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FOREST STRUCTURE SHAPES TROPICAL TERRESTRIAL AND ARBOREAL MESOMAMMAL COMMUNITIES UNDER MODERATE DISTURBANCE

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FOREST STRUCTURE SHAPES TROPICAL TERRESTRIAL AND ARBOREAL MESOMAMMAL COMMUNITIES UNDER MODERATE DISTURBANCE

BY

JULIANA MASSELOUX

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OF

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ABSTRACT

Tropical biodiversity is threatened globally by anthropogenic disturbances, particularly forest degradation and overhunting. Where large mammals have been extirpated, smaller-bodied "mesomammals" may play an important ecological role (e.g., as seed-dispersers). However, mesomammals are routinely understudied as they tend to be rare, cryptic, and nocturnal. Tropical tree-dwelling (arboreal and semi-arboreal) mesomammals are especially vulnerable to forest conversion, particularly when reliant on old growth forest structures. Understanding species- and community-level responses of terrestrial and arboreal mesomammals to changes in forest structure and human activity is crucial for informing management decisions in protected areas where resources are limited. We deployed 20 arboreal and 75 terrestrial camera traps throughout Nam Cat Tien National Park, southern Vietnam. The study objectives of the first chapter were to 1) identify long-term changes in terrestrial mesomammal richness and 2) evaluate the effects of forest structure and anthropogenic disturbance on an 18-species mesomammal community using community occupancy models. The objectives of the second chapter were to 1) evaluate the utility of arboreal camera traps for surveying nine arboreal and four semi-arboreal tropical mesomammals, 2) model the effects of forest structure and anthropogenic disturbance on detection and occurrence of arboreal mesomammals using generalized linear mixed models and single-season occupancy models, and 3) estimate arboreality of semi-arboreal species using multi-scale occupancy models. We found that terrestrial mesomammal site occupancy was driven largely by the interaction between distance to seasonally inundated grassland and absolute forest cover (basal area per hectare). We found no negative effects of anthropogenic factors at the community-level.

However, we did find that four disturbance-tolerant small carnivores have been extirpated since the 1990s and continued human presence in the park suggests that hunting and snaring remains an acute threat to native mesomammals. We also found that canopy connectivity and other mature forest characteristics were important across the arboreal community. The effect of tree and focal limb characteristics on species detection was most likely explained by physiological adaptations and tree use behavior. Mean occupancy was underestimated for most semi-arboreal species when only one method was used. Multi-method occupancy designs may thus improve estimates of species distribution and habitat use, which are important for guiding management and conservation decisions.

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PREFACE

The two chapters of this thesis have been provided in the manuscript format of the respective journals they were submitted to. Manuscript 1 follows the Ecosphere journal guidelines, and Manuscript 2 follows the Animal Conservation journal guidelines. All tables, figures, and appendices for both chapters are included at the end of Manuscript 2. All literature cited for both chapters are combined in the Bibliography section.

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In Review, Submitted to Ecosphere, May 2021

Forest structure and seasonally inundated grassland shapes tropical mammal communities under moderate disturbance

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Data are publicly available via the following link:

https://github.com/jmasseloux/Ecosphere_data

Introduction

Tropical biodiversity is acutely threatened by anthropogenic development and overexploitation (Bradshaw, Sodhi, & Brook, 2009). Land use change, particularly conversion of intact native forests for agriculture, alters habitat structure and resource availability in ways that preclude species persistence and is the greatest driver of biodiversity loss (Newbold et al., 2016; Tilman et al., 2017). While selectively logged forests can retain habitat and thus have value for conserving many species, high-intensity logging and land conversion negatively affects the abundance and species richness of forest-dwelling mammals in the tropics (Laurance et al., 2008; Brodie, Giordano, & Ambu, 2015). Resource specialists and species with small ranges are particularly vulnerable to extinction by habitat loss and anthropogenic disturbances (Pimm & Raven, 2000; Davies, Margules, & Lawrence, 2004), especially when combined with additional pressures, such as unsustainable hunting and climate change (William F. Laurance & Useche, 2009; Wilkie et al., 2011).

Tropical Southeast Asia is a biodiversity hotspot that contains the highest proportion of globally unique (endemic) mammal species (Myers et al., 2000; Olson et al., 2001). However, Southeast Asia also has the highest rate of anthropogenic deforestation of any major tropical region (Sodhi et al., 2010). The region has lost over half of their primary forest (Sodhi et al., 2004) and 20% of their total species richness (Newbold et al., 2016), largely due to land conversion for the production of agricultural commodities (e.g., oil palm; Schipper et al. 2008). Further, the region experiences heavy exploitation of wildlife for subsistence hunting and the rapidly expanding medicine, pet, and bushmeat market (Corlett, 2007). The synergistic combination of anthropogenic pressures on wildlife in Southeast Asia has the potential to rapidly disrupt ecosystems and drive disturbance-sensitive species to local or global extinction.

Protected areas, such as national parks, wilderness areas, and nature reserves have been established globally as refuges for wildlife with the aim of preserving biodiversity and ecosystem integrity. However, the effectiveness and conservation potential of protected areas in the tropics is endangered by human activities and ineffective governance. Over 68% of tropical protected forests have experienced loss of forest cover within a 50 km range of the boundary, and 25% have experienced loss within protected area boundaries, with loss rates highest in South and Southeast Asia (Clark et al., 2013; Brun et al., 2015). Reductions in forest cover surrounding protected areas (i.e., buffer zones) jeopardize the capacity for protected areas to conserve species (DeFries et al., 2005). Further, the fragmentation and potential isolation of high-quality habitat between protected areas can threaten the long-term persistence of wide-ranging species (Crooks et al., 2011). In addition, concentrated development around protected areas in Southeast Asia facilitates illegal hunting, snaring, and the movement of wildlife from parks to urban consumers, especially where local poverty rates are high and alternative livelihood options are limited (Johannesen, 2007; Watson et al., 2013).

Many of Southeast Asia’s larger frugivorous mammals have experienced significant population and range declines in recent years even within national parks (i.e. elephants, gaur, sun bear; Sukumar 2003, IUCN 2016a, 2016b). Frugivorous or partially frugivorous forest mesomammals can play important yet undervalued ecological roles as seed dispersers (Nakashima et al., 2010; Corlett, 2017) and may help maintain ecosystem stability as larger and more disturbance-sensitive species disappear (Cardillo et al., 2004).

Yet, despite similar levels of extinction among smaller-bodied mammals as large mammals (Schipper et al., 2008), there has been relatively little research on these species in tropical areas as they tend to be rare, cryptic, and nocturnal (Brooke et al., 2014). For example, civets, mongoose, and small cats are among the least studied members of the order Carnivora (Brodie 2009; Brooke et al. 2014); 22% of small carnivores are classified as threatened under IUCN due to population declines or range contractions (Schipper et al. 2008). Although forest mesomammals have shown resilience to moderate anthropogenic disturbance in Southeast Asia, such as selective logging, responses can vary by species and fine-scale vegetation structure (e.g., canopy cover; Mathai et al. 2010). However, quantifying anthropogenic and habitat effects can be difficult for Southeast Asian mesomammals, as habitat suitability analyses (e.g., gap analyses) have been shown to be inconsistent with ground-truthed occurrence data (biased estimates of distribution and abundance; Jennings and Veron 2011). Such analyses often ignore edge effects beyond changes in forest structure (Tabarelli, Cardoso da Silva, & Gascon, 2004). For example, hunting in Southeast Asia disproportionally affects distributions of species selectively targeted for the urban wildlife market (e.g., pangolin, civets, wild pigs, and primates) despite availability of suitable habitat (Brodie, Giordano, & Ambu, 2015; Wearn et al., 2017). In addition, community stability is reliant on species and interaction diversity (Mougi & Kondoh, 2012), yet few studies have examined spatio-temporal responses to anthropogenic disturbance by mesomammals at the community level. Identifying community-level sensitivity and responses to disturbance may identify imbalances within an ecosystem that could threaten long-term species persistence.

Our study objectives are to 1) identify long-term changes in terrestrial mesomammal richness and 2) evaluate how current forest structure and encroaching anthropogenic activities affect occurrence of forest dwelling mesomammals within a protected tropical forest of Southeast Asia. The protected area has been increasingly fragmented by landcover change and urbanization within the surrounding buffer zone since its establishment in the 1990s. We hypothesized that park-level terrestrial and semi-terrestrial mesomammal community richness would have declined since the last rigorous biodiversity surveys conducted in the 1990s, with species requiring larger ranges, more intact primary forest, or which are selectively targeted by the wildlife trade no longer occur in the park or occur at very low rates. We also hypothesized that site-level community occurrence and richness throughout the park would increase where forest structure was most intact (i.e., high absolute cover and low understory cover) and would decrease where human use and accessibility was higher. Given the long history of anthropogenic disturbance in and around the park since its establishment, we reasoned that there would be a gradient of species-specific responses, where disturbance-sensitive species would be constrained to less disturbed areas while more adaptable species would be less selective in their use of forest sites.

Methods

Study Area

We surveyed terrestrial and semi-terrestrial forest mesomammals in Cat Tien National Park, located ~150 km north of Ho Chi Minh City in Southern Vietnam. It is one of the largest national parks in the country, at 72,000 ha, and is part of a greater UNESCO Biosphere Reserve buffer zone and Ramsar Site. The park consists of two segments separated by eight kilometers of agricultural land: Cat Loc in the north and Nam Cat Tien and Tay Cat Tien in the south. Our study occurred within the core zone of Nam Cat Tien in Dong Nai province (Figure 1). Nam Cat Tien has several landcover types, including secondary mixed evergreen and deciduous forest, bamboo forest, and seasonally inundated grassland.

Seventy-six mammal species were confirmed to inhabit Cat Tien National Park during surveys conducted between 1993 and 2001, comprising 30% of Vietnam's known mammal species. Of these, 23 species can be classified as terrestrial or semi-terrestrial mesomammals. At least sixteen of the park's mammal species are listed as threatened under IUCN and several are endemic to Vietnam. Most large mammals have been extirpated from the park, including tiger (*Panthera tigris*) and Javan rhinoceros (*Rhinoceros sondaicus*), or restricted to very small local populations, such as Asian elephant (*Elephas maximus*) and gaur (*Bos gaurus*; Murphy 2004, Polet and Ling 2004, Nguyen 2009).

Most of Cat Tien National Park consists of secondary and bamboo-dominated forest due to a legacy of anthropogenic disturbance within and around the park. Portions of the park were sprayed with herbicides, such as Agent Orange, during the U.S.-Vietnam War between 1965-1970 (Stellman et al., 2003). The park was also logged after the war and prior to its establishment as a protected area in 1992. Most logging occurred within the buffer zone of the park (Figure 1; delineated by UNESCO in 2001) between 1973 and 1989, with some forest regeneration during the 1990s accompanying a shift from forest extraction and agriculture to agroforestry (Meyfroidt & Lambin, 2008; Vogelmann et al., 2017). While the core of the park has not much changed in forest cover since the 1970s, the buffer zone and areas beyond have been extensively converted for small-scale agriculture and anthropogenic development (Emerton et al., 2014; Vogelmann et al., 2017; Duong et al., 2018). In addition, harvest of wild animals for trade and subsistence poses a serious threat to the remaining wildlife within the park and has been linked to increasing demand for bushmeat in the cities (Polet & Ling, 2004; Van Song, 2008; An, Markowski, & Bartos, 2018).

Camera trapping

The use of automated cameras to capture animal incidences is a well-documented and preferred method of non-invasively assessing terrestrial mammal populations, species diversity, occurrence patterns, and temporal activity (Tobler et al. 2008, Rovero and Marshall 2009). We set seventy-five terrestrial camera traps in Nam Cat Tien from June 2019 to January 2020 to allow for data collection across wet (June to September 2019) and dry (October 2019 to January 2020) seasons. We used a stratified random sampling approach to select camera sites in proportion to the availability of four different land cover classifications (secondary forest, mixed forest, bamboo, and grassland; ESA Land Cover CCI 2015, Figure 1). Sites were selected at varying proximity to anthropogenic disturbance (urban areas, agricultural land, park edge), with minimum proximity between sites at 500 m. Cameras were set approximately 30-70 cm off the ground to maximize detections of small- to medium-bodied mammals (M. W. Tobler et al., 2008a; Sunarto, Sollman, & Kelly, 2013) and placed on or near (within 5 m) human trails for maximizing detection of human activity and facilitating revisit accessibility. The detection range of each camera (max 24 m detection distance) was limited by obstructing vegetation, especially at night when the infrared flash may be reflected off nearby foliage. We minimized detection range variation across cameras by clearing vegetation in front of the camera to approximately two meters. Cameras were continuously active throughout each season and had large (32 GB) memory cards to limit revisits to once per month. Most trails were not heavily used or significantly altered by people, thus we did not expect mesomammals to avoid trails. Photos were tagged to species by six observers using the Digikam photo manager (https://digikam.org) and all mesomammal tags were reviewed for accuracy by the lead author.

Covariates

We hypothesized that mesomammal occurrence would be affected by various combinations of environmental and anthropogenic variables. A 10x10m landcover classification (i.e., forest, bamboo, grassland) was assigned at each camera site using *ArcGIS v. 10.5* (ESRI 2011; ESA 2015) and was confirmed on the ground with visual observation, capturing broad-scale habitat features. We quantified forest structure at each camera site at the end of each season. Understory cover can influence mammal detection and occurrence (William F. Laurance et al., 2008; Gerber, Karpanty, & Randrianantenaina, 2012) and can act as a proxy for habitat disturbance where dense bamboo has colonized and dominated logged forests, potentially disrupting forest regeneration (Larpkern, Moe, & Totland, 2011). We used the point intercept method to measure understory and percent high canopy (>15 m) within a five-meter radius at the camera location (0 m) and three intervals (17 m, 35 m, 50 m) along three equidistant 50 m transects. We measured nearest tree distances and diameter at breast height (DBH >30 cm) at each point interval to estimate basal area and absolute cover (basal area per ha) using an unbiased point-centered-quarter estimator (Pollard 1971, Appendix S1: Table

S1). Fruit were rarely detected during vegetation surveys and revisits, likely due to short and dispersed fruiting periods, so could not be included as a variable.

We evaluated anthropogenic activity in three ways. We used a cost-path analysis in ArcGIS from urban areas (from Duong et al. 2018) as an index of site accessibility to humans. The cost raster included four variables that we reasoned would most affect accessibility to the camera site from urban areas: roads (associated cost = 1), open landscape (e.g. grassland, agriculture, rice plantations; cost = 2), forest (cost = 10), and water (cost = 30). Water, such as the Dong Nai river, was considered the highest barrier to forest entry, but according to park staff it is easily traversed by locals who own or have access to small motorized boats and pirogues. We also obtained site-level counts of independent (>30 min) human detections for each season from camera data. When possible, we identified five different types of human presence (e.g., hunter, tourist, ranger) to better understand types of risk, but all human detections were collated for the human count covariate. Lastly, we conducted a point density analysis within 300 m cells using ArcGIS as an index of site protection effort from available ranger tracklog data (2017-2019) which is expected to capture the general spatial variation of patrolling effort. All environmental and anthropogenic variables are summarized in Appendix S1. We tested for pair-wise correlation among covariates and highly correlated variables ($r > 0.6$) were removed or not included within the same model. A few sites missing field measurements were assigned the mean covariate value and all covariates were standardized at a mean of zero and a standard deviation of one for analyses.

Modelling framework

We analyzed our photographic data using community occupancy modelling (Dorazio & Royle, 2005; Mathias W. Tobler et al., 2015), which uses detection/non-detection data to estimate species richness and community- and species-level responses to predictor variables. Occupancy analyses are able to accommodate for imperfect detections, such as the probability that a species uses a site but is not detected by the camera (MacKenzie et al., 2002). This is a common issue when sampling wild animals, especially rare and elusive species. Point-sampling, such as using camera traps, does not allow for inference to a strict definition of species occurrence, as individuals are able to move in and out of a site within the season, violating the assumptions of site closure. As such, we interpret our inference on occupancy as the probability a species uses the site during the sampling period (asymptotic occupancy; (Mackenzie & Royle, 2005; Efford & Dawson, 2012). Hereafter, "occupancy" refers to site "use" for each species. We considered differences in species occurrence across the dry and wet season using a stacked modeling approach, where season was represented as a categorical variable (Monterroso et al., 2020). We did not explicitly model the dynamic changes (i.e., site colonization and extirpation) in occurrence as two seasons were inappropriate to capture these processes.

We used a Bayesian framework to fit and compare models and estimate parameter effects, such as on mean community-level detection (μ_p) and occupancy (μ_ψ), using JAGS via the 'runjags' package (Denwood 2016, Plummer 2003). Species-specific parameters were treated as random effects with a community-level distribution (i.e., Normal distribution). We standardized all covariates and fit the models using diffuse priors on all logit-scaled effects on detection and occupancy using a Logistic distribution (hyperparameters of 0 and 1 for location and scale, respectively; (Northrup & Gerber, 2018)) and a half-Cauchy distribution on the standard deviation (hyperparameter of 2.5 for the scale; (Gelman, 2006). Occupancy probability of species i at site j (ψ_{ij}) were modelled as a Bernoulli random variable, such as $z_{ij} \sim \text{Bernoulli}(\psi_{ij})$, where z_{ij} is the latent state occurrence and is equal to1 if a species occurred at a site and 0 if it did not occur. Surveys were defined as a period of seven camera trap days. Observations for each survey k (y_{ijk}) are a joint product of occurrence and detection probability, such that, $y_{ijk} \sim \text{Bernoulli}(p_{ij} \times z_{ij})$, where p_{ij} is the detection probability for each species at each site, but assumed to not vary by survey occasion. Detection and occupancy probabilities can be a function of hypothesized covariates and specified as a logit-linear model, as

$$\text{logit}(\psi_{ij}) = x_{ij}\beta_i \qquad (2)$$

$$\text{logit}(p_{ij}) = w_{ij}\alpha_i \qquad (3)$$

with covariates in design matrices x_{ij} and w_{ij}, a vector of species occupancy coefficients, β_i, and a vector of species detection coefficients, α_i. The community level distributions are then

$\beta_i \sim \text{Normal}(\mu_\psi, \sigma_\psi)$ and $\alpha_i \sim \text{Normal}(\mu_p, \sigma_p)$.

We fit 18 candidate models that hypothesized species occurrence to vary by only environmental variables or a combination of anthropogenic and environmental variables; all models considered the same variables to influence detection: understory cover, counts of human detections, and season. Detailed explanations of model structures, hypotheses, and predictions are specified in Appendix S2. For each model, we fit two parallel Markov-chain Monte Carlo chains of 40,000 iterations with a burn in of 10,000 and a thinning rate of 2. We assessed parameter convergence by visually inspecting trace plots and using the Gelman-Rubin statistic to ensure values were close to 1. To evaluate model fit, we used a goodness-of-fit (GOF) approach to derive a Bayesian p-value from a posterior predictive check (Gelman & Hill, 2007) based on differences in the observed and predicted deviance residuals. We compared models via 10-fold (across sites) cross validation using a logarithmic scoring rule based on predicted deviances (Broms, Hooten, & Fitzpatrick, 2016); models with smaller log-scores indicate more support in terms of out-of-sample prediction. We make inference using the top supported model and present estimated mean effects with associated Bayesian credible intervals (BCI). We quantify support for estimated species and community effects by reporting the proportion of posterior samples <0 or >0, which are indicative of the probability that the effect is negative or positive, respectively; we qualitatively evaluate strong support as a proportion >0.9 and moderate support >0.7 and <0.9.

We estimated site-level species richness using the mesomammal community as our species pool and did not use data augmentation to estimate undetected species within our community (Guillera-Arroita, Kéry, & Lahoz-Monfort, 2019). We assessed changes in mesomammal community composition by comparing our community to the results of previous large-scale biodiversity surveys conducted in the park between 1993 and 2001 (Polet and Ling 2004).

Results

Species richness

We obtained data from 60 of the 75 camera trap sites for a total of 7,699 effective camera trap nights and 10,197 independent detections (30 minutes between subsequent detections of the same species) of vertebrate animals and humans. Fifteen cameras were stolen and were not replaced. We detected 18 mesomammals (Appendix S3: Table S1), as well as several non-target species, including birds, reptiles, bats, and small mammals. Predicted site-level community richness from the top model varied from one to 15, with a seasonal decline in occurrence between seasons from a mode of eight species in the wet season to seven in the dry season (Appendix S4: Figure S1). No sites were estimated to be used by all 18 mesomammals.

When compared to biodiversity assessments compiled by Polet and Ling from 1993-2001, we found a 17% (19/23) decline in total terrestrial mesomammal richness. We failed to detect large Indian civet (*Viverra cibetha*), binturong (*Arctictis binturong*), sun bear (*Helarctos malayanus*), and hog badger (*Arctonyx collaris*), all of which are small carnivores. Given that these species have also not been detected in other small-scale camera surveys and ranger patrols it is unlikely that viable populations of any of these species still exist in the park. All other previously-confirmed terrestrial mesomammals were detected on our cameras (Appendix S3: Table S1).

Model support

We found all models converged (mean Gelman-Rubin <1.1) and fit the data (0.1 > GOF p-value <0.9). The most supported (lowest log-score; Appendix S5: Table S1) model included effects of absolute cover, distance to grassland, the interaction between absolute cover and distance to grassland, and season on occupancy (Figure 2). The second most supported model (increase in log-score of 4.22; Appendix S5: Table S1) differed in that it did not include an effect of grassland or an interaction of grassland with absolute cover. Considering the top model, we found community-level detection probability declined as understory increased (Figure 3; mean = -0.15; 95% BCI = 0.26, -

0.12; Pr<0 = 0.999); all species showed strong support for this effect (Appendix S6: Table S1). The effect of human counts on detection probability was not supported overall at the community-level (mean = 0.02; 95% BCI = -0.11, 0.12; PR>0 = 0.650), while we identified strong positive effects only for the common palm civet (*Paradoxurus hermaphroditus*), Malayan porcupine (*Hystrix brachyura*), and pig-tailed macaque (*Macaca leonina*). In addition, the effect of season on detection probability was not strongly supported at the community-level (mean = -0.02, 95% BCI = -0.29, 0.24; Pr<0 = 0.559) because effects varied by species with some strong positive effects (brush-tailed porcupine *Atherurus macrourus*, Eurasian wild pig *Sus scrofa*), some strong negative (common palm civet, pig-tailed macaque), and some without evidence of an effect (e.g., leopard cat *Prionailurus bengalensis*, long-tailed macaque *Macaca fascicularis*). Overall, detection covariate effects varied by species and were generally small in size ($|\boldsymbol{\alpha_i}|<1$) suggesting that these covariates did not have a large effect on community-level detection.

