	*Atherurus macrourus*	(Jones et al., 2009)
Capricornis milneedwardsii	NAK	0.5	*Capricornis crispus*	(Takada et al., 2020)
Capricornis sumatraensis	PSH	0.5	*Capricornis crispus*	(Takada et al., 2020)
Catopuma temminckii	BBS, NAK	47.7	*Catopuma temminckii*	(Grassman, L. I., Jr. et al., 2005)
Elephas maximus	BBS	38.36	*Elephas maximus*	(Jones et al., 2009)
Helarctos malayanus	BBS, NAK, PSH	14.8	*Helarctos malayanus*	(Te Wong et al., 2004)
Hemigalus derbyanus	BBS, PSH	2.88	*Paguma larvata*	(Jones et al., 2009)
Herpestes brachyurus	PSH	2.33	*Herpestes brachyurus*	(Jennings et al., 2010)
Herpestes urva	NAK	2.33	*Herpestes brachyurus*	(Jennings et al., 2010)
Hystrix brachyura	BBS, NAK, PSH	0.4	*Hystrix africaeaustralis*	(Ngcobo et al., 2019)
Macaca fascicularis	PSH	0.46	*Macaca fascicularis*	(Jones et al., 2009)
Macaca leonina	NAK	4.49	*Macaca leonina*	(José-Domínguez et al., 2015)
Macaca nemestrina	BBS, PSH	1.75	*Macaca nemestrina*	(Jones et al., 2009)
Manis javanica	PSH	0.05	*Manis javanica*	(Lim & Ng, 2008)
Martes flavigula	PSH	7.2	*Martes flavigula*	(Grassman, L. I. et al., 2005)
Muntiacus montanus	BBS	1.1	*Muntiacus reevesi*	(McCullough et al., 2000)

Muntiacus muntjak	BBS, NAK,PSH	0.77	*Muntiacus muntjak*	(Wegge & Mosand, 2015)
Neofelis diardi	BBS	2.2	*Neofelis diardi*	(Pallemaerts et al., 2019)
Neofelis nebulosa	PSH	30.8	*Clouded leopard*	(Grassman, L. I., Jr. et al., 2005)
Paguma larvata	BBS, PSH	2.88	*Paguma larvata*	(Jones et al., 2009)
Panthera tigris	BBS	64.89	*Panthera tigris*	(Jones et al., 2009)
Paradoxurus hermaphroditus	BBS, NAK	4.15	*Paradoxurus hermaphroditus*	(Jones et al., 2009)
Pardofelis marmorata	BBS, PSH	5.3	*Pardofelis marmorata*	(Grassman, L. I., Jr. et al., 2005)
Presbytis melalophos	BBS	14.3	*Presbytis melalophos*	(Nijman et al., 2020)
Prionailurus bengalensis	BBS, NAK, PSH	1.87	*Prionailurus bengalensis*	(Jones et al., 2009)
Prionailurus planiceps	PSH	4	*Prionailurus bengalensis*	(Wilting et al., 2010)
Ratufa bicolor	PSH	0.017	*Ratufa indica*	(Baskaran et al., 2011)
Rusa unicolor	BBS, PSH	15	*Rusa unicolor*	(Leslie, 2011)
Sus scrofa	BBS, NAK, PSH	1.18	*Sus scrofa*	(Jones et al., 2009)
Tapirus indicus	BBS, PSH	9.4	*Tapirus indicus*	(Jones et al., 2009)
Trachypithecus obscurus	PSH	0.18	*Trachypithecus obscurus*	(Jones et al., 2009)
Tragulus javanicus	NAK	5.9	*Tragulus javanicus*	(Matsubayashi et al., 2003)
Tragulus kanchil	BBS, NAK, PSH	0.06	*Tragulus kanchil*	(Jones et al., 2009)
Tragulus napu	BBS	0.06	*Tragulus kanchil*	(Yuan, 2016)
Viverra megaspila	PSH	9.36	*Viverra zibetha*	(Jones et al., 2009)
Viverra zibetha	PSH	9.36	*Viverra zibetha*	(Jones et al., 2009)