Mesomammal community occurrence was best explained by the interaction between absolute cover and grassland, where higher absolute cover increased the probability of occupancy at sites closer to grassland, but reduced probability of occupancy at sites further from grassland for all species (Figure 3; Appendix S6: Table S1; mean = -0.46; 95% BCI = -0.77, -0.16; Pr>0 = 0.998). Community and species-level occupancy probability increased with higher absolute cover when distance to grassland was zero (mean = 0.20; 95% BCI = 0.03, 0.39; Pr>0 = 0.991). Occupancy probability decreased with distance to grassland when absolute cover was zero (mean = -0.31; 95% BCI = -0.56, -0.08; Pr<0 = 0.996) with the effect being strong for most species and moderate for Eurasian wild pig, Malayan porcupine, and stump-tailed macaque (*Macaca* *arctoides*). Community and species-level occupancy probability also increased strongly in the wet season compared to the dry season (mean = 0.29; 95% BCI = -0.04, 0.61; Pr<0 = 0.960). Overall, the effects of the occupancy covariates were similar across the community and were not large ($|\boldsymbol{\beta}_i|<1$).

The difference in deviance residuals between the top model and several subsequent competing models was marginal (<4), suggesting that several other environmental covariates could predict occupancy similarly to the top model (Appendix S5: Table S1). Across these other models, absolute cover and percent high canopy generally had a positive effect on community occurrence, and distance to grassland, distance to water, and understory cover generally had a negative effect on community occurrence. Contrary to our hypotheses, few of the competing models included anthropogenic covariates, and the parameter effects on occurrence of those anthropogenic covariates were not strongly negative. Thus, human accessibility and use of the national park does not appear to have a strong negative effect on the current resident mesomammal community.

Discussion

Protected areas are vital to conserving wildlife populations and natural ecosystems. There is increasing acknowledgement of the conservation value of secondary and historically disturbed landscapes (Barlow et al., 2007; Chazdon et al., 2009; Sodhi et al., 2010). With less than one percent of Vietnam's primary forest remaining (Vogelmann et al., 2017), future conservation planning will need to prioritize moderately disturbed and regenerating forests. Still, continued monitoring of protected area biodiversity and drivers of species occurrence is important for ensuring the effectiveness of protected areas, especially where additive and synergistic types of disturbance occur. Even in a relatively biodiverse and well-protected park, like Cat Tien, hunting and genetic isolation has already extirpated several of the park's larger-bodied mesomammals and threatens the persistence of many others.

All four mesomammal species previously confirmed to inhabit Nam Cat Tien but not detected in our study (sun bear, hog badger, large Indian civet, and binturong) are moderate-to-high disturbance-tolerant (Appendix S3: Table S1), suggesting that other factors, such as hunting and snaring, may have contributed to their absence from the park. Given the low number of detections of these species from past surveys (Murphy & Duy Thuc, 2002; Polet & Ling, 2004) and the isolated geography of the park in relation to other intact forest habitat, it is increasingly unlikely that genetically viable populations of these four species still occur in Nam Cat Tien. Additional surveys should be extended to include Cat Loc as this region has previously supported some of these species, including sun bear and binturong. Interestingly, species richness varied across the landscape and by season and never exceeded 15, suggesting a degree of niche separation or interspecies competition within the community.

We found support that high absolute cover (more and/or larger trees typical of more intact evergreen forest) is important for mesomammal occurrence closer to grasslands, but in more interior areas of the park further from grassland, mesomammals are more likely to use sites with lower absolute cover (fewer/smaller trees, typical of more disturbed bamboo forest). This is consistent with our hypotheses given that most of the remaining mesomammals among our community are habitat generalists and known to occur in a wide variety of disturbed and undisturbed environments (see Appendix S3). In addition, frugivore distribution and space use depends heavily on fruit availability (Nakashima et al., 2013). Many of the fruiting trees which make up frugivorous and omnivorous species' diets in disturbed forests are early-successional and pioneer species (e.g., *Calamus* and *Ficus* spp) and are often located near water, regenerating stands, and forest edges ((Vandekerkhove, De Wulf, & Chinh, 1993; Nakashima, Nakabayashi, & Sukor, 2013; Nakabayashi & Ahmad, 2018). In addition, fruit availability in Cat Tien varies seasonally and is highest in the wet season (Bach et al., 2017) which may explain higher detection rates as individuals moved around the landscape in search of dispersed fruiting trees. Disentangling the effects of water, grassland, and forest edge is also difficult as the three are moderately correlated due to the park's geography (r ~ 0.5-0.6; Appendix S8; most supported models included water or grassland; Appendix S5: Table S1). Many of the grassland areas occur close to rivers and streams and tend to be seasonally inundated. Crocodile Lake, a 13,759-ha open wetland and semi-seasonal floodplain located in the core of the park and surrounded by relatively intact forest (Appendix S7: Figure S1), is likely to play an important role in mesomammal occurrence. Further, absolute cover was correlated with tree hollows (Appendix S8), so regions of intact forest with high absolute cover are more likely to provide denning and nesting cavities important to semi-arboreal mesomammals even as they move around forest edges in search of food. Distance to grassland and water was also moderately correlated with distance to ranger station. Thus, hunting and harvesting activities may be reduced in areas closer to water and grassland due to the possible deterring presence of ranger stations.

Anthropogenic variables, including cost distance to urban areas and site-level human detections, did not affect mesomammal community landscape use. This may be due to a combination of factors. Most mesomammals detected within the park have high or medium tolerance to forest disturbance (Appendix S3: Table S1), meaning that they have previously been detected in secondary and regenerating forest, plantations, and grasslands. The high occurrence of these species in more disturbed bamboo-dominated forest provides further evidence that regenerating and secondary forest can still accommodate high mesomammal biodiversity. There is a large quantity of low-risk human activity within the park, including collection of non-timber forest products (NTFP) and tourism, which may have habituated many wildlife species to human presence. These activities are relatively low-impact and may not directly affect wildlife populations except by propagating bamboo regrowth within the forest. NTFP users also use the park largely during the day (Appendix S9: Figure S2), while many mesomammal species are nocturnal, so temporal differentiation may reduce any conflict that would otherwise preclude the species from utilizing high human-use sites.

Hunter presence in the park overall was low, with only 20 confirmed independent hunter detections over the seven-month study period, and exclusively nocturnal (Appendix S9: Figure S1). However, many of our cameras and SD cards were stolen from the higher-risk, high-human-use areas including Dat Do and Ta Lai (Appendix S7: Figure S1), limiting availability of data and precluding generalizations about species occurrence within these high-risk areas. This may bias our occurrence estimates away from the highest-risk areas. In 2016 the Cat Tien National Park Forest Protection Department made 122 arrests and confiscated 42 animals including common palm civet, lesser chevrotain, and stump-tailed macaque. Hundreds to thousands of snares and traps are removed or confiscated from Cat Tien every year (Cat Tien National Park, Unpublished data, 2020). These devices indiscriminately capture a variety of medium-bodied species and have contributed to the depauperate state of many of Southeast Asia's protected areas (Gray et al., 2018). Thus, understanding human activity levels and hotspots within the park and where they overlap sites with high species richness can help identify high conflict zones where conservation actions can be prioritized (Appendix S8: Supplemental information S1). Future enforcement efforts should aim to increase nocturnal patrol efforts particularly in the higher-risk areas identified by our study.

The future of wildlife in Southeast Asia hangs in precarious balance. Well-funded protected areas, such as Cat Tien National Park, can act as a refuge for a wide range of tropical species even under conditions of moderate disturbance. However, the increasing number of "empty forests" globally (Sreekar et al., 2015; Wilkie et al., 2011) are evidence that without adequate measures for minimizing hunting and snaring, protected areas hold little value for preserving biodiversity. All of Vietnam's largest mammals have been extirpated (tiger, Javan rhinoceros) or fragmented into small, isolated populations (Asian elephants, sun bear). The mesomammal community, which is more resilient to disturbance, persists in a few well-managed protected areas but is under constant threat from local and international wildlife trade markets. The loss of Javan rhinoceros from Cat Tien serves as a warning that even under high levels of funding and support, insufficient staffing capacity, low motivation, and complacency in the face of limited data can condemn conservation efforts to failure (Brooke et al., 2014). Community education programs on the economic and intrinsic value of conservation, targeted marketing campaigns to reduce demand for wildlife products, and efficient enforcement of wildlife protection laws are strongly recommended to reduce hunting pressure and forest encroachment. Without these continued efforts, Southeast Asia's remaining mesomammals are at risk of meeting the same fate as their larger predecessors.

MANUSCRIPT 2

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Estimating arboreality and the effects of forest structure on detection of tropical tree-dwelling mesomammals using arboreal camera traps

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Running head: Detection and arboreality of tropical mesomammals

Data are publicly available via the following link:

https://github.com/jmasseloux/AnimalCon2-021_data

Introduction

Tropical forests are the most species-rich biomes in the world due to a year-round abundance of resources and spatial and structural complexity which allows for diverse speciation (Barlow et al. 2007; Gibson et al., 2011). Forest conversion for agriculture and high-intensity logging are among the greatest drivers of tropical biodiversity loss and species extinctions (Newbold et al. 2016; Tilman et al. 2017). Such forest degradation disproportionately affects habitat specialists preferring undisturbed primary forests (Brodie, Giordano, and Ambu 2015; Laurance et al. 2008), and results in homogenized forests composed largely of habitat generalists and edge species (Tabarelli et al. 2012).

Tropical tree-dwelling (arboreal and semi-arboreal) mammals are especially vulnerable to forest conversion (Whitworth et al. 2019; Laurance 1990; Laurance et al. 2008), particularly when reliant on old growth forest structures, such as canopy height, complexity, and connectivity (Cannon and Leighton, 1994). Ecological traits, such as degree of arboreality can also affect species-level responses to forest degradation, where populations of more specialized, strictly arboreal species are more vulnerable to changes in forest structure (Laurance & Laurance 1996; Villaseñor et al. 2014). Forests under moderate levels of disturbance (e.g., low-intensity selective logging) can still retain conservation value and high levels of species richness (Berry et al. 2010; Wearn and Glover-Kapfer 2017; Masseloux et al. In Review). However, overharvest of targeted species, including small carnivores, primates, and pangolins, for the bushmeat, pet, and medicine trade can further endanger forest-dwelling populations (Corlett 2007). The increasing number of “empty forests” (Sreekar et al. 2015; Wilkie et al. 2011) suggests that without adequate measures for minimizing hunting and snaring, even intact forests can experience dramatic declines in species richness and abundance.

Rigorous research on responses to anthropogenic disturbances by arboreal mammal species is crucial for guiding informed decision-making and allocation of limited resources to conservation efforts in tropical regions. However, with the exception of primates, little is known about tropical canopy mammals (Kays & Allison, 2001; Lowman, 2009), due largely to the paucity of research and inefficient sampling methodology. Tropical canopy vertebrates have historically been studied using animal-follows or line transect methods, which involve walking through a forest and counting species as they are detected (e.g., Nekaris, Blackham, & Nijman, 2008). These methods are however limited, as many canopy-dwelling species are rare, cryptic, nocturnal, or behaviorally avoid humans (Duckworth, 1998; Brooke et al., 2014), precluding accurate estimates of abundance or species distribution. Camera trapping (use of automated cameras to capture animal incidences) is a well-documented and preferred method of non-invasively assessing terrestrial mammal populations (Tobler et al., 2008; Rovero & Marshall, 2009), but has rarely been applied to arboreal species. A few recent and novel studies have shown that arboreal camera traps can be useful in detecting species not observed by traditional ground-based techniques (e.g., (Whitworth et al., 2016; Bowler et al., 2017; Moore et al., 2020). However, there is still much to be learned on how to appropriately and efficiently design arboreal camera trapping studies. Furthermore, jointly sampling the terrestrial and arboreal environments via camera traps not only provides a more complete survey of the entire non-volant mammal community, it allows for a new methodology for studying arboreality. The degree of behavioral arboreality of semi-arboreal mammals can be related to forest structure and disturbance (Mekonnen et al., 2018) as well as perceived presence of terrestrial threats (e.g., humans, predators; McGraw & Bshary, 2002; Makin et al., 2012). Estimating degree of arboreality has traditionally been conducted by following semi-arboreal species, mostly primates, which is time and energy intensive and usually limited to diurnal species. Multi-method sampling designs that include arboreal and terrestrial camera traps, in combination with multi-scale occupancy models (Nichols et al., 2008), could be useful to expand these types of studies to rarer and nocturnal species.

Our study objectives were to 1) evaluate the utility of arboreal camera traps as a method of surveying arboreal and semi-arboreal mesomammals, particularly rare and cryptic species, 2) assess the effects of forest structure and anthropogenic disturbance on detection and occurrence of arboreal and semi-arboreal tropical mesomammals within a historically-disturbed protected forest, and 3) estimate degree of arboreality of semi-arboreal species at paired arboreal and terrestrial camera trap sites. We hypothesized that arboreal camera traps will be a useful method for detecting arboreal species not detected on terrestrial cameras, particularly rare and nocturnal species. We also hypothesized that site-level arboreal and semi-arboreal species detection and occurrence would increase where forest structure was most intact (i.e., high absolute cover, high canopy cover, and high canopy connectedness) and would decrease closer to roads (a proxy for human accessibility). Given the long history of anthropogenic disturbance in and around the protected forest, we reasoned that there would be a gradient of species-specific responses. Finally, due to the absence of large predators and low human presence in the park, we hypothesized most semi-arboreal species would display high levels of terrestrial activity.

Methods

Study area

Our study was conducted in Cat Tien National Park, located ~150 km north of Ho Chi Minh City in Southern Vietnam. Tropical Southeast Asia is a biodiversity hotspot that contains the highest proportion of globally unique (endemic) mammal species (Myers et al., 2000; Olson et al., 2001), but suffers from the highest rate of anthropogenic deforestation of any major tropical region (Sodhi et al., 2010). Cat Tien National Park is one of the largest (72,000 ha) and most well-funded national parks in Vietnam and is part of a greater UNESCO Biosphere Reserve buffer zone (https://whc.unesco.org) and Ramsar Site (https://rsis.ramsar.org).

Our study occurred within the core zone of Nam Cat Tien in Dong Nai province (Figure 1a). Nam Cat Tien is composed of secondary mixed evergreen and deciduous lowland dipterocarp forest, bamboo forest, wetland, and grassland. The wide distribution of secondary and bamboo-dominated forest is due to a legacy of anthropogenic disturbance within and around the park. This includes herbicide spraying during the U.S.-Vietnam War between 1965-1970 (Stellman et al., 2003) and logging after the war and prior to its establishment as a protected area in 1992. While forest cover in the core of the park has not changed much since the 1970s, the buffer zone and areas beyond have been extensively converted for small-scale agriculture and anthropogenic development (Vogelmann et al., 2017).

Seventy-six mammal species were confirmed to inhabit Cat Tien National Park during surveys conducted between 1993 and 2001, comprising 30% of Vietnam's known mammal species. Of these, 12 can be classified as native arboreal or semi-arboreal mesomammals (<50 kg; Appendix A), of which 10 (42%) are listed as threatened under IUCN, including Sunda pangolin (*Manis javanicus*) and Elliot's silver langur (*Trachypithecus margarita).*

Camera trapping

We set twenty terrestrial and arboreal camera trap pairs in Nam Cat Tien from June 2019 to September 2020. All cameras (Browning Strikeforce Pro XD) were set in the eastern evergreen and deciduous secondary forest region of the park (Figure 1b). Sites were selected at varying proximity to anthropogenic disturbance (urban areas, park edge, roads), with minimum proximity between adjacent sites at 500 m. Terrestrial cameras were set approximately 30-70 cm off the ground on or near human trails (within 5 m) from June 2019 to January 2020 across three seasons: wet 2019 (June 2019 to October 2019), dry 2020 (November 2019 to April 2020) and wet 2020 (May 2020 to September 2020). Terrestrial cameras were moved off-trail (within 50 meters of the original site) from January to September 2020 due to high theft rates. Arboreal cameras were set within 50 m of the terrestrial camera pair, on a horizontal limb or facing a vertical trunk at a height between 7 and 28 m. All cameras were set to take five successive photographs with a delay period of 1 second and were continuously active for the duration of the study unless tampered with, stolen, or affected by mechanical problems. All cameras had large (32 GB) memory cards to limit revisits. Plans to expand the study in 2020 were annulled by the COVID pandemic and further limited revisits to arboreal cameras. Photos were tagged to species by three observers using the Digikam photo manager (https://digikam.org) and all mesomammal tags were reviewed for accuracy by the lead author.

Covariates

We hypothesized that mesomammal site use would be affected by both environmental and anthropogenic factors. Preliminary analyses suggest that detection rates between seasons were similar in magnitude and terrestrial site type (on vs. off trail) did not vary significantly ($\alpha = 0.05$; Appendix B), thus we pooled our data into two methods (arboreal and terrestrial) per site for the following analyses.

We conducted vegetation surveys at each camera site to quantify forest structure. Site-level terrestrial variables included absolute cover (basal area per hectare, strongly correlated with understory cover) and canopy height. Site-level arboreal variables included focal branch slope, canopy connectivity, and tree diameter at breast height. Spatial variables were calculated in ArcGIS (10.8.1; ESRI 2011) and included Euclidian distance to grassland, water, and roads. We used roads as our metric of anthropogenic disturbance as all roads within the park are regularly used for a variety of human activities (tourism, hunting, bamboo collection) and were not correlated with landscape features. Hypotheses, predictions, and data source for all variables are summarized in Appendix C. We tested for pair-wise correlation among covariates and highly correlated variables ($r > 0.5$) were removed or not included within the same model (Appendix B). All covariates were standardized at a mean of zero and a standard deviation of 1.

Modelling framework

To address objective 1, we assessed the adequacy of our sampling scheme for detecting all possible species using species accumulation curves, estimated in the R package 'vegan' (Oksanen et al. 2020). To address objectives 2 and 3, we used occupancy modeling (MacKenzie et al., 2017) and generalized linear mixed models (GLMMs) for all species with a naïve occupancy greater than 0.1.

General Linearized Mixed Models

We evaluated the effects of forest structure and proximity to roads on the count of independent arboreal mesomammal species detections at camera trap sites using negative binomial generalized linear mixed models. Species-level detection rates can vary due to a species' group size and sociality, activity rates, and abundance. Thus, all models included species as a random effect to account for differences in species-level detection rates and responses within the community. Each hypothesis was represented by two models: one with all variables as fixed effects, and one with up to two variables as random slopes when the slope of the effect was hypothesized to vary by species (Appendix D: Table D1). Models were fit using a Bayesian framework in the R programming language using the package 'rstanarm' (Goodrich, Gabry, and Brilleman 2020). We compared models within a model set using the expected log pointwise predictive density, which was estimated using approximate leave-one-out cross-validation (package 'loo'; Vehtari, Gelman, and Gabry 2017). Default weakly informative priors were used for all parameters.

Single-species and multi-scale occupancy models

We used single-season occupancy modeling (MacKenzie et al., 2002) to estimate the effects of predictor variables on species' detection (p) and occupancy (ψ) probability of all arboreal and semi-arboreal species using detection/non-detection data (Appendix D

Table D2). Occupancy models account for imperfect detections (MacKenzie et al. 2002). Given the variation in range-size by our focal species, it is likely that individuals were able to move in and out of a site within the sampling period. Thus, we interpret our inference on occupancy as the probability a species uses a site during a primary sampling period (asymptotic occupancy; (Mackenzie & Royle, 2005; Efford & Dawson, 2012). We considered differences in species occurrence across the dry and wet season using a stacked modeling approach, where season was a categorical variable (see (Monterroso et al., 2020); due to data sparsity we did not include season as a covariate on occurrence. We did not explicitly model the dynamic changes (i.e., site colonization and extirpation) in occurrence as three seasons were inappropriate to capture these dynamic processes. We used a Bayesian framework to fit and compare models for each arboreal species and estimated parameter effects on p and ψ using the software program MARK (White & Burnham, 1999).

To evaluate differences in occupancy and detection between terrestrial and arboreal methods for semi-arboreal mammals, we used multi-scale occupancy modeling (Nichols et al., 2008). This model permits simultaneous use of data from multiple methods to make method- and site-level inferences about occupancy and detection without the assumption of independence between methods. In our study, site refers to the larger-scale paired camera trap sampling unit and station refers to the method-specific camera trap sampling unit (arboreal or terrestrial). In a single-species multi-scale model, ψ is the probability that the site is occupied, p_t^s is the probability of detection on occasion t by method s, given that the site is occupied and the species is present at the sample station, and θ^s is the probability that the species is present at the immediate sample station given that the site is occupied. Comparing $\theta^{\text{Terrestrial}}$ and θ^{Arboreal} allows us to evaluate the degree of arboreality by a species. All parameters can be modelled as functions of site-specific covariates, and p^s and θ^s can be modelled as a function of method-specific co-variates. To minimize overparameterization, we built the candidate model set for each species using the most supported model from our single-species arboreal occupancy analyses. Specifically, we used the same variables on arboreal detection probability and added absolute cover as a terrestrial-level detection covariate as it was strongly (r ~ 0.96) correlated with understory cover, which may constrain terrestrial species' movement and camera trap detection distance (Appendix C; Table C1). We also considered a categorical covariate for dry vs wet season across both arboreal and terrestrial detection. The sample station parameter (θ^s) was always modeled with a difference in arboreal and terrestrial station occurrence. Lastly, we included one of five possible covariates on ψ (Appendix D Table D2). We fit and compared multi-scale models in a Bayesian framework for each semi-arboreal species and estimated parameter effects using MARK (White & Burnham, 1999).

All occupancy models were fit using diffuse normally distributed priors on all logit-scaled effects on detection and site-level occupancy ($\mu = 0$, $\sigma = 1.75$; Cooch and White, 2020). For each model, we fit two parallel Markov-chain Monte Carlo chains of 10,000 iterations with a tuning of 4,000 and a burn in of 2,000. We assessed parameter convergence by visually inspecting trace plots and using the Gelman-Rubin statistic to ensure values were less than 1.1 (Gelman & Rubin, 1992). We compared models using Watanabe-Akaike Information Criterion (WAIC; Watanabe, 2013); smaller WAIC values indicate greater support for the model. We make inference using estimated mean effects and 95% Bayesian credible intervals (BCI) from the top supported model. We quantify support for estimated species and community effects by reporting the probability of a non-zero effect, derived as the proportion of posterior samples <0 or >0; we qualitatively evaluate strong support as a proportion >0.9 and moderate support >0.7 and <0.9.

Results

We detected a total of 13 species on the arboreal cameras and 17 species on the terrestrial cameras (Appendix A). Six species were only detected arboreally (e.g., yellow-cheeked gibbon *Nomascus gabriellae*, small-toothed palm civet *Arctogalidia trivirgata*), 10 species were only detected terrestrially (e.g., lesser chevrotain *Tragulus kanchil*, crab-eating mongoose *Herpestes urva*), and 7 species were detected both on the ground and in the trees (e.g., yellow-throated marten *Martes flavigula*, pig-tailed macaque *Macaca nemestrina*; Appendix A). The species accumulation curves suggest all or almost all species were detected, although we have greater confidence for terrestrial species richness (Figure 2; Appendix B). In addition, according to the Polet and Ling (2004) and Murphy and Duy Thuc (2002) CTNP biodiversity list, our arboreal surveys detected all arboreal and semi-arboreal mesomammals previously detected in the park with the exception of binturong (which have not been sighted in the park since 2002; Murphy & Duy Thuc, 2002). In the following analyses, we did not include Elliot's silver langur, Sunda pangolin, pygmy slow loris (*Nycticebus pygmaeus*), and stump-tailed macaque due to the sparsity of detections.

General Linearized Mixed Models

We fit 18 arboreal multi-species GLMM models (Appendix E: Table E2). The most supported model included canopy connectivity and distance to road as varying across the community of species (i.e., random slopes) and distance to grassland as a fixed effect for the community (Figure 3a; Appendix E Table E1). There was strong support for the positive effect of distance to grassland across all species ($\beta = 0.52$; 95% BCI = 0.34, 0.72; Pr>0 = 1). The effect of canopy connectivity was positive with strong to moderate support for all species except for yellow-cheeked gibbon (Figure 3a; Appendix F Table F1). There was also strong to moderate support for most species displaying greater detections close to roads (e.g., black-shanked douc-langur, common palm civet). A competing model (Appendix E: Table E2) included camera height and focal branch slope as varying across the community of species with canopy connectivity as a fixed community effect (Figure 3b; Appendix E Table E1). Canopy connectivity had a positive effect across all species ($\beta = 0.81$; 95% BCI = 0.65, 0.98; Pr>0 = 1.00) while the effects of branch slope and camera height varied widely by species (Figure 3b; Appendix F Table F1). The number of independent detections increased at lower branch slopes for black-shanked douc-langur and yellow-cheeked gibbon and increased at higher branch slopes for all three small carnivores. The macaque species and black giant squirrel did not appear to have a strong preference in branch slope. Species-level responses to camera height varied from a positive effect (e.g., black giant squirrel, yellow-cheeked gibbon), to a negative effect (e.g., common palm civet, long-tailed macaque) and no clear effect (e.g., small-toothed palm civet, black-shanked douc-langur).

Single-species arboreal occupancy models

We fit and compared 35 candidate models for each arboreal and semi-arboreal species (arboreal data only; Appendix E Table E2). Estimated mean occupancy probabilities for arboreal species varied from 0.27 (yellow-cheeked gibbon) to 0.76 (pig-tailed macaque; Table 1a). The most supported model varied by species, but recurring detection covariates were canopy connectivity, camera height, and focal branch diameter (Figure 4; Appendix F Table F2). Canopy connectivity and camera height had medium positive effects on most species except black giant squirrel, for which camera height had no effect, and yellow-throated marten, for which canopy connectivity had no effect (Figure 4). Larger branch size increased detection for most species except pig-tailed macaque, small-toothed palm civet, and flying squirrel. Detection of long-tailed macaque was strongly associated with increasing distance from the canopy, and a negative effect of camera height (from the second most supported that included the covariate; Appendix E: Table E2d), suggests that long-tailed macaque detections increase in the sub-canopy. Dry season had a small to moderate effect ($|\beta| <1$) on detection of most species. Several model sets included parsimonious occupancy covariates, likely due to the high naive occupancy for several of our species and the low number of sample sites. There was strong support for the positive effect of distance to water on occurrence of long-tailed macaque and canopy height on occurrence of gibbon and flying squirrel. There was strong support for the negative effect of absolute cover on occurrence of black-shanked douc-langur and yellow-throated marten, and distance to road on the occurrence of black giant squirrel, pig-tailed macaque, and common palm civet (Figure 4; Appendix F Table F2).

Single-species multi-scale occupancy models

We fit 5 candidate models for each semi-arboreal species (terrestrial and arboreal data; Appendix E: Table E3). There was strong support for a negative difference of the effect between terrestrial and arboreal station-level occupancy (Θ_{Arb}) for all species (Pig-tailed macaque: mean = -2.77, 95% BCI = -4.15, -1.5, Pr<0 = 1; long-tailed macaque:

mean = -1.24, 95% BCI = -2.02, -0.55, Pr<0 = 1; common palm civet: mean = -3.64, 95% BCI = -4.98, -2.5, Pr<0 = 1; yellow-throated marten: mean = -0.74, 95% BCI = -2.17, 0.57, Pr<0 = 0.88). Arboreal occurrence and detection were consistently lower than terrestrial, but differences in probability varied widely by species. We found the pig-tailed macaque to be highly arboreal, but also almost equally terrestrial (Table 1b), while the long-tailed macaque was almost half as arboreal as terrestrial. The common palm civet was highly terrestrial and was more arboreal than the long-tailed macaque, but less than the pig-tailed macaque. Lastly, yellow-throated marten was highly terrestrial and only 18% less arboreal. There was substantial model selection uncertainty for ψ for all species (all WAIC values were within a difference of 2) except the long-tailed macaque. For long-tailed macaque, distance to road had a large positive effect on occurrence and absolute cover had a small negative effect on terrestrial detection (Figure 5; Appendix F Table F3). Dry season had a medium positive effect on civet detection and a medium negative effect on pig-tailed and long-tailed macaque detection. The effect of absolute cover on terrestrial detection was small and had low support for all species (Figure 5; Appendix F Table F3). Mean occupancy estimates using the multi-scale models were significantly higher than occupancy estimates from the single-species arboreal models for all species, and significantly higher than occupancy estimates from the single-species terrestrial models for yellow-throated marten and long-tailed macaque (Table 1a and 1b; Appendix E: Table E4).

Discussion

Environmental and anthropogenic spatial and structural characteristics can affect species' use of and distribution within a landscape (Gehring & Swihart, 2003; Grelle, 2003). Quantifying these dynamics for arboreal species has been traditionally constrained to costly, time-intensive methods mostly suited for diurnal, larger bodied species. More cryptic, small-bodied, nocturnal, and rare species are often forgotten, resulting in data deficiencies which may endanger conservation efforts for threatened species. Our study supports arboreal camera trapping as a promising new field technique for monitoring the entire community of semi- and fully-arboreal mesomammals. In addition, we highlight the importance of camera placement (camera height, branch placement, canopy structure), which can help guide future studies in improving detection of focal species. Further, we offer a new method for quantifying arboreality by semi-arboreal mammals using multi-scale occupancy models.

Based on our species accumulation curves and aggregated species detections from previous surveys, we are relatively confident that we detected most arboreal and terrestrial mesomammal species currently known to inhabit Nam Cat Tien. Our study recorded 8 independent detections of the endangered Elliot’s silver langur (IUCN, 2015), providing the first camera-trap evidence of these species ever recorded in Cat Tien National Park; a small population is known to occur, but has been rarely sighted. Surprisingly, Sunda pangolin were only detected once on our arboreal camera traps, compared to 15 detections on the ground, suggesting they may be less arboreal than previously thought. However, their low detections precluded any formal modeling or strong conclusions. Such findings support how arboreal camera traps are a promising tool that still require further study for optimizing the passive monitoring of the presence and distribution of rare and cryptic species.

We found several structural forest characteristics can affect detections of mesomammals by arboreal cameras. As we hypothesized, canopy connectivity was a strong determinant of species detections, as trees with more connections to proximate trees can act as arboreal highways, facilitating movement through the canopy. Arboreal mammals generally prefer to move through the canopy along established routes that maximize revisits to known resource locations (e.g., fruiting trees) while avoiding large gaps in the canopy (Cannon and Leighton 1994). While no species displayed an aversion to roads, wide roads that create large canopy gaps can impede the movement and distribution of more strictly arboreal species, such as gibbon and black-shanked douc-langur. Reduced arboreal connectivity may also force arboreal and semi-arboreal species to spend more time moving on the ground, increasing exposure to terrestrial predators, human hunters, and snares (Mekonnen et al., 2018).

The effect of tree and focal limb characteristics on species detection appears to be most likely explained by morphological adaptations and tree use behavior. Species which were predominantly detected at higher canopy height or within the emergent canopy level (e.g., yellow-cheeked gibbon, black-shanked douc-langur, black giant squirrel) were detected more often on more vertically sloped tree limbs. These species are more likely to spend time climbing for access to the high canopy and may spend less time crossing or resting on horizontal limbs within the mid- or sub-canopy. Preference for higher canopy has been previously documented in gibbons and giant squirrels (Cannon & Leighton, 1994; Datta & Goyal, 1996). Indian giant flying squirrel detections were also strongly associated with more vertical tree slopes, likely due to their primary mode of locomotion, which involves climbing and gliding between tree trunks. Semi-arboreal species were detected more at sites with higher canopy connectivity and at lower camera heights, suggesting they may spend more time in mid- and sub-canopy where access to terrestrial resources is easier. This effect varied among species, suggesting a possibility of niche partitioning, particularly among primates. While arboreal specialists, such as gibbons, occur and utilize resources more in higher canopy, semi-arboreal long-tailed and pig-tailed macaques utilize resources at lower canopy levels.

Snares, which indiscriminately capture medium-bodied mammals, are deployed in vast quantities within Southeast Asian forests and are likely a primary cause of the current defaunation crisis in the region (Gray et al., 2018). The degree a species is arboreal may thus be a useful metric for assessing vulnerability of semi-arboreal fauna to this terrestrial threat. While all four of our semi-arboreal species occurred more terrestrially than arboreally, the degree of difference varied by species. For example, common palm civet was half as likely to occur arboreally than terrestrially at our sites (Table 1b). Thus, we could infer that common palm civet spend more time moving and foraging terrestrially through the forest and are thus likely to be more at risk from terrestrial snares and/or hunters compared to the other semi-arboreal species. This risk may be further exacerbated by their higher occurrence close to roads, where human accessibility is greater.

Our study provides preliminary suggestions of important metrics for species-specific detection in tropical forests at the canopy level. Arboreal station detection rates were lower than terrestrial stations for almost all species. Future studies on the arboreality and occurrence of arboreal mesomammals should set cameras to maximize detection of the focal species. In addition, mean occupancy was underestimated for most semi-arboreal species when only one method was used. Multi-method sampling designs coupled with multi-scale occupancy models may thus improve estimates of species distribution and habitat use, which are important for guiding management and conservation decisions. Our limited sample size precluded use of covariates on method-specific occupancy (θ^s), but future research efforts could expand on this application of the multi-scale method by examining changes in degree of arboreality over more explicit gradients of forest structure and anthropogenic activity. While costly and time-intensive to set up (we set an average of 1-2 arboreal cameras per day), we demonstrated that arboreal-terrestrial camera trapping studies can be maintained long-term with minimal revisit effort, are useful for detecting and monitoring rare arboreal species of conservation concern, and provide inference to the entire mesomammal community. Our study demonstrates the importance of canopy connectivity and other mature forest characteristics, especially for highly arboreal species. Thus, conservation actions in the region should prioritize the protection of mature forest and mitigate terrestrial threats to ensure the persistence of arboreal and semi-arboreal mesomammals.

TABLE 1.

(a)

	ψ		p	
Species	*Mean*	*SE*	*Mean*	*SE*
Black-shanked douc-langur	0.65	0.07	0.19	0.02
Yellow-cheeked gibbon	0.27	0.09	0.05	0.02
Pig-tailed macaque	0.76	0.06	0.26	0.02
Long-tailed macaque	0.29	0.08	0.12	0.03
Common palm civet	0.53	0.11	0.10	0.02
Small-toothed palm civet	0.48	0.09	0.11	0.02
Yellow-throated marten	0.54	0.11	0.06	0.01
Black giant squirrel	0.36	0.07	0.18	0.02
Indian giant flying squirrel	0.44	0.08	0.13	0.02

(b)

	ψ		$\theta^{\text{Terrestrial}}$		θ^{Arboreal}	
Species	*Mean*	*SE*	*Mean*	*SE*	*Mean*	*SE*
Pig-tailed macaque	0.99	0.01	0.98	0.01	0.77	0.04
Long-tailed macaque	0.85	0.08	0.61	0.08	0.31	0.06
Common palm civet	0.98	0.01	0.97	0.02	0.51	0.06
Yellow-throated marten	0.90	0.06	0.78	0.09	0.64	0.10

	$p^{\text{Terrestrial}}$		p^{Arboreal}	
Species	*Mean*	*SE*	*Mean*	*SE*
Pig-tailed macaque	0.43	0.01	0.43	0.01
Long-tailed macaque	0.17	0.02	0.17	0.02
Common palm civet	0.33	0.01	0.33	0.01
Yellow-throated marten	0.08	0.01	0.08	0.01

FIGURE 1.

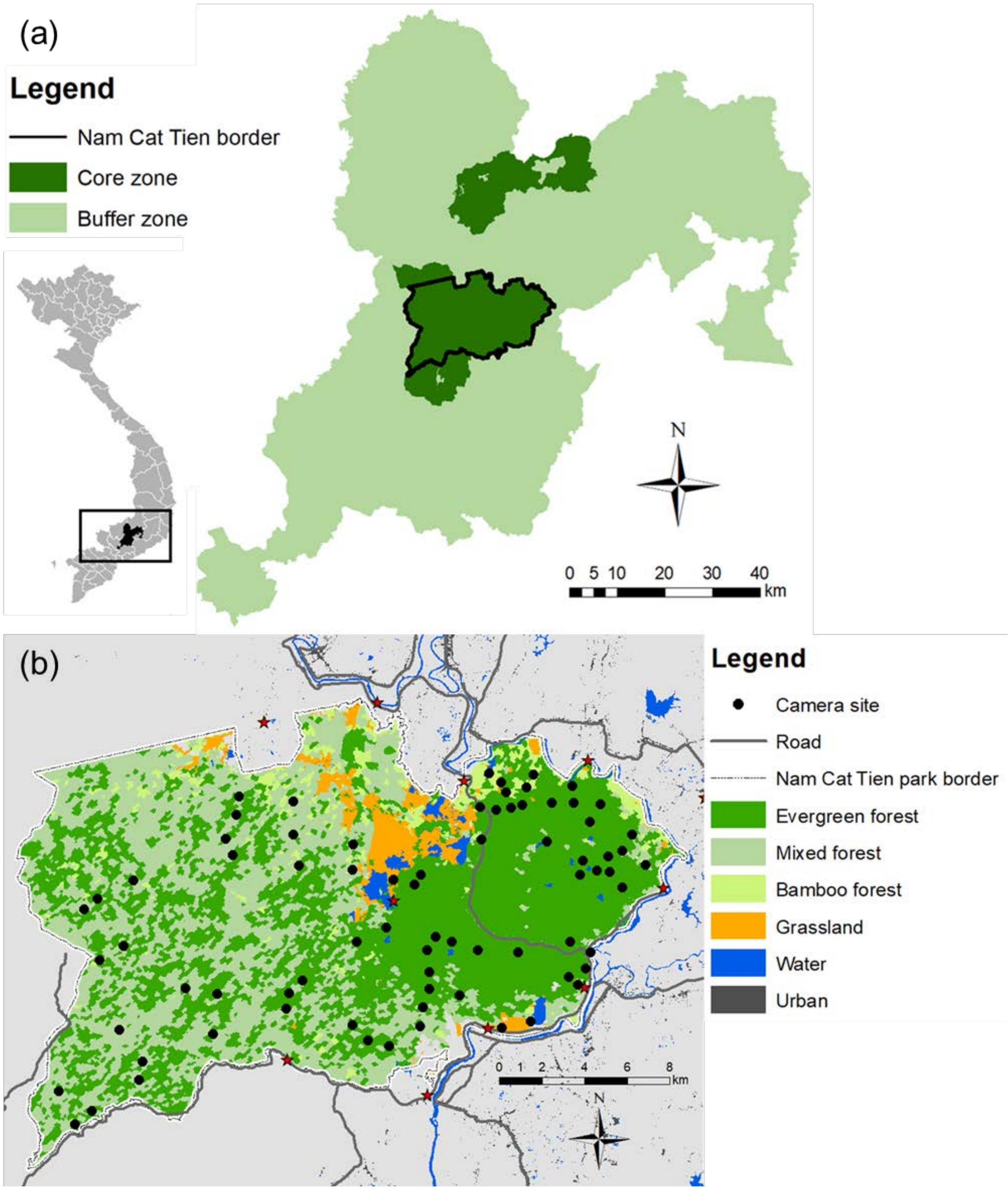

(a)
Legend
Nam Cat Tien border
Core zone
Buffer zone
N
0 5 10 20 30 40
km
(b)
Legend
Camera site
Road
Nam Cat Tien park border
Evergreen forest
Mixed forest
Bamboo forest
Grassland
Water
Urban
0 1 2 4 6 8
km
N

FIGURE 2.

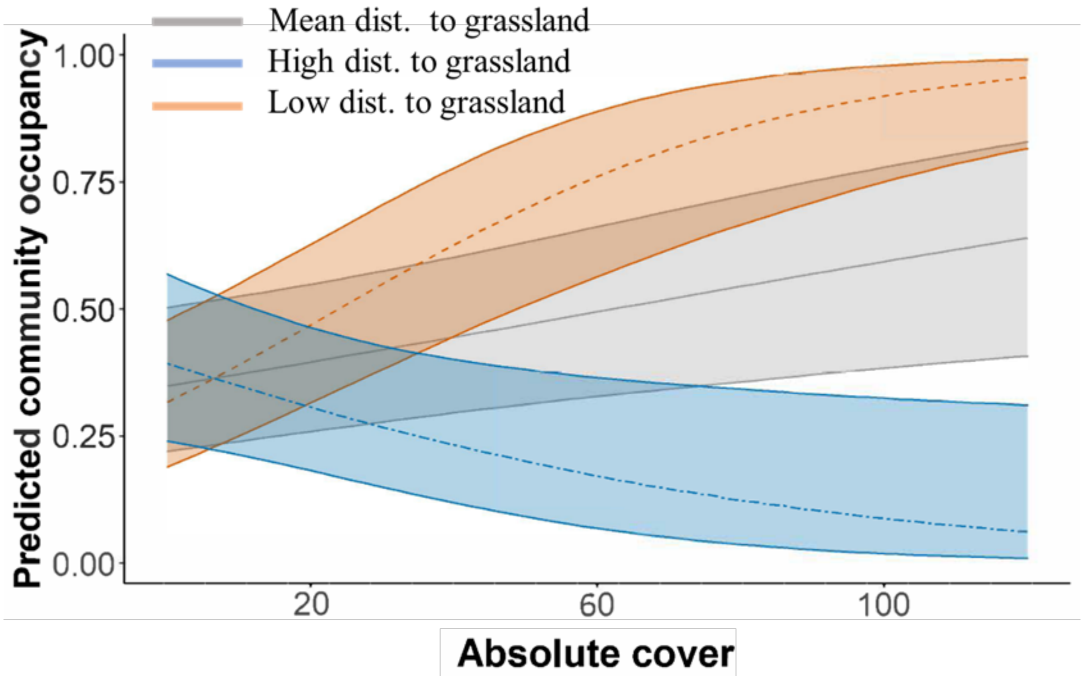

Mean dist. to grassland
High dist. to grassland
Low dist. to grassland
Predicted community occupancy
1.00
0.75
0.50
0.25
0.00
20
60
100
Absolute cover

FIGURE 3.

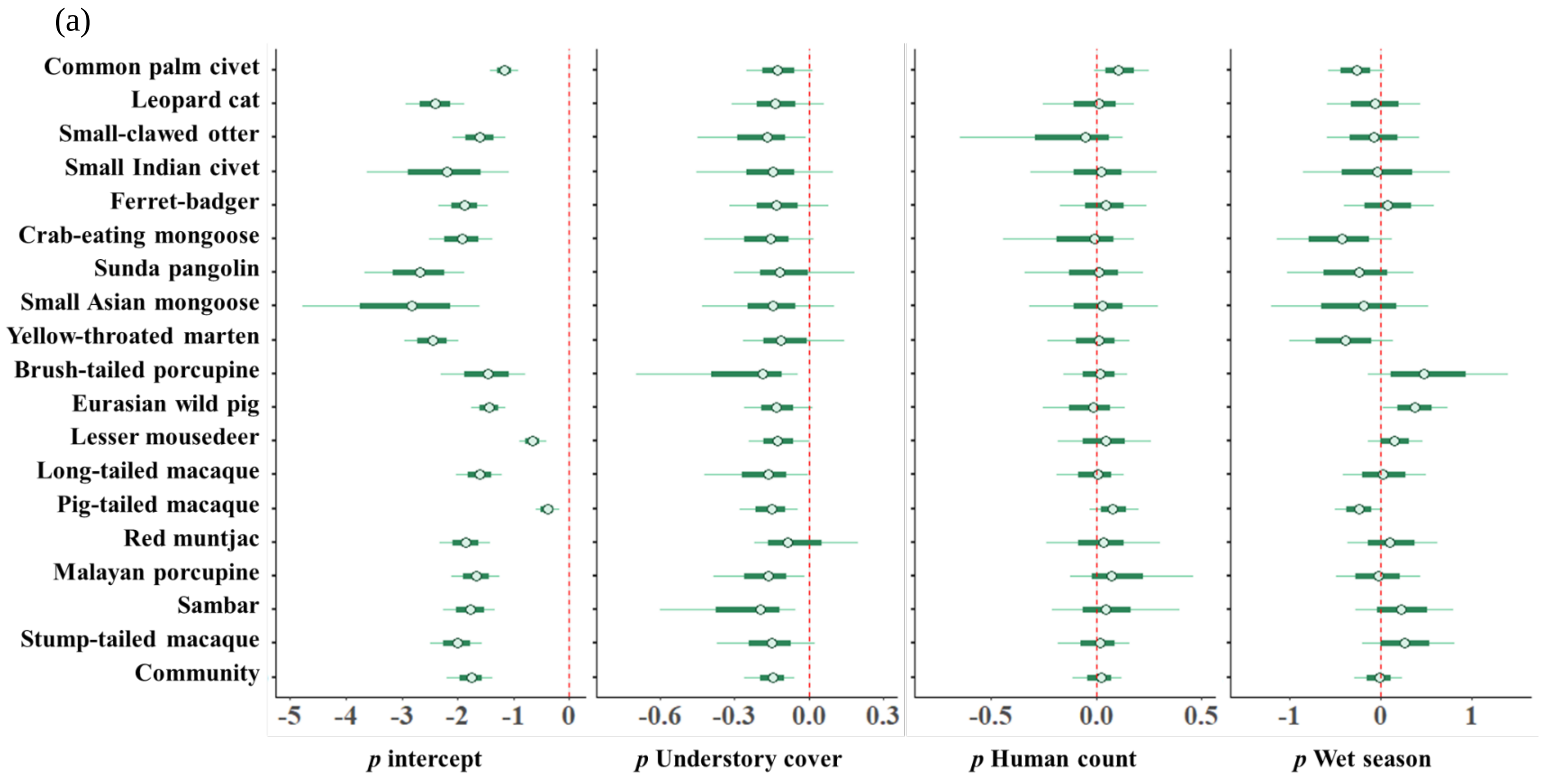

(a)
Common palm civet
Leopard cat
Small-clawed otter
Small Indian civet
Ferret-badger
Crab-eating mongoose
Sunda pangolin
Small Asian mongoose
Yellow-throated marten
Brush-tailed porcupine
Eurasian wild pig
Lesser mousedeer
Long-tailed macaque
Pig-tailed macaque
Red muntjac
Malayan porcupine
Sambar
Stump-tailed macaque
Community
-5
-4
-3
-2
-1
0
p intercept
-0.6
-0.3
0.0
0.3
p Understory cover
-0.5
0.0
0.5
p Human count
-1
0
1
p Wet season

FIGURE 3.