** = For some species whose home ranges were not found in the literature, home ranges of closely related species (reference species) were used*

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Annex 2: Functional traits of the species

Species	**Feeding guild**	**Body mass (g)**	**Habitat breadth**	**Habitat specialisation: Forest**
Arctictis binturong	Omnivorous	9875	4	Specialist
Atherurus macrourus	Herbivorous	2000	2	Specialist
Capricornis milneedwardsii	Herbivorous	130000	3	Non specialist
Capricornis sumatraensis	Herbivorous	87500	4	Non specialist
Catopuma temminckii	Carnivorous	11500	7	Non specialist
Elephas maximus	Herbivorous	3160000	7	Non specialist
Helarctos malayanus	Omnivorous	46500	4	Non specialist
Hemigalus derbyanus	Insectivorous	2322.5	3	Specialist
Herpestes brachyurus	Omnivorous	1853.5	3	Specialist
Herpestes urva	Omnivorous	1863.2	7	Non specialist
Hystrix brachyura	Herbivorous	8450	10	Non specialist
Macaca fascicularis	Omnivorous	3991.5	8	Non specialist
Macaca leonina	Herbivorous	6500	4	Specialist
Macaca nemestrina	Herbivorous	6296.5	7	Non specialist
Manis javanica	Insectivorous	5150	6	Non specialist
Martes flavigula	Carnivorous	1842.5	7	Non specialist
Muntiacus montanus	Herbivorous	17619.8	1	Specialist
Muntiacus muntjak	Herbivorous	15925.8	6	Non specialist
Neofelis diardi	Carnivorous	20500	2	Specialist
Neofelis nebulosa	Carnivorous	20500	3	Specialist
Paguma larvata	Omnivorous	4300	5	Non specialist
Panthera tigris	Carnivorous	162564	7	Non specialist
Paradoxurus hermaphroditus	Omnivorous	3156.7	11	Non specialist
Pardofelis marmorata	Carnivorous	2854.3	3	Specialist
Presbytis melalophos	Herbivorous	6300	2	Specialist
Prionailurus bengalensis	Carnivorous	3300	9	Non specialist
Prionailurus planiceps	Carnivorous	6750	7	Non specialist
Ratufa bicolor	Herbivorous	2050	2	Specialist

Rusa unicolor	Herbivorous	180344.4	13	Non specialist
Sus scrofa	Herbivorous	101052.1	25	Non specialist
Tapirus indicus	Herbivorous	296250	4	Non specialist
Trachypithecus obscurus	Herbivorous	7000	1	Specialist
Tragulus javanicus	Herbivorous	2775	3	Non specialist
Tragulus kanchil	Herbivorous	2000	7	Non specialist
Tragulus napu	Herbivorous	4000	3	Non specialist
Viverra megaspila	Omnivorous	9250	7	Non specialist
Viverra zibetha	Carnivorous	9500	8	Non specialist

Annex 3: Coefficients for the forest cover parameter and standard error for the species included in the functional trait analysis

Species	Forest specialisation	β_Forest cover	SE
Atherurus macrourus	Specialist	-0.147	0.375
Hemigalus derbyanus	Specialist	1.257	0.996
Herpestes brachyurus	Specialist	2.125	2.602
Hystrix brachyura	Non specialist	-1.305	0.692
Macaca fascicularis	Non specialist	-0.002	0.34
Macaca nemestrina	Non specialist	-0.076	0.645
Muntiacus muntjak	Non specialist	0.053	0.232
Panthera tigris	Non specialist	0.677	2.889
Pardofelis marmorata	Specialist	4.46	6.076
Rusa unicolor	Non specialist	6.635	8.159
Sus scrofa	Non specialist	0.214	0.269
Tragulus kanchil	Non specialist	0.333	0.339

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