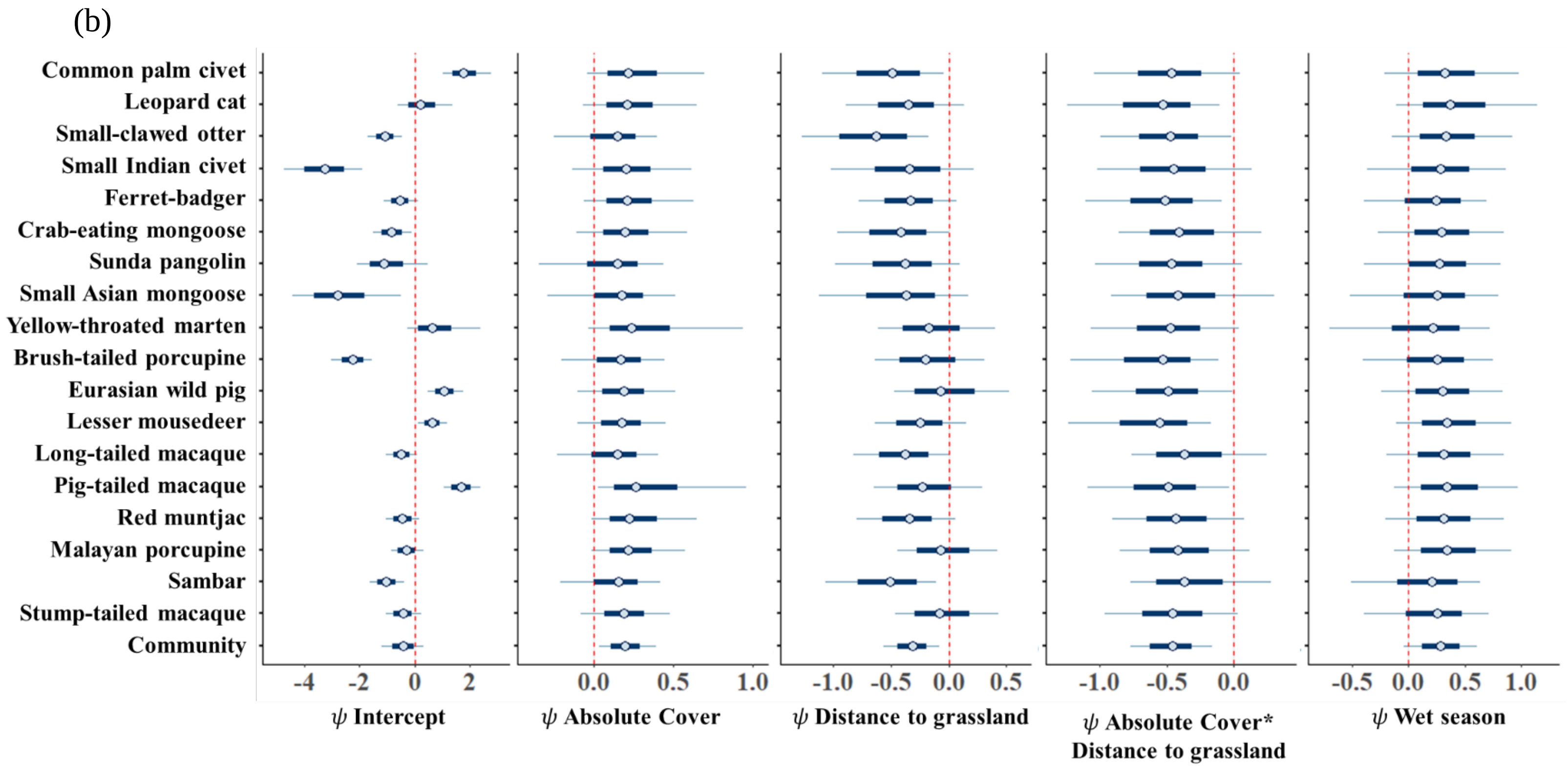

(b)
Common palm civet
Leopard cat
Small-clawed otter
Small Indian civet
Ferret-badger
Crab-eating mongoose
Sunda pangolin
Small Asian mongoose
Yellow-throated marten
Brush-tailed porcupine
Eurasian wild pig
Lesser mousedeer
Long-tailed macaque
Pig-tailed macaque
Red muntjac
Malayan porcupine
Sambar
Stump-tailed macaque
Community
-4
-2
0
2
ψ Intercept
0.0
0.5
1.0
ψ Absolute Cover
-1.0
-0.5
0.0
0.5
ψ Distance to grassland
-1.0
-0.5
0.0
ψ Absolute Cover* Distance to grassland
-0.5
0.0
0.5
1.0
ψ Wet season

FIGURE 4.

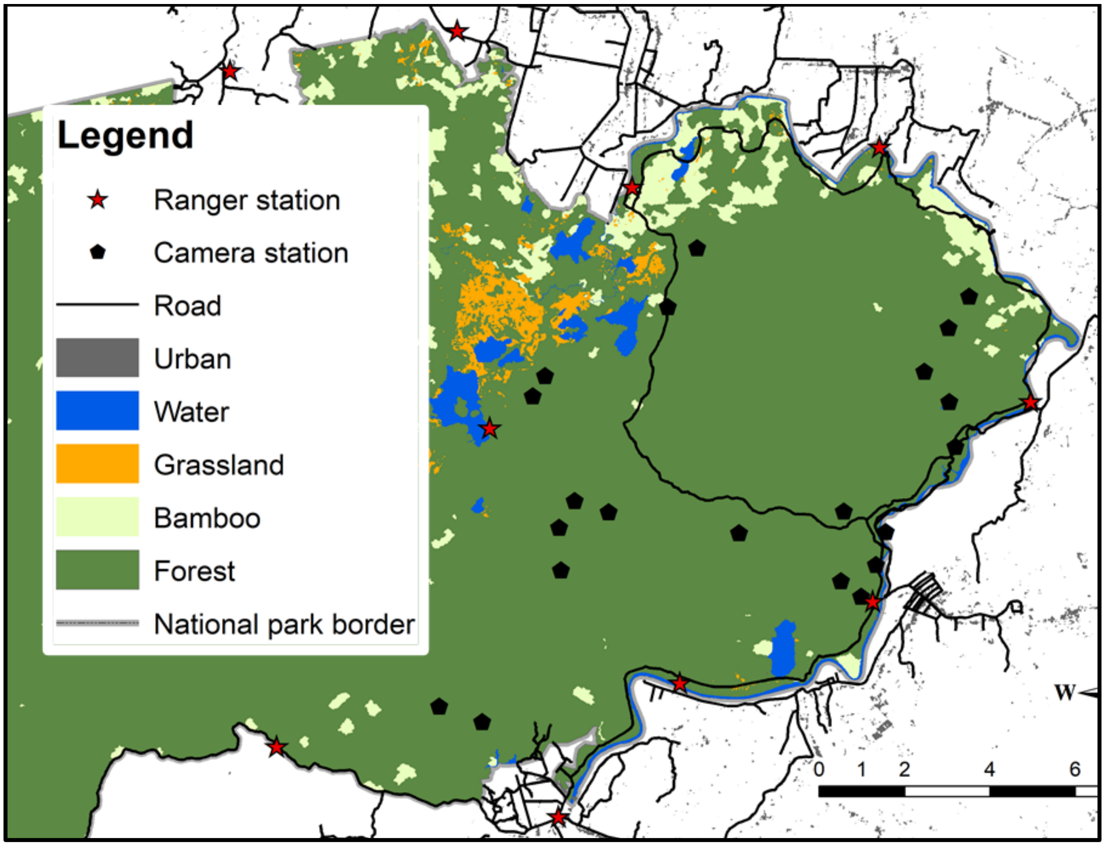

Legend
Ranger station
Camera station
Road
Urban
Water
Grassland
Bamboo
Forest
National park border
W
0
1
2
4
6

FIGURE 5.

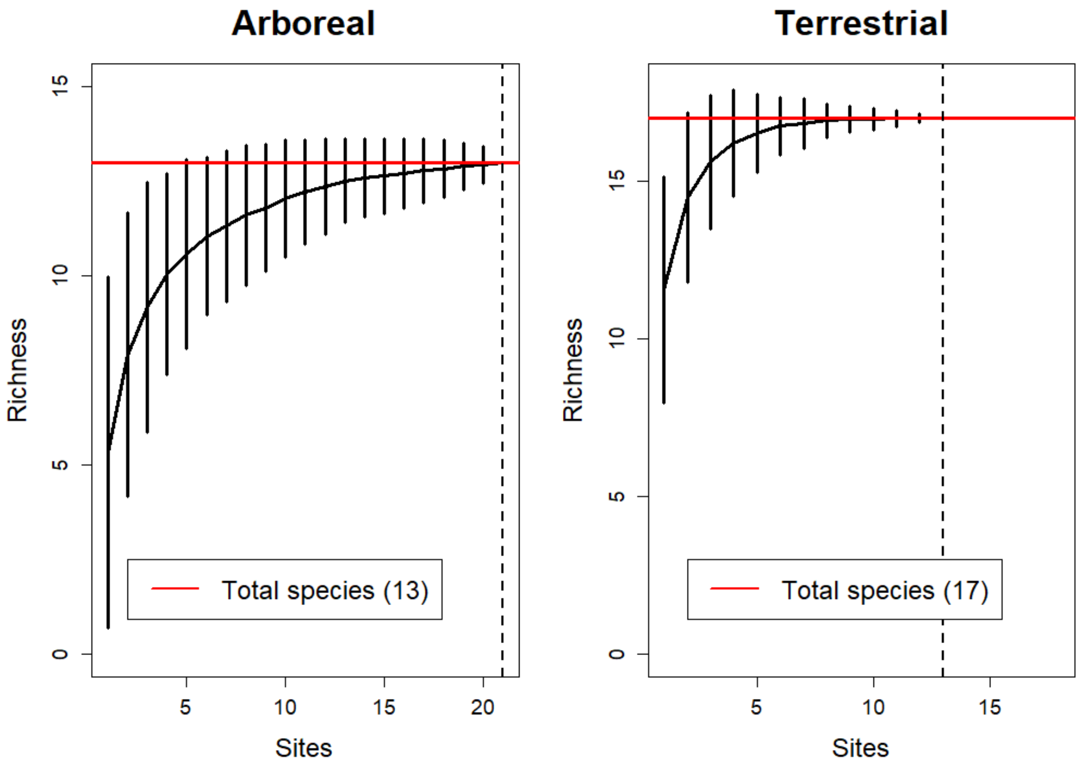
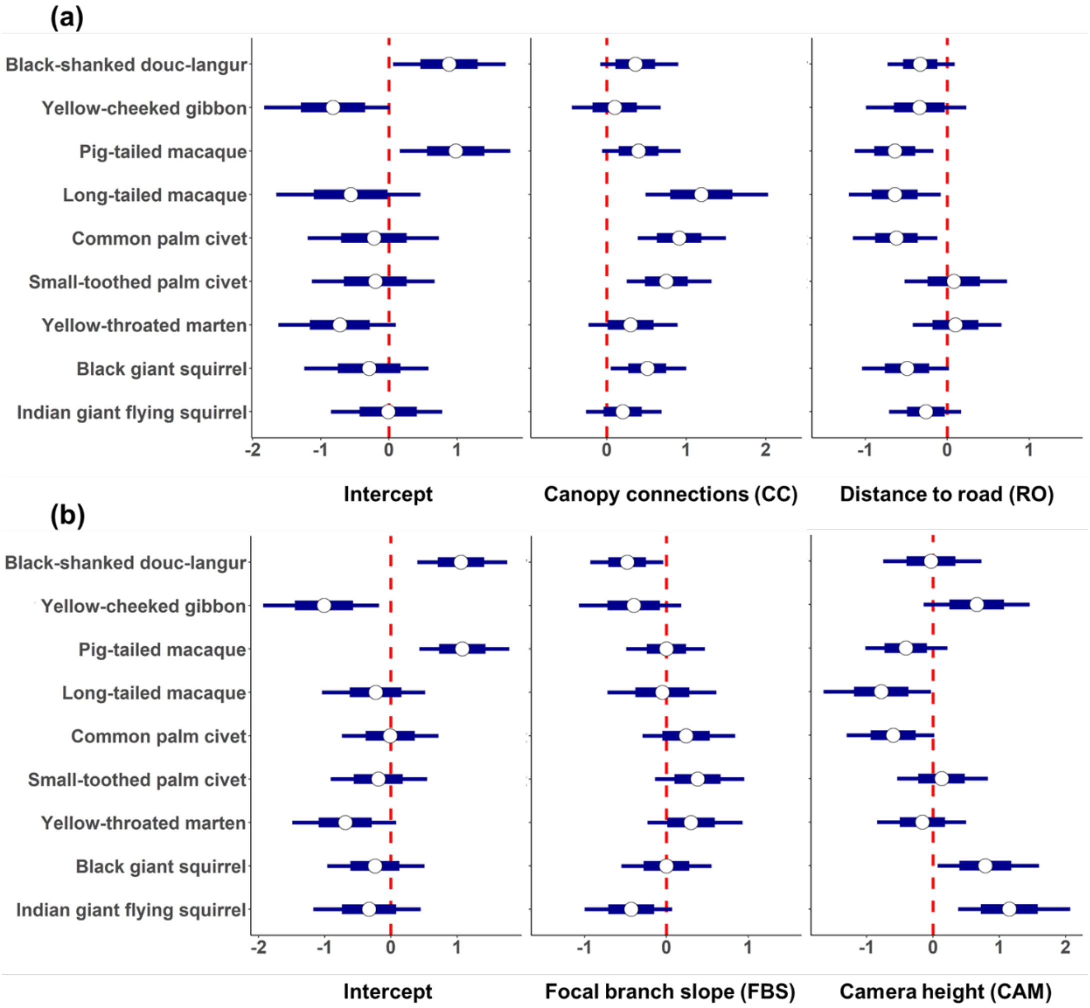
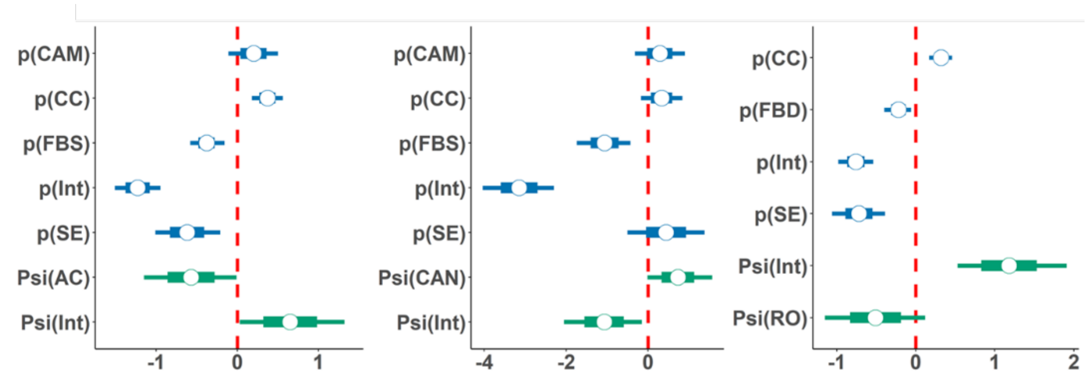

Arboreal
Terrestrial
Richness
Sites
Total species (13)
Total species (17)
0
5
10
15
20

FIGURE 6.

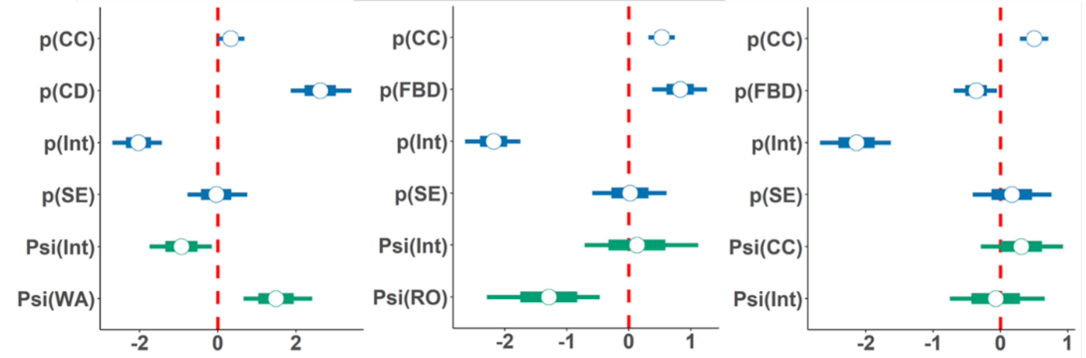


(a)
Black-shanked douc-langur
Yellow-cheeked gibbon
Pig-tailed macaque
Long-tailed macaque
Common palm civet
Small-toothed palm civet
Yellow-throated marten
Black giant squirrel
Indian giant flying squirrel
-2
-1
0
1
Intercept
0
1
2
Canopy connections (CC)
-1
0
1
Distance to road (RO)
(b)
Black-shanked douc-langur
Yellow-cheeked gibbon
Pig-tailed macaque
Long-tailed macaque
Common palm civet
Small-toothed palm civet
Yellow-throated marten
Black giant squirrel
Indian giant flying squirrel
-2
-1
0
1
Intercept
-1
0
1
Focal branch slope (FBS)
-1
0
1
2
Camera height (CAM)

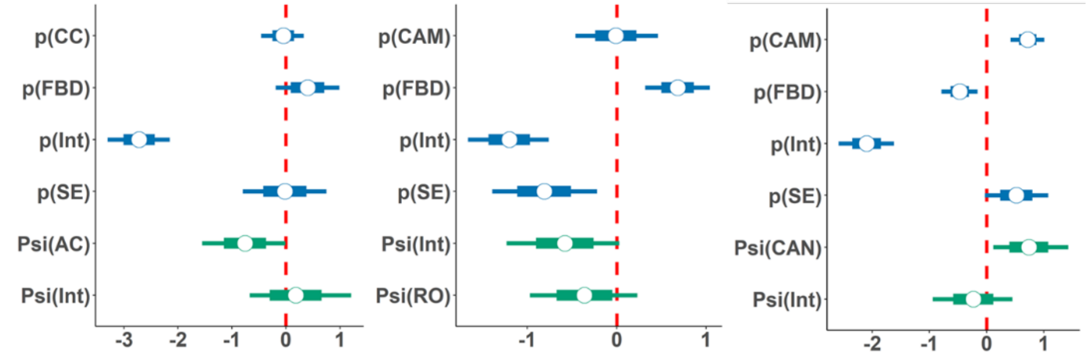
FIGURE 7.



Black-shanked douc langur Yellow-cheeked gibbon Pig-tailed macaque

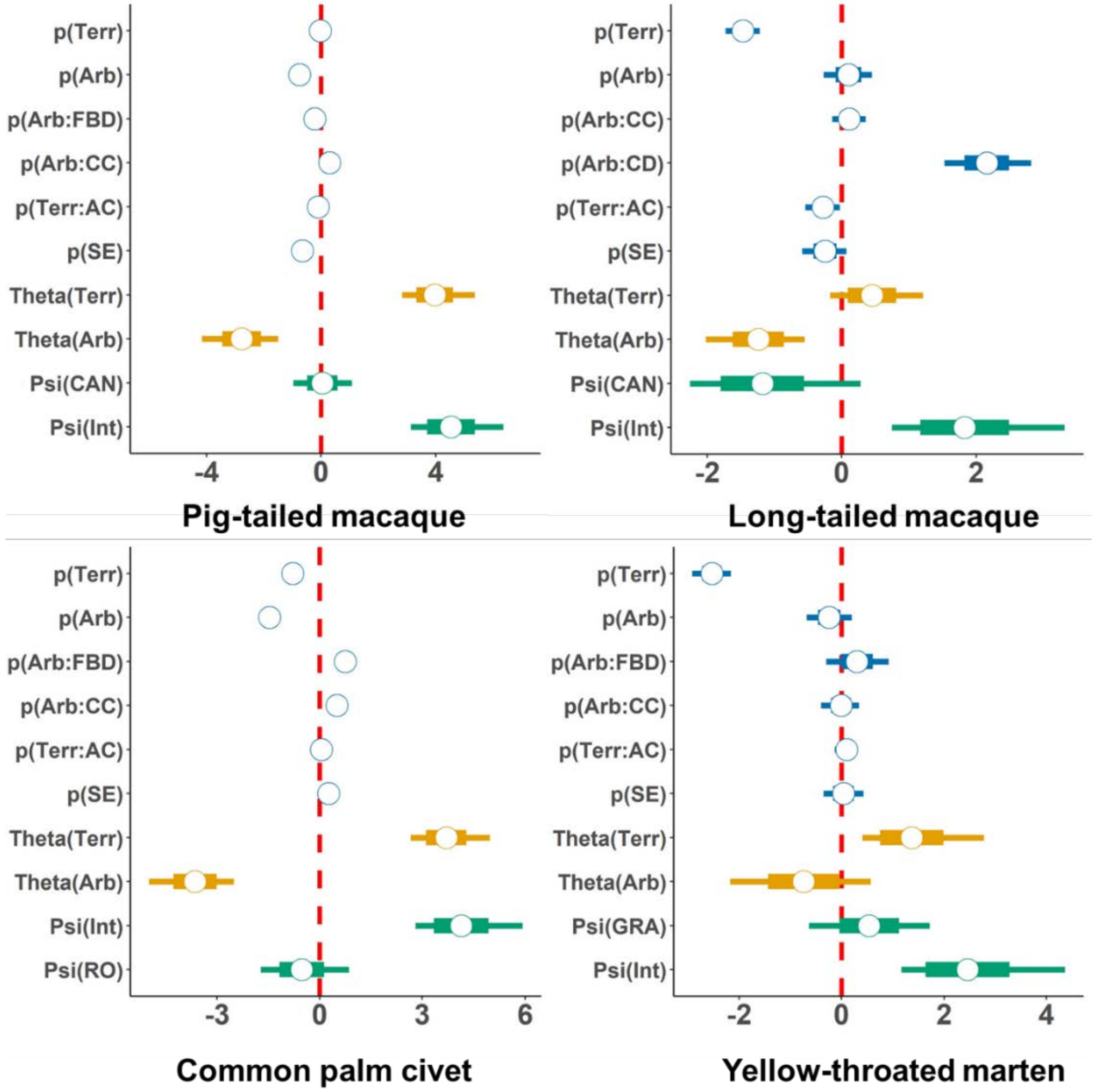


Long-tailed macaque Common palm civet Small-toothed palm civet



Yellow-throated marten Black giant squirrel Indian giant flying squirrel

FIGURE 8.


p(Terr)
p(Arb)
p(Arb:FBD)
p(Arb:CC)
p(Terr:AC)
p(SE)
Theta(Terr)
Theta(Arb)
Psi(CAN)
Psi(Int)
-4
0
4
Pig-tailed macaque
p(Terr)
p(Arb)
p(Arb:CC)
p(Arb:CD)
p(Terr:AC)
p(SE)
Theta(Terr)
Theta(Arb)
Psi(CAN)
Psi(Int)
-2
0
2
Long-tailed macaque
p(Terr)
p(Arb)
p(Arb:FBD)
p(Arb:CC)
p(Terr:AC)
p(SE)
Theta(Terr)
Theta(Arb)
Psi(Int)
Psi(RO)
-3
0
3
6
Common palm civet
p(Terr)
p(Arb)
p(Arb:FBD)
p(Arb:CC)
p(Terr:AC)
p(SE)
Theta(Terr)
Theta(Arb)
Psi(GRA)
Psi(Int)
-2
0
2
4
Yellow-throated marten

APPENDICES

APPENDIX S1

Table 1: Variable information and estimation methods used for all covariates included in the mesomammal occupancy models.

Covariate	Data type	Literature	Resolution	Measurement method	Estimation method
Environmental					
Understory cover	Continuous	Weller 2019	50m x 50m	Point centered quarter estimator (Pollard 1971)	A Photograph of a red 2x1-meter tarp was taken five meters from each PCQ interval point (0m, 17m, 35m) for a total of 9 photos per site. For each photo, we estimated the proportion of vegetation obstructing the red tarp by using the CountColors package in R to calculate the proportion of green color pixels (Weller 2019). The mode across all photos at a site was used for site-level covariate.
Basal area	Continuous	Mitchell 2007	50m x 50m	Point centered quarter estimator (Pollard 1971)	We measured nearest tree distances, height, and diameter at breast height (DBH >30 cm) at each PCQ interval location to estimate basal area and used Mitchell 2007's PCQ method to correct for missing values where trees were inaccessible or >200m away
Absolute cover	Continuous	Mitchell 2007	50m x 50m	Point centered quarter estimator (Pollard 1971)	We measured nearest tree distances, height, and diameter at breast height (DBH >30 cm) at each PCQ interval location to estimate absolute cover (basal area/ha) and used Mitchell 2007's PCQ method to correct for missing values where trees were inaccessible or >200m away
Distance to grassland	Continuous	Duong 2018	10m	ArcGIS analysis	Proximity to grassland was measured from high-resolution remote-sensing Geographic Information Systems data (Duong 2018) and geospatial vectors using the Near tool in ArcGIS and constrained to within park boundaries to reduce confounding with crop or grazing land

Distance to water	Continuous	Duong 2018	10m	ArcGIS analysis	Proximity to water was measured from high-resolution remote-sensing Geographic Information Systems data (Duong 2018) and geospatial vectors using the Near tool in ArcGIS
Latitude	Continuous	NA	NA	NA	Site latitude was obtained from geographic coordinates
Percent high canopy	Continuous	NA	50m x 50m	Point centered quarter estimator (Pollard 1971)	The percent of canopy above 15m in height was estimated by eye in 20% increments at each PCQ interval. The mode across all estimates was used for the site-level covariate.
Bamboo forest	Categorical	NA	50m x 50m	Point centered quarter estimator (Pollard 1971)	Landcover classifications were assigned to each camera site during vegetation surveys; bamboo forest was defined as secondary forest dominated by Bambusoideae
Season	Categorical	NA	Regional	Online historical database	Seasons were determined from changes in daily precipitation in Ho Chi Minh City (from World Weather Online). This was calculated from monthly rainfall divided by number of rain days, whereby the wet season had higher average daily precipitation (12.7-15.2 cm) and dry season had lower average daily precipitation (0.25-8.25).
Anthropogenic					
Pathcost to urban area	Continuous	Duong 2018	10m	ArcGIS analysis	A least-cost path analysis was used to determine path cost from each site to the nearest urban landcover classification cell (defined as land covered by buildings and other man-made structures; Duong 2018) using a cost raster which incorporated roads and urban build up (cost = 1), forest and other (cost = 10), and large water bodies (cost = 30) which could be easily traversed by boat. Final cost paths were validated by national park staff.

Human count	Continuous	NA	NA	Camera trap	The count of independent (>30 minute) camera trap detections of humans was summed across surveys within a season (wet and dry) for each site. Counts were strongly (99.9%) correlated with counts scaled for effort.
Protection effort	Continuous	NA	300m	Tracklog data	Protection effort was calculated by performing a kernal density analysis in ArcGIS using ranger tracklog data from 2017 to 2020 converted into points with a 100m search radius (assumed to be a realistic detection zone of humans by rangers). Points within 50m of a ranger station or road were removed, as these areas tended to over-accumulate points and would skew true patrol densities. The mean kernal density within a 300m buffer zone around each camera trap site was used as a metric of protection effort by rangers.

APPENDIX S2

Table S1. Hypotheses and predictions of candidate models describing how habitat and anthropogenic disturbance affects occurrence of small carnivores and mesomammals in Cat Tien National Park, Vietnam. Note that the first row indicates the hypotheses and predictions for the sub-model on detection probability (p), while all other rows indicate the sub-model on occupancy (ψ).

Name	**Model**	**Hypothesis**	**Prediction**
All Models	p(UC + HUM + SE)	Understory cover may restrict species' terrestrial movement or, alternatively, increase use of human trails to facilitate movement; human use of trails may have a deterring effect on shy and/or hunted species, reducing detection rates at the camera site; rainfall may affect species' daily activity rates	Detection will decrease with understory cover, human counts, and wet season
Model 1	ψ(AC + SE)	Absolute cover is a measure of basal area per hectare, or a combination of tree size and density within the landscape, and is likely to be a strong predictor of occurrence for species reliant on tree cover and spatial complexity (e.g. semi-arboreal species). In addition, seasonal flooding may affect site-level occurrence as individuals move out of inundated areas or increase arboreal activity levels.	Occurrence will increase as absolute cover increases and during the dry season.
Model 2	ψ(AC + UR + LAT + SE)	Due to the east-to-west gradient of landscape-level differences in forest structure and anthropogenic disturbance, there may be a latitudinal difference in occurrence within the park not explained by other variables included in our models.	Occurrence will increase eastward in latitude given changes in absolute cover and site-level accessibility to urban areas.
Model 3	ψ(AC + UC + GR + SE)	Habitat 1: Dense understory cover is associated with secondary and degraded forests, which may be avoided by species preferring intact forest structure. Absolute cover, understory cover, and distance to grassland therefore	Occurrence will increase with higher absolute cover, lower understory cover, and greater distance from grassland

		encompass numerous levels of forest intactness that may affect species site use.	
Model 4	ψ(AC + UC + WA + SE)	Habitat 2: In addition to spatial habitat characteristics such as absolute cover and understory cover, reliable year-round water sources such as rivers and wetlands are important for wildlife especially during the dry season when seasonal water sources (creeks, waterholes) dry up.	Occurrence will increase with higher absolute cover, lower understory cover, and greater proximity to water
Model 5	ψ(AC + UC + FB + SE)	Habitat 3: Bamboo forest is a broad-scale habitat classification for a degraded and often homogenized forest type that may be avoided by species which prefer intact forest	Occurrence will be lower in bamboo habitat compared to non-bamboo habitat, given the additional effects of absolute cover and understory cover.
Model 6	ψ(BA + UC + WA + SE)	Habitat 4: Basal area is a metric of average tree size at a site. Sites with larger trees and lower understory cover are more indicative of unlogged or moderately logged forests preferred by disturbance-sensitive species.	Occurrence will increase as basal area and proximity to water increases and understory cover decreases.
Model 7	ψ(AC + GR + GR*AC + SE)	Habitat 5: The effect of absolute cover on species occurrence may differ depending on proximity to grassland, as forest quality will be more important when close to forest edges compared to within the forest interior.	Occurrence will increase in areas closer to grassland with higher absolute cover, but the effect of absolute cover will be marginal when far from grassland (within more interior parts of the park).
Model 8	ψ(AC + WA + WA*SE + SE)	Habitat 7. The importance of year-round water sources for species occurrence varies seasonally as the availability of other water sources fluctuates.	Occurrence will increase at sites in proximity to water during the dry season, but the effect will be marginal or negative during the wet season.
Model 9	ψ(AC + WA + SE + AC*SE)	Habitat 8: Given the topography and seasonal flooding schemes in Nam Cat Tien, use of habitat with high absolute cover may change seasonally as species move westward or vertically into the canopy	Occurrence will increase at areas with higher absolute cover during the wet season with seasonal flooding, but the effect of season on absolute cover will be marginal during the dry season.

Model 10	ψ(AC + WA + UC + HC + SE)	Habitat 9: Fine-scale habitat variables that incorporate vertical complexity, such as understory cover and percent high canopy, are likely to affect site use by arboreal and semi-arboreal species.	Occurrence will increase with greater absolute cover and percent canopy and lower understory cover
Model 11	ψ(AC + UC + WA + AC*UC + SE)	Habitat 10: Density of understory cover may preclude use of forest sites despite higher absolute cover, indicating more recently disturbed forest and lower quality habitat.	The positive effect of absolute cover on species occurrence will be stronger when understory cover is low than when understory cover is high.
Model 12	ψ(AC + UR + HUM + SE)	Anthropogenic 1: Accessibility of sites from urban areas surrounding the park in combination with direct counts from camera traps provide a metric of human risk levels which may affect species detection and occurrence due to behavioral avoidance or direct population removal.	Occurrence will decrease with higher human presence and accessibility from urban areas. Detection will also decrease at sites with high human counts as individuals may avoid using trails or occupy a more arboreal niche as a method of risk avoidance.
Model 13	ψ(AC + GR + HUM + SE)	Anthropogenic 2: Human activity may affect site use due to behavioral avoidance or direct removal of individuals	Occurrence will increase as human count decreases and proximity to grassland and absolute cover increases.
Model 14	ψ(AC + WA + UR + SE)	Anthropogenic 3: Human risk levels are likely to compromise habitat use that would otherwise be driven largely by forest structure and resource availability.	Occurrence will increase as accessibility from urban areas decreases and proximity to water increases.
Model 15	ψ(AC + UR + PE + UR*PE + SE)	Anthropogenic 4: Human accessibility to urban areas are likely to be a large risk factor that reduces species occurrence only if protection effort by rangers is low.	Occurrence will decrease at sites with higher accessibility from urban areas when protection effort is low, but will be higher at those sites when protection effort is high.
Model 16	ψ(AC + UR + AC*UR + SE)	Anthropogenic 5: Human risk is likely to compromise species occurrence in otherwise suitable intact forest habitat	At sites with high absolute cover, occurrence will increase at sites less accessible from urban areas but will

			decrease at sites more accessible from urban areas.
Model 17	ψ(AC + UR + UR*SE + SE)	Anthropogenic 6: Seasonal flooding and rainfall will impede human use and thus anthropogenic risk during the wet season compared to the dry season	Occurrence will decrease at sites more accessible from urban areas, with the effect being greater during the dry season.
Model 18	ψ(AC + HUM + HUM*AC + SE)	Anthropogenic 7: Human activity is likely to compromise site use that would otherwise be driven largely by forest structure and resource availability especially as hunters may actively target areas of high absolute cover where species richness and abundance is assumed to be higher	Occurrence will increase as absolute cover increases when human counts are low, but will decrease when human counts are high

Covariates: AC = absolute cover, FB = Forest bamboo, GR = distance to grassland, HC = % high canopy, HUM = count of site-level human detections, LAT = latitude, PE = protection effort, SE = season, UC = understory cover, UR = pathcost to urban area, WA = distance to water

Appendix S3

Table S1. Body mass and diet classification of mesomammal species confirmed to occur within Cat Tien National park (Vietnam) in 2001 (Polet and Ling 2004) and 2019.

Species name	**2001 Status in CTNP†**	**2019 Status in CTNP**	**Diet Classification‡**	**Body Mass (kg)§**	**IUCN Red List status**	**Disturbance tolerance¶**	**Diel activity**
Pangolins (Pholidota, Manidae)							
Sunda pangolin *Manis javanica*	Confirmed	Confirmed	Insectivore [1]	5.15	CR	Medium [2]	Nocturnal [2]
Bears (Ursidae)							
Sun bear *Helarctos malayanus*	Confirmed	Not detected	Omnivore [3]	46.00	VU	Medium [4,5]	Diurnal [6]
Weasels, otters (Mustelidae)							
Yellow-throated marten *Martes flavigula*	Confirmed	Confirmed	Carnivore [7]	2.50	LC	High [8,9]	Diurnal [9]
Greater hog badger *Arctonyx collaris*	Confirmed	Not detected	Omnivore [10]	6.36	VU	High [11]	Diurnal [11]
Ferret badger *Melogale spp.*	Confirmed	Confirmed	Omnivore [12]	3.23	LC	High [11]	Nocturnal [13]
Asian small-clawed otter *Aonyx cinerea*	Confirmed	Confirmed	Carnivore [14,15]	3.60	VU	High [11,16]	Diurnal [17]
Civets (Viverridae)							
Large Indian civet *Viverra zibetha*	Confirmed	Not detected	Omnivore [17]	3.95	LC	Medium [18]	Nocturnal [19,20]
Small Indian civet *Viverricula indica*	Confirmed	Confirmed	Omnivore [12]	2.98	LC	High [11,18]	Nocturnal [19,20]
Common palm civet *Paradoxurus hermaphroditus*	Confirmed	Confirmed	Omnivore [21]	3.20	LC	High [11,19]	Nocturnal [19,20]
Binturong *Arctictis binturong*	Confirmed	Not detected	Frugivore [22]	13.00	VU	Medium [11,19,22]	Cathemeral [9,19]
Mongooses (Herpestidae)							

Small Asian mongoose *Herpestes javanicus*	Confirmed	Confirmed	Carnivore [23]	0.75	LC	High [11,18,24]	Diurnal [17]
Crab-eating mongoose *Herpestes urva*	Confirmed	Confirmed	Carnivore [12]	1.86	LC	Medium [18]	Diurnal [19]
Cats (Felidae)							
Leopard cat *Prionailurus bengalensis*	Confirmed	Confirmed	Carnivore [25,26]	3.30	LC	High [25–28]	Cathemeral [25,27,29]
Old-world monkeys (Cercopithecidae)							
Northern pig-tailed macaque *Macaca nemestrina*	Confirmed	Confirmed	Frugivore [30]	6.09	VU	High [30–32]	Diurnal [30–32]
Rhesus macaque *Macaca mulatta*	Confirmed	Not detected	Frugivore [33]		LC	High [34]	Diurnal [17]
Long-tailed macaque *Macaca fascicularis*	Confirmed	Confirmed	Frugivore [35]	3.23	LC	High [36,37]	Diurnal [17]
Stump-tailed macaque *Macaca arctoides*	Confirmed	Confirmed	Frugivore [38,39]	5.00	VU	Medium [39]	Diurnal [39]
Pigs (Suidae)							
Eurasian wild pig *Sus scrofa*	Confirmed	Confirmed	Omnivore [40]	117.29	LC	High [17,40,41]	Cathemeral [31,32]
Chrevotains (Tragulidae)							
Lesser oriental chevrotain *Tragulus kanchil*	Confirmed	Confirmed	Herbivore [42]	3.30	LC	High [42,43]	Cathemeral [42]
Deer (Cervidae)							
Sambar *Rusa unicolor*	Confirmed	Confirmed	Herbivore [44]	211.62	VU	High [45]	Cathemeral [32]
Northern red muntjac *Muntiacus vaginalis*	Confirmed	Confirmed	Herbivore [46]	14.00	LC	High [31,45]	Cathemeral [31]
Porcupines (Hystricidae)							
Malayan porcupine *Hystrix brachyura*	Confirmed	Confirmed	Herbivore [17]	8.00	LC	High [31,47,48]	Nocturnal [31]
Asiatic brush-tailed porcupine *Atherurus macrourus*	Confirmed	Confirmed	Herbivore [17]	2.00	LC	Medium [48]	Nocturnal [32]

† 2001 status from Polet and Ling 2004

‡ Diet classifications: Herbivore: >50% of diet composed of fruits, seeds, and vegetation; Carnivore: >50% of diet composed of vertebrates and carrion; Insectivore: >50% of diet composed of invertibrates; Omnivore: Diet opportunistically composed of available resources

§ Adult body mass averaged across males and females and geographic locations; estimates obtained from Macroecological database of mammalian body mass, Smith et al. 2003

¶ Disturbance tolerance based on habitat distributions: low = only occur in undisturbed primary forest; medium = occur in primary and secondary forest; high = occur in primary and secondary forest as well as forest edges and plantations

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Supporting information S1. Previously confirmed species undetected during our study

Four mesomammal species previously confirmed to inhabit Nam Cat Tien were not detected in our study: sun bear, hog badger, large Indian civet, and binturong. Non-native captive-bred rhesus macaque (*Macaca mulatta*) were released in CTNP in 1999 but rhesus macaque were not detected on our cameras, suggesting removal efforts in 2003 and 2004 may have been effective at extirpating or reducing the population. In December of 2020, a sun bear was caught on a baited camera trap set by the national park in western Nam Cat Tien. This is the most recent sighting since fresh sign and sightings of wild sun bear were reported in the park in 2009 by Scotson et al. 2009, The low frequency of fresh bear sign and recent sightings suggests that the remaining wild sun bear population is very small and may not be a viable population. Sun bear are hunted for their meat and body parts for use in traditional medicine and thus have low occurrence despite their generalist habits. Hog badger sightings were last reported in 2002 by park visitors (Murphy and Duy Thuc 2002), but have not subsequently been captured by camera traps, also suggesting a small or extirpated population. Cat Tien has previously been described as the southern-most extent of the hog badger's range in Vietnam due to lack of suitable forest habitat in the region. Large Indian civet were last reported in 2002 by Polet and Ling, and their greater body size and largely terrestrial nature compared to other civets may make them more vulnerable to snaring and hunting. There was one possible binturong sighting in Nam Cat Tien in 2002 (Murphy and Duy Thuc), but no confirmed sightings since. As binturong are highly arboreal and prefer tall trees and intact forest, they are less tolerant to disturbance and may be limited to patches of less degraded forest. Their arboreal and nocturnal nature also make them difficult to detect on terrestrial camera traps or by diurnal ranger patrols and tourists. Binturong were also reported to occur in the northern Cat Loc region of the park, so extending a camera trap survey to this region may increase likelihood of detection if the species persists.

Scotson, L., Downie, A., Hai, B.T., Morkel, B., Nguyen, T.L., 2009. Wild bear population status, Cat Tien National Park, Vietnam Asiatic black bear (*Ursus thibetanus*) and Malayan sun bear (*Helarctos malayanus*).

APPENDIX S4

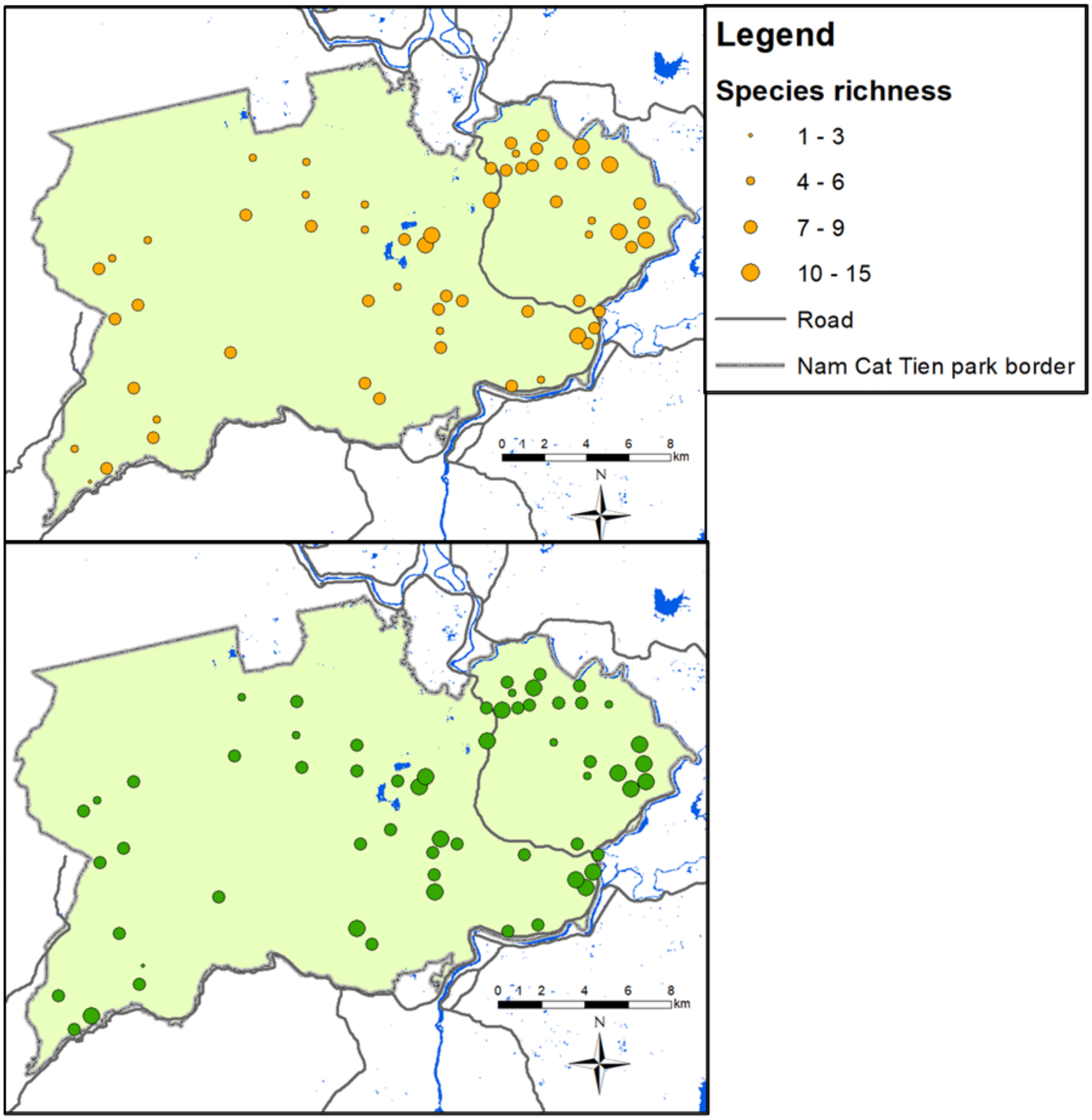


Figure S1. Estimated site-level mode mesomammal richness in Nam Cat Tien National Park during the dry (left, red circles) and wet (right, green circles) seasons.

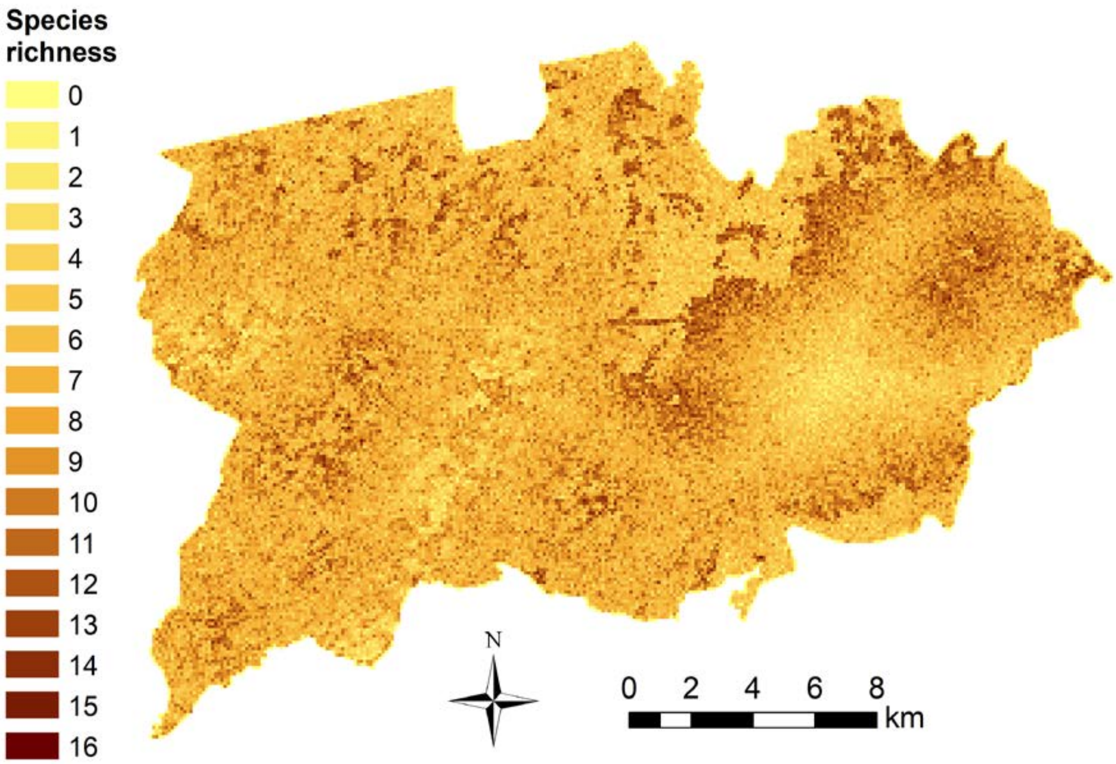


Figure S2. Map of median estimated species richness in Nam Cat Tien National Park from the top community occupancy model. The regions in dark brown indicate higher species richness and regions in yellow indicate lower species richness. We applied mean estimated absolute cover to five land cover types (grassland, bamboo, secondary forest, and mixed bamboo and secondary forest). Mean absolute cover and distance to grassland was calculated at a 100x100m resolution within Nam Cat Tien and used to predict species richness.

APPENDIX S5

Table S1. Model comparison of mesomammal community occupancy models using 10-fold cross validation and a logarithmic scoring rule based on predicted deviances. UC = understory cover; HUM = human count; SE = season; AC = absolute cover; GR = distance to grassland, WA = distance to water, UR = pathcost distance to urban area, LAT = latitude, FB = bamboo forest.

Name	**Model**	**Log Score**	**Delta Log Score**
Model 7	*p*(UC + HUM + SE) ψ(AC + GR + AC*GR + SE)	994.35	0.00
Model 1	*p*(UC + HUM + SE) ψ(AC + SE)	998.57	4.22
Model 4	*p*(UC + HUM + SE) ψ(AC + UC + WA + SE)	999.11	4.76
Model 6	*p*(UC + HUM + SE) ψ(BA + UC + WA + SE)	999.61	5.27
Model 8	*p*(UC + HUM + SE) ψ(AC + WA + WA*SE + SE)	999.76	5.41
Model 3	*p*(UC + HUM + SE) ψ(AC + UC + GR + SE)	1000.00	5.66
Model 17	*p*(UC + HUM + SE) ψ(AC + UR + UR*SE + SE)	1000.13	5.79
Model 13	*p*(UC + HUM + SE) ψ(AC + GR + HUM + SE)	1000.15	5.81
Model 16	*p*(UC + HUM + SE) ψ(AC + UR + AC*UR + SE)	1000.18	5.84
Model 10	*p*(UC + HUM + SE) ψ(AC + GR + UC + HC + SE)	1000.30	5.95
Model 14	*p*(UC + HUM + SE) ψ(AC + UC + WA + UR + SE)	1000.45	6.10
Model 9	*p*(UC + HUM + SE) ψ(AC + WA + SE + AC*SE)	1000.63	6.28
Model 11	*p*(UC + HUM + SE) ψ(AC + UC + WA + AC*UC + SE)	1000.86	6.52
Model 5	*p*(UC + HUM + SE) ψ(AC + UC + FB + SE)	1001.79	7.44
Model 12	*p*(UC + HUM + SE) ψ(AC + UC + UR + HUM + SE)	1003.10	8.76
Model 2	*p*(UC + HUM + SE) ψ(AC + UR + LAT + SE)	1003.70	9.36
Model 15	*p*(UC + HUM + SE) ψ(AC + UR + PE + UR*PE + SE)	1004.92	10.58
Model 18	*p*(UC + HUM + SE) ψ(AC + UC + HUM + AC*HUM + SE)	1009.60	15.25

APPENDIX S6

Table S1. Posterior mean effects of detection and occupancy covariates from the top model by species and for the community. Bold values indicate strong support (probability of an effect is greater than 0.9), italicized values indicate moderate support (probability of an effect is between 0.7 and 0.9), and remaining values indicate low support (probability of an effect is below 0.7). UC = understory cover; HUM = human count; SE = season; AC = absolute cover; GR = distance to grassland.

Species	Covariate effects						
	Detection Probability Variables			Occupancy Probability Variables			
	UC	*HUM*	*SE*	*AC*	*GR*	*AC*GR*	*SE*
Common palm civet	**-0.963**	**0.966**	**-0.960**	**0.957**	**-0.983**	**-0.968**	**0.911**
Leopard cat	**-0.933**	0.543	-0.597	**0.944**	**-0.935**	**-0.991**	**0.946**
Small-clawed otter	**-0.981**	-0.655	-0.617	*0.830*	**-0.999**	**-0.977**	**0.931**
Small Indian civet	**-0.929**	0.598	-0.541	**0.921**	**-0.902**	**-0.952**	*0.868*
Ferret badger	**-0.919**	0.696	0.622	**0.947**	**-0.953**	**-0.989**	*0.828*
Crab-eating mongoose	**-0.964**	-0.542	**-0.932**	**0.924**	**-0.974**	**-0.928**	*0.890*
Sunda pangolin	*-0.855*	0.545	*-0.785*	*0.813*	**-0.945**	**-0.963**	*0.853*
Small Asian mongoose	**-0.926**	0.600	*-0.704*	*0.859*	**-0.925**	**-0.917**	*0.823*
Yellow-throated marten	*-0.860*	0.555	**-0.924**	**0.964**	*-0.759*	**-0.967**	*0.760*
Brush-tailed porcupine	**-0.992**	0.601	**0.922**	*0.877*	*-0.794*	**-0.992**	*0.840*
Eurasian wild pig	**-0.965**	-0.563	**0.983**	**0.921**	-0.600	**-0.977**	*0.897*
Lesser chevrotain	**-0.974**	0.676	*0.842*	**0.917**	*-0.897*	**-0.996**	**0.943**
Long-tailed macaque	**-0.976**	0.519	0.549	*0.833*	**-0.973**	**-0.903**	**0.915**
Pig-tailed macaque	**-0.996**	**0.925**	**-0.966**	**0.987**	*-0.830*	**-0.981**	**0.937**
Red muntjac	*-0.764*	0.623	0.666	**0.971**	**-0.957**	**-0.957**	**0.910**
Malaysian porcupine	**-0.983**	*0.797*	-0.550	**0.969**	-0.616	**-0.948**	**0.938**

Sambar	**-0.996**	0.682	*0.803*	*0.855*	**-0.994**	*-0.895*	*0.779*
Stump-tailed macaque	**-0.962**	0.593	*0.853*	**0.935**	-0.621	**-0.969**	*0.836*
Community	**-0.999**	0.650	-0.559	**0.991**	**-0.996**	**-0.998**	**0.960**

APPENDIX S7

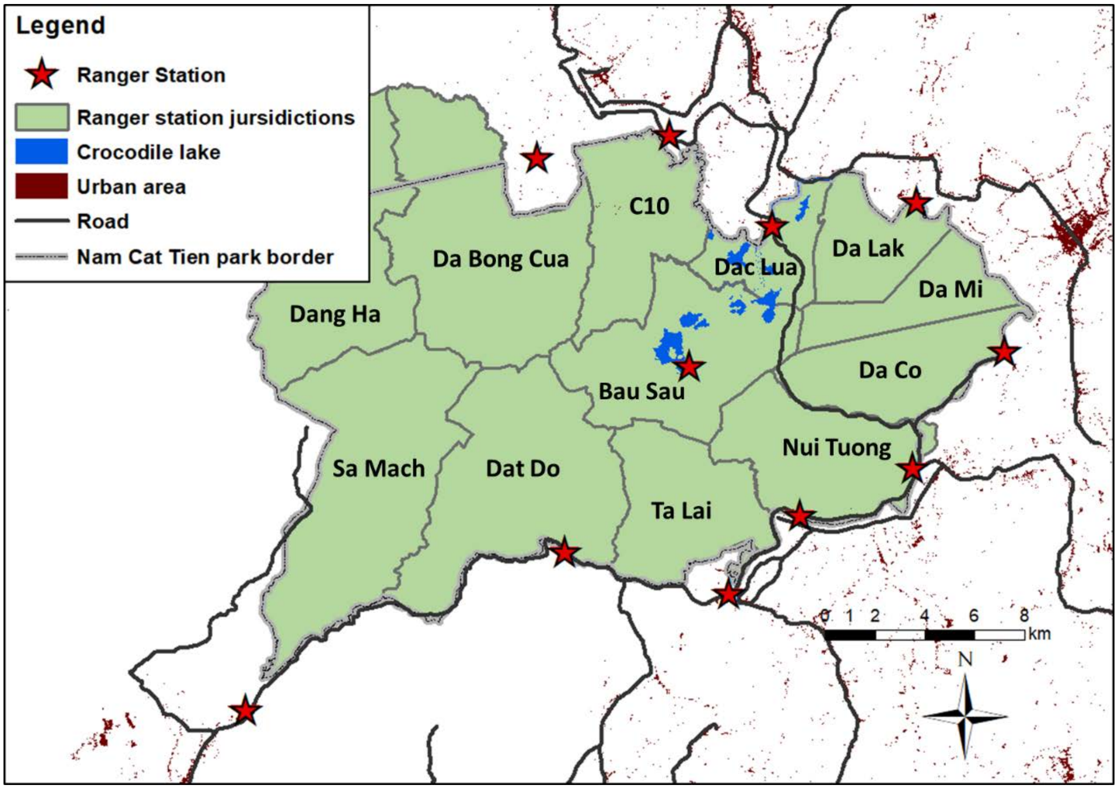


Figure S1. Map of ranger stations, jurisdictions, urban areas, and the Crocodile Lake RAMSAR site at Cat Tien National Park, Vietnam in 2019.

APPENDIX S8

1. Description of covariates

Site-level: Measured at camera site by field researchers

cc_wet = canopy cover wet season

cc_dry = canopy cover dry season

uc_wet = understory cover wet season

uc_dry = understory cover dry season

tree_dens = mean absolute tree density (#trees/ha) corrected using Mitchell 2007 correction factor*

basal_area = mean basal area (cm^2)*

absolute_cover = mean basal area by hectare (m^2/ha)*

tree_height = mean tree height (m)

hum_dry = Dry season human frequency of occurrence**

hum_wet = Dry season human frequency of occurrence**

rod_dry = Dry season rodent frequency of occurrence**

rod_wet = Wet season rodent frequency of occurrence**

sm_dry = Dry season small mammal frequency of occurrence**

sm_wet = Wet season small mammal frequency of occurrence**

- Calculated using Point-Centered Quarter Method (Pollard 1971)

** Calculated as the sum of independent detections (>30 min) at each site using a CamtrapR detection history matrix

Spatial: Calculated using spatial analysis methods in ArcGIS and the 2017 Land Use and Land Cover maps for southern Vietnam from ALOS. Distances in meters.

NEAR_RANGER = Euclidian distance to park ranger station

NEAR_EDGE = Euclidian distance to park edge, spatially delimited as grassland, rice field, agriculture, or urban area

NEAR_WATER = Euclidian distance to year-round water source

NEAR_URBAN = Euclidian distance to urban development

NEAR_ROAD = Euclidian distance to vehicle-access road

COST_DIST_URBAN = Cost distance to urban area

PATHCOST_EDGE = Path cost to edge

PATHCOST_URBAN = Path cost to urban development

point_mean = Index of protection effort by rangers calculated as mean point density within a 100m buffer around each site

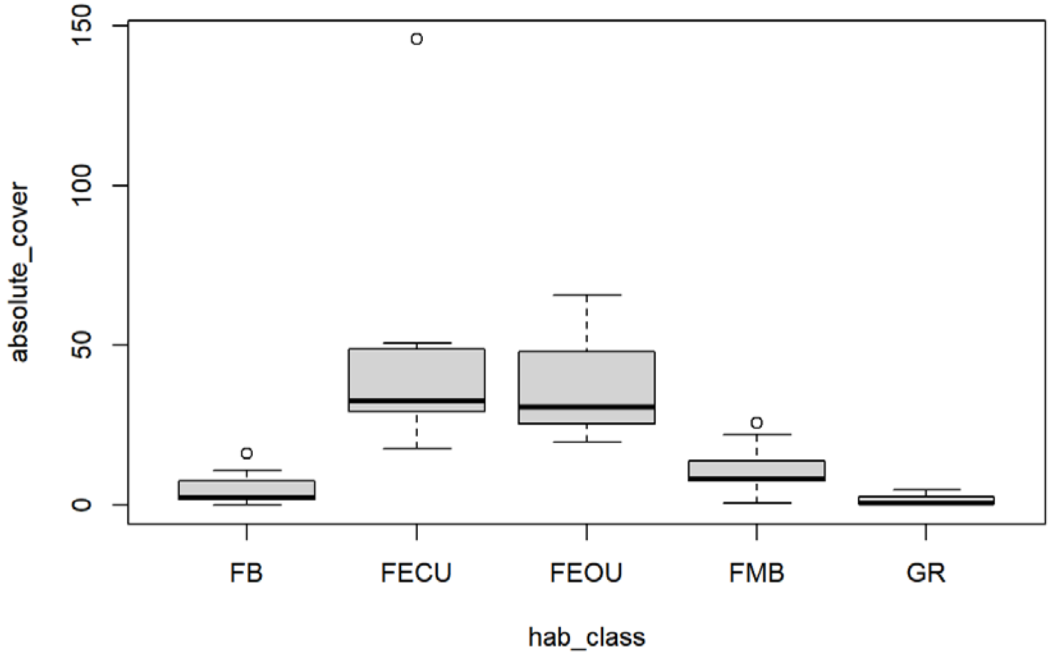
point_sum = Index of protection effort by rangers calculated as mean point density within a 100m buffer around each site

See Appendix A.1 for details on measurement methods.

2. Identifying and parsing through correlated covariates

Categorical habitat variable

We tested whether absolute cover could accurately capture broad-scale changes in habitat classification by plotting site-level absolute cover estimates against habitat classifications.



Absolute cover estimates appear to match habitat classifications as predicted, with higher AC values in more intact secondary evergreen forest and lower AC values in the more degraded mixed bamboo and bamboo forest, with lowest values in open grassland habitat. There does appear to be overlap between evergreen forest types (Forest Evergreen Open Understory (FEOU), Forest Evergreen Closed Understory (FECU)) and bamboo forest types (Forest Bamboo Mixed (FBM), Forest Bamboo (FB)).

We clumped habitat into FB (Forest Bamboo), FS (Forest Secondary), and GR (Grassland) and tested for differences in absolute cover.

```
##
## Call:
## lm(formula = allcov$absolute_cover ~ allcov$hab_class)
##
## Residuals:
##     Min      1Q  Median      3Q     Max
```

```
## -0.9449 -0.3532 -0.0693  0.1362  4.4381
##
## Coefficients:
##                     Estimate Std. Error t value Pr(>|t|)
## (Intercept)          -0.6009     0.1384  -4.343 5.83e-05 ***
## allcov$hab_classFS   1.3196     0.1974   6.684 1.07e-08 ***
## allcov$hab_classGR  -0.2974     0.4519  -0.658    0.513
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 0.7451 on 57 degrees of freedom
## Multiple R-squared:  0.4636, Adjusted R-squared:  0.4448
## F-statistic: 24.64 on 2 and 57 DF,  p-value: 1.948e-08
```

Absolute cover for forest bamboo and forest grassland are not significantly different, meaning the absolute cover covariate cannot differentiate between the two, but there are only 2 grassland sites and no grassland obligate species in our species list so we decided only to include bamboo forest as a possible habitat classification covariate to determine whether species actively avoided bamboo forest.

Selecting spatial variables

Spatial index for proximity to human development

All correlated, so selected PATHCOST_URBAN as it is likely to be a more accurate and informative index of proximity to human development.

Checking remaining spatial variables

```
cor(allcov[,c(10,12,14:16,23)], method = "pearson", use="pairwise.complete.obs")
```

```
##                 NEAR_EDGE NEAR_URBAN COST_DIST_URBAN Pathcost_Edge
## NEAR_EDGE       1.0000000  0.8285310       0.8474273     0.6325362
## NEAR_URBAN      0.8285310  1.0000000       0.9200033     0.6458111
## COST_DIST_URBAN 0.8474273  0.9200033       1.0000000     0.6696788
## Pathcost_Edge   0.6325362  0.6458111       0.6696788     1.0000000
## Pathcost_Urban  0.5392586  0.5818029       0.5703571     0.7958445
## Pathcost_Pop    0.5321717  0.6826670       0.6378666     0.7486116
##                 Pathcost_Urban Pathcost_Pop
## NEAR_EDGE            0.5392586    0.5321717
## NEAR_URBAN           0.5818029    0.6826670
## COST_DIST_URBAN      0.5703571    0.6378666
## Pathcost_Edge        0.7958445    0.7486116
## Pathcost_Urban       1.0000000    0.7804354
## Pathcost_Pop         0.7804354    1.0000000
```

```
##                NEAR_RANGER NEAR_WATER  NEAR_ROAD Pathcost_Urban   KDA_mean
## NEAR_RANGER      1.0000000  0.7654142  0.2491036      0.4872942 -0.3135698
## NEAR_WATER       0.7654142  1.0000000  0.2398261      0.4543684 -0.3494721
## NEAR_ROAD        0.2491036  0.2398261  1.0000000      0.2818653 -0.2046265
## Pathcost_Urban   0.4872942  0.4543684  0.2818653      1.0000000 -0.2130982
## KDA_mean        -0.3135698 -0.3494721 -0.2046265     -0.2130982  1.0000000
## KDA_sum         -0.3203925 -0.3588953 -0.2169800     -0.2048574  0.9964933
##                   KDA_sum
## NEAR_RANGER    -0.3203925
## NEAR_WATER     -0.3588953
## NEAR_ROAD      -0.2169800
## Pathcost_Urban -0.2048574
## KDA_mean        0.9964933
## KDA_sum         1.0000000
```

Distance to year-round water source may be an important seasonal variable as a resource during the dry season and an index of flooding with potential for affecting species displacement during the wet season. Grassland is also a possible index of habitat quality and resource availability, especially due to the presence of a large, intact wetland ecosystem (Crocodile Lake) in the center of the park. However, distance to water and distance to grassland are moderately correlated due to the geographical layout of the park, so we chose to keep both covariates but not include them together in our analyses to determine which covariate has the strongest effect on species occurrence.

Distance to ranger station was strongly correlated with proximity to grassland and water, so we chose to remove it.

Point sum and point mean are strongly correlated and very similar so chose to use the mean as our measure of protection effort. Neither were correlated with distance to ranger station, suggesting rangers do a good job of focusing patrol efforts away from the ranger station.

Selecting site-level variables

```
cor.mat=cor(allcov[,c(5:8)], method = "pearson", use="pairwise.complete.obs")
index=which(abs(cor.mat)>0.5,arr.ind=TRUE)
index=index[-which(index[,1]==index[,2]),]
R = cor.mat[index]
var = paste(rownames(cor.mat)[index[,1]],"vs",rownames(cor.mat)[index[,2]])
cor.var = cbind(var, R)
cor.var[-which(duplicated(cor.var[,2])),]
```

```
##      var                           R
## [1,] "absolute_cover vs tree_dens" "0.807719324473719"
## [2,] "tree_height vs basal_area"   "0.733378380000579"
```

Absolute cover is correlated with tree density (unsurprisingly, as it is calculated from tree density and basal area). We parsed out tree density, as absolute cover is more indicative of total tree cover which is relevant to microhabitat selection by mesomammals.

Basal area and tree height are also correlated, so we parsed out tree height as it is likely less relevant to the terrestrial dataset.

Checking for correlation between remaining variables

```
##      var                              R
## [1,] "tree_hollows vs absolute_cover" "0.621"
## [2,] "NEAR_GRASS vs NEAR_WATER"       "0.674"
## [3,] "Elevation vs NEAR_WATER"        "0.612"
## [4,] "Latitude vs Pathcost_Urban"     "-0.517"
## [5,] "Elevation vs NEAR_GRASS"        "0.783"
```

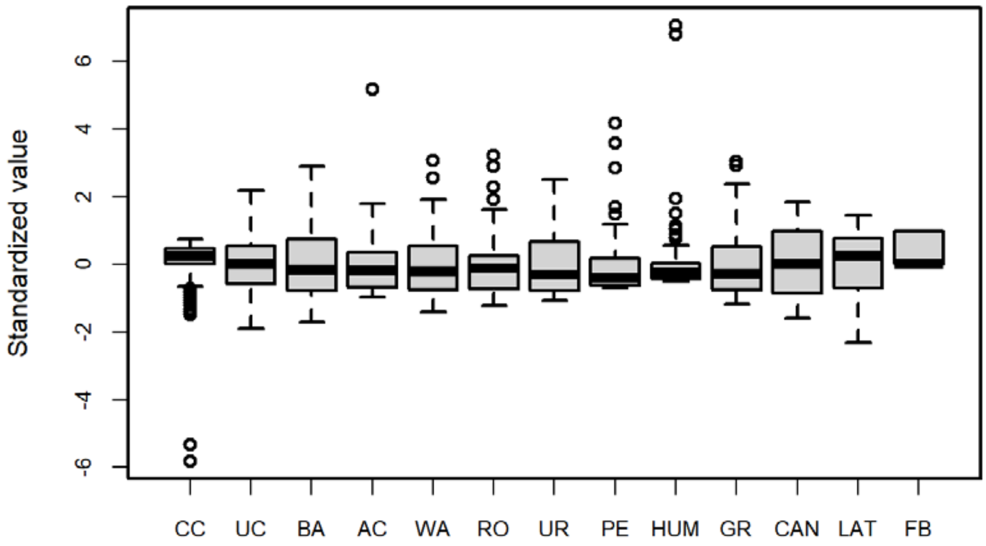
Elevation is correlated with distance to grassland and distance to water, and the variation in elevation is low so we elected to remove it.

Absolute cover is positively correlated with number of tree hollows. This is a reasonable association as absolute cover is generally indicative of greater size and density of trees, and thus greater availability of denning/nesting sites for semi-arboreal wildlife.

Head of the final covariate matrix, standardized and stacked by season for multi-season occupancy modeling

```
##             CC         UC         BA         AC      Water     Road      Urban
## S001 0.7483906 -0.4010423  1.2726134 -0.5176633 -0.3898020  1.912235 -1.0067690
## S004 0.4686184 -0.1423053 -0.8648979 -0.2935697  1.1317618  3.209394  0.3526633
## S005 0.5385614  1.9275904 -0.6306501 -0.9007365 -0.3802027  1.500597 -0.7299421
## S006 0.6784475  1.7723482 -0.6306501 -0.9421727  0.5748816  2.283454  0.2103722
## S007 0.6085045 -0.1940527 -1.3813079 -0.8686023  0.8065975  2.909994  1.3345743
## S008 0.4686184  0.9961373  0.4740413  0.2307248 -0.9439954 -1.224294 -0.9723944
##               PE     Human       Grass        Canopy  Latitude FB
## S001  0.27243893 0.3059050 -0.52469235 -0.3802041520 1.2319593  1
## S004 -0.05718795 0.5798497 -0.03222153 -0.7025955081 0.5921481  1
## S005 -0.58032488 1.9495734 -0.64693227 -1.5759088018 1.1730101  1
## S006 -0.05617754 0.7624795  0.24752355 -1.5799897050 0.8110049  1
## S007 -0.65120007 0.5798497  0.65920001 -0.0006801505 0.4684447  1
## S008  0.34805342 1.0364243 -0.90109441  1.7010565012 0.7344528  0
```

Plot of variation within standardized covariates



APPENDIX S8

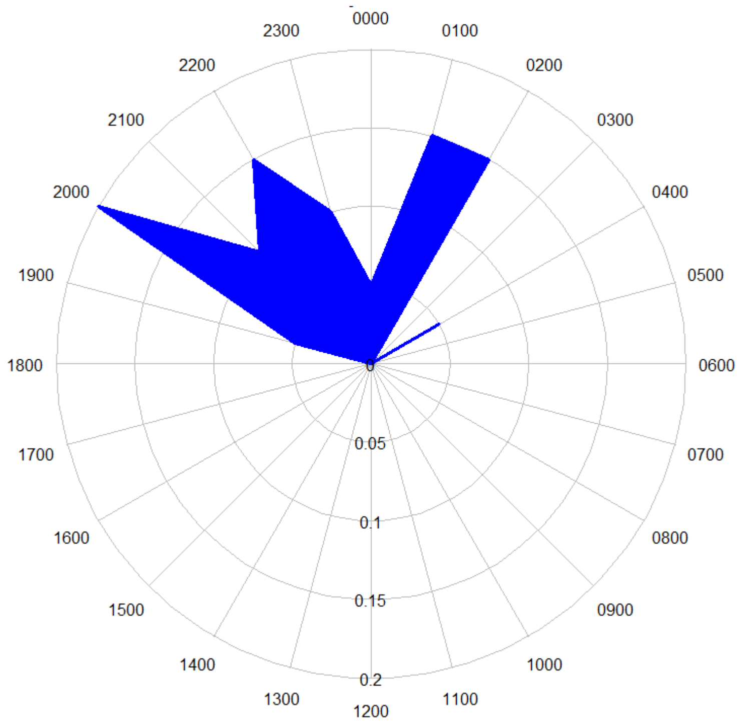


Figure S1. Radial plot of hunter activity detected by camera traps in Cat Tien National Park displayed on a 24 hour clockface from 20 detections between June 2019 and January 2020.

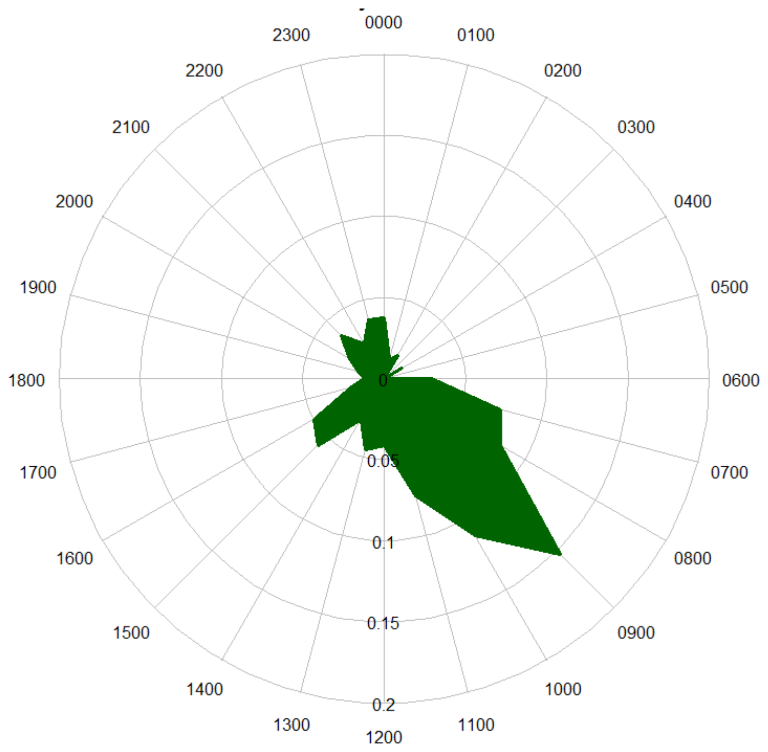


Figure 2 Radial plot of non-timber forest product user activity detected by camera traps in Cat Tien National Park displayed on a 24 hour clockface from 242 detections between June 2019 and January 2020.

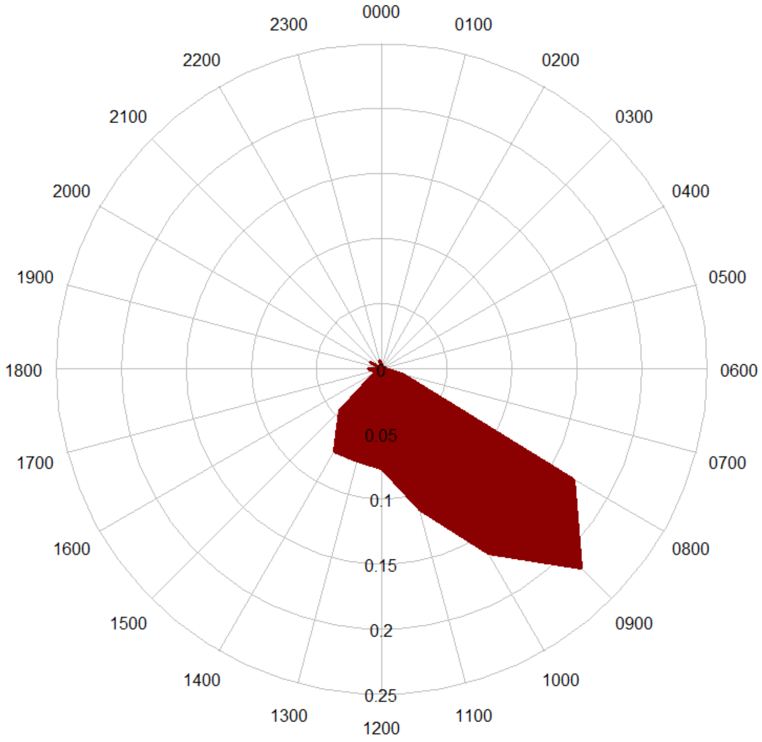


Figure 3. Radial plot of ranger activity detected by camera traps in Cat Tien National Park displayed on a 24 hour clockface from 287 detections between June 2019 and January 2020.

Supplemental information 1. Hunter activity within Nam Cat Tien

Hunter activity detected by our cameras was exclusively nocturnal and highest around the east and south near Sa Mach and Ta Lai villages, with some activity near the park headquarters in Nui Tuong (see Appendix S13). This overlaps strongly with the nocturnal nature of several mesomammals targeted by the wildlife trade including Sunda pangolin, common palm civet, and Eurasian wild pig. The high occurrence of these species at sites easily accessible from urban areas suggests a continued risk to these species from hunters. Patrol effort by park rangers, contrarily, is concentrated in the eastern part of the park and is primarily diurnal. This may preclude detection of hunters by rangers even where they spatially overlap since their temporal activity differs.

APPENDIX S10

Table S1. Habitat, diet, disturbance tolerance, and diel activity classifications of mesomammal species detected within Cat Tien National park in 2019 by arboreal and terrestrial camera traps.

Species name	Diet classification	Spatial habitat classification	Body mass (kg)	IUCN Red List status	Disturbance tolerance	Diel activity
Pangolins (Pholidota, Manidae)						
Sunda pangolin *Manis javanica*	Insectivore[1]	Semi-arboreal	5.15	CR	Medium[2]	Nocturnal[2]
Weasels, otters (Mustelidae)						
Yellow-throated marten *Martes flavigula*	Carnivore[3]	Semi-arboreal	2.50	LC	High[4,5]	Diurnal[5]
Ferret badger *Melogale spp.*	Omnivore[6]	Terrestrial	3.23	LC	High[7]	Nocturnal[8]
Asian small-clawed otter *Aonyx cinerea*	Carnivore[9,10]	Terrestrial	3.60	VU	Low[7,11]	Diurnal[12]
Civets (Viverridae)						
Small Indian civet *Viverricula indica*	Omnivore[6]	Terrestrial	2.98	LC	High[7,13]	Nocturnal[14,15]
Small-toothed palm civet *Arctogalidia trivirgata*	Frugivore[16]	Arboreal	2.25	LC	High[17,18]	Nocturnal[16,17]
Common palm civet *Paradoxurus hermaphroditus*	Omnivore[19]	Semi-arboreal	3.20	LC	High[7,14]	Nocturnal[14,15]
Mongooses (Herpestidae)						
Small Asian mongoose *Herpestes javanicus*	Carnivore[20]	Terrestrial	0.75	LC	High[7,13,21]	Diurnal[12]
Crab-eating mongoose *Herpestes urva*	Carnivore[6]	Terrestrial	1.86	LC	Medium[13]	Diurnal[14]
Cats (Felidae)						
Leopard cat *Prionailurus bengalensis*	Carnivore[22,23]	Terrestrial	3.30	LC	High[22–25]	Cathemeral[22,24,26]
Old-world monkeys (Cercopithecidae)						
Northern pig-tailed macaque *Macaca leonina*	Frugivore[27]	Semi-arboreal	6.09	VU	High[27–29]	Diurnal[27–29]

Long-tailed macaque *Macaca fascicularis*	Frugivore[30]	Semi-arboreal	3.23	LC	High[31,32]	Diurnal[12]
Stump-tailed macaque *Macaca arctoides*	Frugivore[33,34]	Semi-arboreal	5.00	VU	Medium[34]	Diurnal[34]
Langurs (Colubridae)						
Elliot's silver langur *Trachypithecus margarita*	Herbivore[35]	Arboreal	8.35	EN	High[36]	Diurnal[36]
Black-shanked douc-langur *Pygathrix nigripes*	Herbivore[37]	Arboreal	N/A	CR	Medium[38]	Diurnal[38]
Gibbons (Hylobatidae)						
Yellow-cheeked gibbon *Nomascus gabriellae*	Herbivore[39]	Arboreal	N/A	EN	Medium[40]	Diurnal[40]
Lorises (Loridae)						
Pygmy slow loris *Nycticebus pygmaeus*	Omnivore[41]	Arboreal	0.9	EN	Medium[42,43]	Nocturnal[42]
Pigs (Suidae)						
Eurasian wild pig *Sus scrofa*	Omnivore[44]	Terrestrial	117.29	LC	High[12,44,45]	Cathemeral[28,29]
Chrevotains (Tragulidae)						
Lesser oriental chevrotain *Tragulus kanchil*	Herbivore[46]	Terrestrial	3.30	LC	High[46,47]	Cathemeral[46]
Deer (Cervidae)						
Sambar *Cervus unicolor*	Herbivore[48]	Terrestrial	211.62	VU	High[49]	Cathemeral[29]
Northern red muntjac *Muntiacus muntjak*	Herbivore[50]	Terrestrial	14.00	LC	High[28,49]	Cathemeral[28]
Porcupines (Hystricidae)						
Malayan porcupine *Hystrix brachyura*	Herbivore[12]	Terrestrial	8.00	LC	High[28,51,52]	Nocturnal[28]
Asiatic brush-tailed porcupine *Atherurus macrourus*	Herbivore[12]	Terrestrial	2.00	LC	Medium [52]	Nocturnal[29]
Squirrels (Sciuridae)						
Black giant squirrel *Ratufa bicolor*	Herbivore[53]	Arboreal	0.9	NT	Medium[54]	Nocturnal[55]
Flying squirrels (Pteromyidae)						
Indian giant flying squirrel *Petaurista philippensis*	Herbivore[56]	Arboreal	2.05	LC	Medium[56,57]	Diurnal[58]

2019 status compared to status from Polet and Ling 2004

Herbivore: >50% of diet composed of fruits, seeds, and vegetation; Carnivore: >50% of diet composed of vertebrates and carrion; Insectivore: >50% of diet composed of invertibrates; Omnivore: Diet opportunistically composed of available resources

Adult body mass averaged across males and females and geographic locations; estimates obtained from Macroecological database of mammalian body mass, Smith et al. 2003

Disturbance tolerance based on habitat distributions: low = only found in undisturbed primary forest; medium = found in primary and secondary forest; high = found in primary and secondary forest as well as grassland and/or plantations

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APPENDIX S11

References

Species list

- Black-shanked douc-langur (BSDL)
- Elliot’s silver langur (ISLA)
- Yellow-cheeked gibbon (YCGI)
- Pig-tailed macaque (PTMA)
- Long-tailed macaque (LTMA)
- Stump-tailed macaque (STMA)
- Pygmy slow loris (LORI)
- Leopard cat (LECA)
- Common palm civet (CPCI)
- Small-toothed palm civet (STPC)
- Small Indian civet (SICI)
- Crab-eating mongoose (CEMO)
- Ferret-badger (FEBA)
- Yellow-throated marten (YTMA)
- Sunda pangolin (SUPA)
- Black giant squirrel (BGSQ)
- Indian giant flying squirrel (IGFS)
- Brush-tailed porcupine (BTPO)
- Malayan Porcupine (MAPO)
- Lesser oriental chevrotain (LEMA)
- Red muntjac (REMU)
- Sambar (SAMB)
- Eurasian wild pig (EWPI)

Sites

- Arboreal (June 2019 to September 2020)
- Terrestrial 2019 - on-trail (June 2019 to January 2020)
- Terrestrial 2020 - off-trail (January to September 2020)

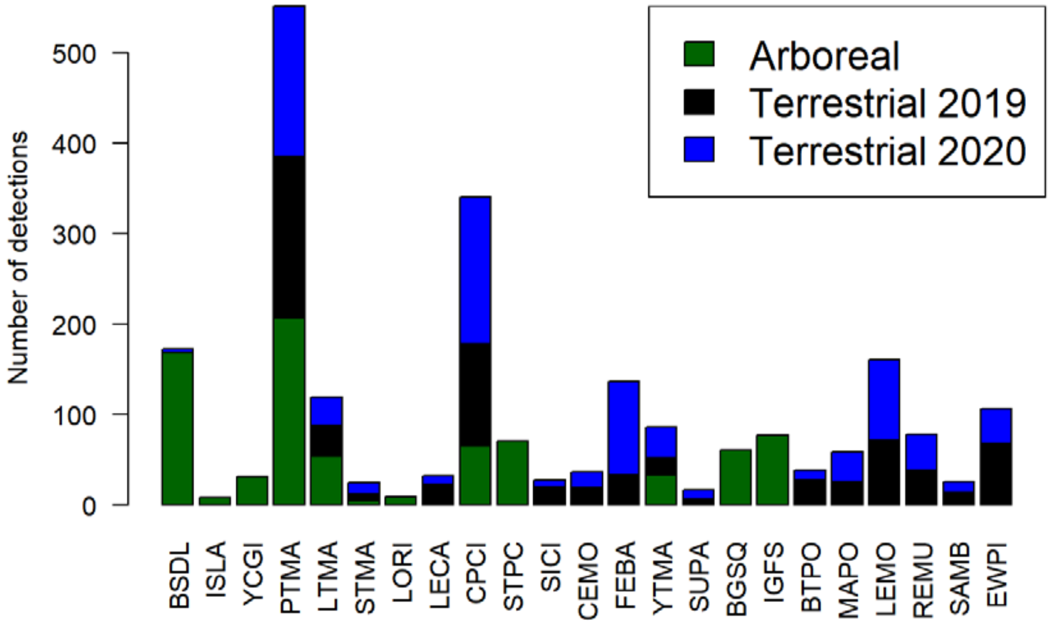
Seasons

- Wet Season 2019: June to October 2019
- Dry Season: November 2019 to April 2020
- Wet Season 2020: May to September 2020

1 Examining the data

Number of independent species detections (> 30 minutes apart) at different site types

```
##                    BSDL ISLA YCGI PTMA LTMA STMA LORI LECA CPCI STPC SICI CE
MO

## Arboreal           168    8   31  206   54    4    9    0   65   70    0
0

## Terrestrial 2019     0    0    0  179   34    8    0   23  113    0   20
19

## Terrestrial 2020     4    0    0  166   31   12    0    9  162    0    7
17

##                    FEBA YTMA SUPA BGSQ IGFS BTPO MAPO LEMO REMU SAMB EWPI

## Arboreal             0   33    1   60   77    0    0    0    0    0    0

## Terrestrial 2019    33   19    5    0    0   27   25   71   38   13   68

## Terrestrial 2020   103   34   10    0    0   11   33   89   40   12   38
```



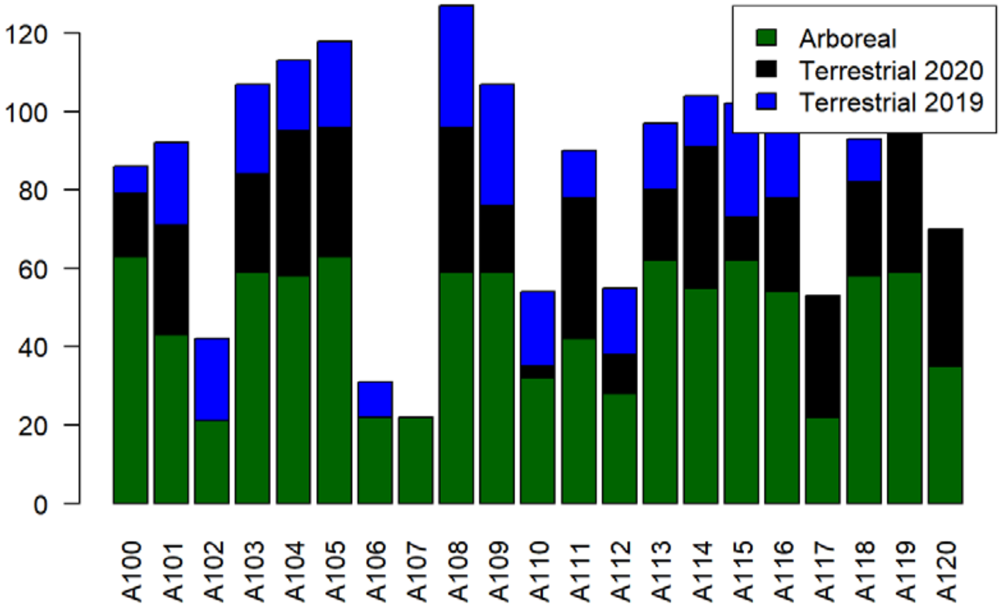
We detected a total of 13 species on the arboreal cameras and 17 species on the terrestrial cameras. 6 species were only detected arboreally (eg. yellow-cheeked gibbon, small-toothed palm civet), 10 species were only detected terrestrially (eg. lesser oriental chevrotain, crab-eating mongoose), and 7 species were detected both on the ground and in the trees (e.g. yellow-throated marted, Sunda pangolin).

```
length(which(mat_all[1,] >= 1)) #Total arboreal
## [1] 13
length(which(mat_all[2,] >= 1)) #Total terrestrial 2019
## [1] 16
length(which(mat_all[3,] >= 1)) #Total terrestrial 2020
## [1] 17
#Species only detected arboreally

which(mat_all[1,] >= 1 & mat_all[2,] == 0 & mat_all[3,] == 0)
## ISLA YCGI LORI STPC BGSQ IGFS
##    2    3    7   10   16   17
#Species only detected terrestrially

which(mat_all[1,] == 0 & mat_all[2,] >= 1 & mat_all[3,] >= 1)
## LECA SICI CEMO FEBA BTPO MAPO LEMO REMU SAMB EWPI
##    8   11   12   13   18   19   20   21   22   23
#Species detected both arboreally and terrestrally

which(mat_all[1,] >= 1 & mat_all[2,] >= 1)
## PTMA LTMA STMA CPCI YTMA SUPA
##    4    5    6    9   14   15
which(mat_all[1,] >= 1 & mat_all[3,] >= 1)
## BSDL PTMA LTMA STMA CPCI YTMA SUPA
##    1    4    5    6    9   14   15
```

Comparison of effort (# of surveys) between paired cameras at each station

```
##      Arboreal Terrestrial_2020 Terrestrial_2019
## A100       63               16                7
## A101       43               28               21
## A102       21                0               21
## A103       59               25               23
## A104       58               37               18
## A105       63               33               22
## A106       22                0                9
## A107       22                0                0
## A108       59               37               31
```

```
## A109        59               17               31
## A110        32                3               19
## A111        42               36               12
## A112        28               10               17
## A113        62               18               17
## A114        55               36               13
## A115        62               11               29
## A116        54               24               24
## A117        22               31                0
## A118        58               24               11
## A119        59               37                0
## A120        35               35                0
```

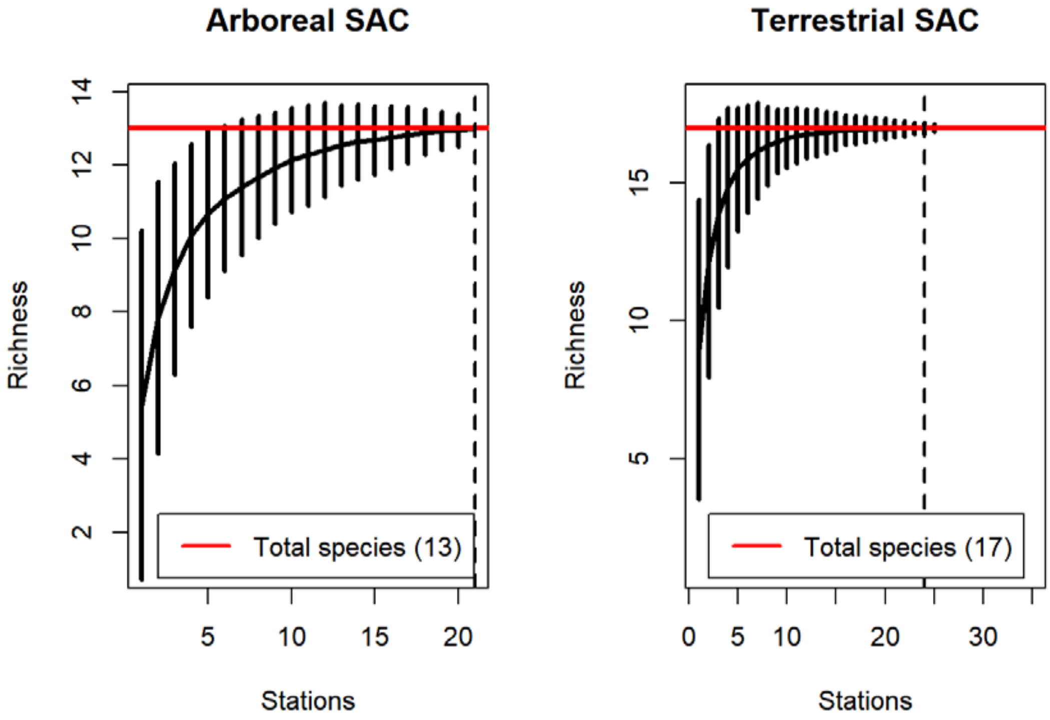


Direct arboreal-terrestrial comparisons may be difficult given the gaps in terrestrial data for several stations (eg. A102, A106, A107). May combine terrestrial data if the difference between site type (on vs. off trail) does not significantly affect detection.

2 Species accumulation curves

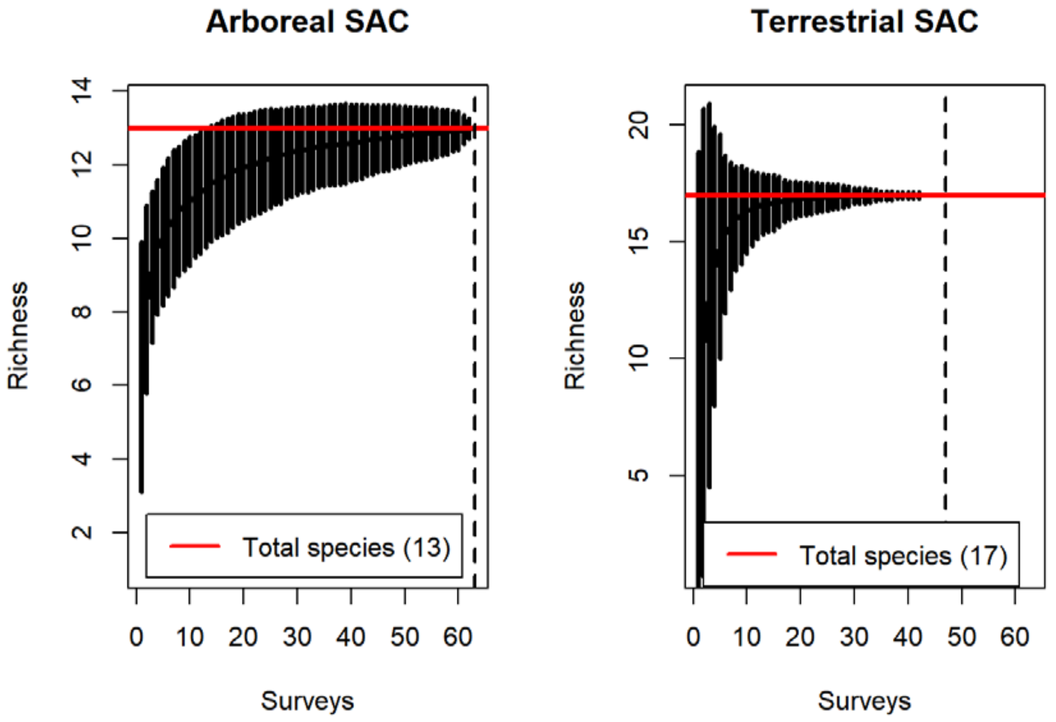
Species accumulation curves by station

- Require 21 stations to detect 13 arboreal species, and 24 stations to detect 17 terrestrial species

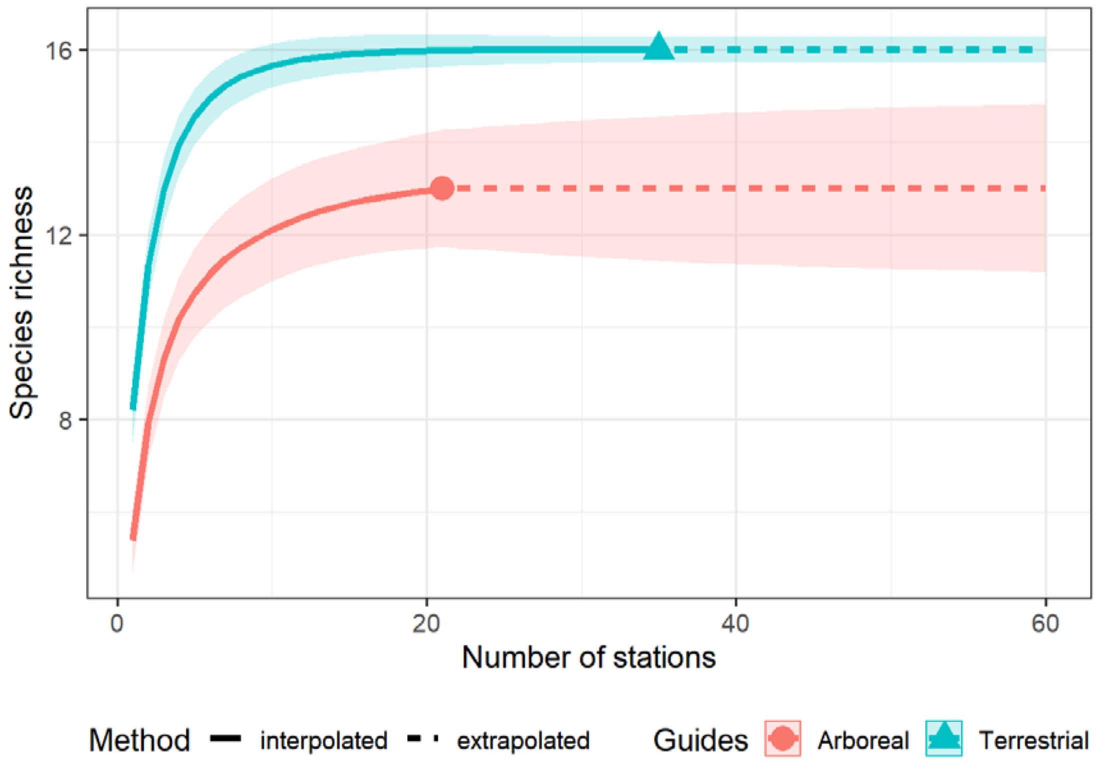


Species accumulation curve by survey (~7 camera trap days per survey)

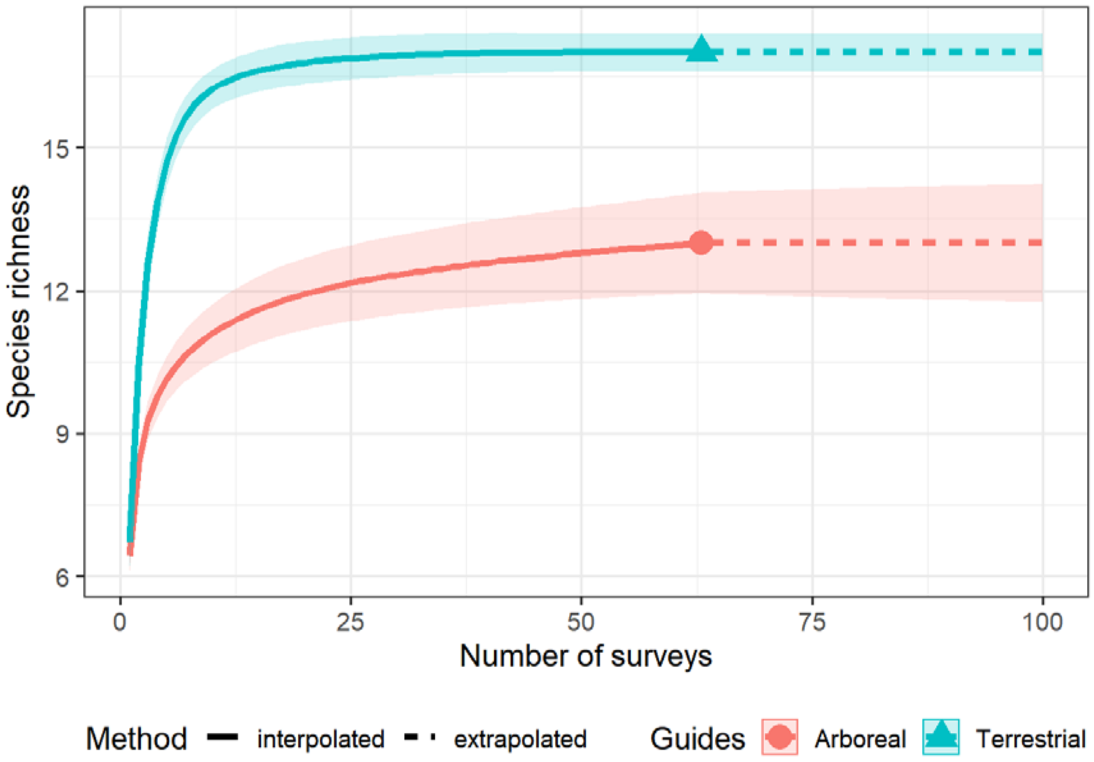
- Require 63 surveys to detect 13 arboreal species, and 47 surveys to detect 17 terrestrial species



Extrapolated species accumulation by station



Extrapolated species accumulation by surveys



From the curves above we can see that we have greater confidence in having arrived at the true species terrestrial richness estimate within the sampling period than for arboreal species richness, which has greater uncertainty around the extrapolated estimates. Both terrestrial and arboreal richness curves did begin to plateau, however, for both the stations and surveys, so there is room to assume that to true species richness was not very different from our final estimates. In addition, according to the Polet and Ling (2004) and Murphy and Phan (2002) CTNP biodiversity list, our arboreal surveys detected all arboreal and semi-arboreal mesomammals previously detected in the park with the exception of binturong (which have not been sighted in the park since 2002).

3 Generalized Linear Models

Modeling the effects of site type and season on naive detection rates

```
#Negative binomial GLM for the effect of site on detections (count) offset by
effort (number of active camera trap days)


glm.site.nb <- glm.nb(count ~ site + offset(log(mat.effort)), data = mat.anov
a)

summary(glm.site.nb)
##

## Call:
```

```
mat.anova.rl$site = relevel(mat.anova$site, ref = "Terrestrial_19")


glm.site.nb.rl <- glm.nb(count ~ site + offset(log(mat.effort)), data = mat.a
nova.rl)

summary(glm.site.nb.rl)
```

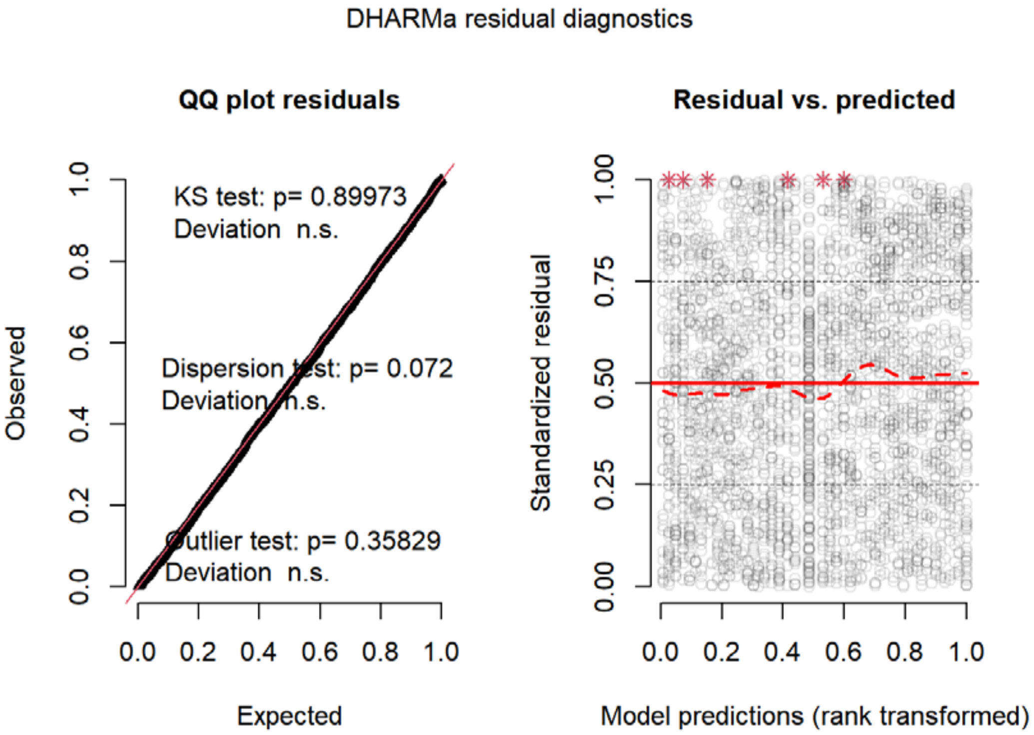
```
## 
## Call:
## glm.nb(formula = count ~ site + offset(log(mat.effort)), data = mat.anova.
rl, 
##     init.theta = 0.1433948764, link = log)
## 
## Deviance Residuals: 
##     Min       1Q   Median       3Q      Max  
## -0.8345  -0.7270  -0.6838  -0.5269   2.5967  
## 
## Coefficients:
##                     Estimate Std. Error z value Pr(>|z|)    
## (Intercept)          -4.9723     0.1028 -48.368   <2e-16 ***
## siteArboreal         -1.4769     0.1298 -11.377   <2e-16 ***
## siteTerrestrial_20   -0.2453     0.1437  -1.706   0.0879 .  
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
## 
## (Dispersion parameter for Negative Binomial(0.1434) family taken to be 1)
## 
##     Null deviance: 1728.7  on 3058  degrees of freedom
## Residual deviance: 1572.4  on 3056  degrees of freedom
## AIC: 5829.7
## 
## Number of Fisher Scoring iterations: 1
## 
## 
##               Theta:  0.14339 
##           Std. Err.:  0.00804 
## 
```

```
## glm.nb(formula = count ~ site + offset(log(mat.effort)), data = mat.anova,
##     init.theta = 0.1433948764, link = log)
##
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -0.8345  -0.7270  -0.6838  -0.5269   2.5967
##
## Coefficients:
##                     Estimate Std. Error z value Pr(>|z|)
## (Intercept)         -6.44925    0.07927 -81.353   <2e-16 ***
## siteTerrestrial_19  1.47690    0.12982  11.377   <2e-16 ***
## siteTerrestrial_20  1.23160    0.12798   9.624   <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for Negative Binomial(0.1434) family taken to be 1)
##
##     Null deviance: 1728.7  on 3058  degrees of freedom
## Residual deviance: 1572.4  on 3056  degrees of freedom
## AIC: 5829.7
##
## Number of Fisher Scoring iterations: 1
##
##               Theta:  0.14339
##           Std. Err.:  0.00804
##
##  2 x log-likelihood:  -5821.66500
#Relevel to compare differences between wet seasons

mat.anova$site = as.factor(mat.anova$site)

mat.anova.rl = mat.anova
```

```
glm.site.nb.coef <- glm.nb(count ~ site - 1 + offset(log(mat.effort)), data =
mat.anova)

glm.site.nb.coef$coefficients
```

```
##       siteArboreal siteTerrestrial_19 siteTerrestrial_20

##          -6.449245          -4.972347          -5.217642
```

```
#Checking residuals


simulationOutput <- simulateResiduals(fittedModel = glm.site.nb, plot = T)
```



There appears to be a significant difference between arboreal and terrestrial, but not between on- and off-trail terrestrial survey methods. In addition, the coefficients are similar in size and direction which suggests the effect on detection is similar across site types.

Residuals are close to 1, indicating that a negative binomial GLM does a good job of accounting for any overdispersion potentially caused by zero-inflation.

```
#Negative binomial GLM for the effect of season on detections (count) offset
by effort (number of active camera trap days)


#glm.season.nb <- glm.nb(count ~ season + offset(log(mat.effort)), data = mat
.anova)

#summary(glm.season.nb)
```

```
#Relevel to compare differences between wet seasons


mat.anova$season = as.factor(mat.anova$season)


mat.anova.rl$season = relevel(mat.anova$season, ref = "Wet.19")


glm.season.nb.rl <- glm.nb(count ~ season + offset(log(mat.effort)), data = m
at.anova.rl)

summary(glm.season.nb.rl)
```

```
##

## Call:

## glm.nb(formula = count ~ season + offset(log(mat.effort)), data = mat.anov
a.rl,

##     init.theta = 0.1216694866, link = log)

##

## Deviance Residuals:

##     Min       1Q   Median       3Q      Max

## -0.8506  -0.7524  -0.6634  -0.4913   2.3660

##

## Coefficients:

##               Estimate Std. Error z value Pr(>|z|)

## (Intercept)   -5.2727     0.1006 -52.412  < 2e-16 ***

## seasonDry.20  -0.3659     0.1325  -2.761  0.00577 **

## seasonWet.20  -0.5863     0.1503  -3.901 9.58e-05 ***

## ---

## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##

## (Dispersion parameter for Negative Binomial(0.1217) family taken to be 1)

##

##     Null deviance: 1555.1  on 3058  degrees of freedom

## Residual deviance: 1539.2  on 3056  degrees of freedom

## AIC: 5958.6

##

## Number of Fisher Scoring iterations: 1
```

```
##                Theta:  0.12167
##            Std. Err.:  0.00653
##
##  2 x log-likelihood:  -5950.63600
```

```r
#Coefficient estimates for all seasons


glm.season.nb.coef <- glm.nb(count ~ season - 1 + offset(log(mat.effort)), da
ta = mat.anova)

glm.season.nb.coef$coefficients
```

```
## seasonDry.20 seasonWet.19 seasonWet.20
##    -5.638561    -5.272666    -5.858920
```

```r
#Checking residuals


#simulationOutput <- simulateResiduals(fittedModel = glm.season.nb, plot = T)


#Some underdispersion
```

There is a significant effect of dry season on detection, as well as Wet season 2019 though the effect size is small. The coefficients are also similar in size and direction which suggests the effect on detection is similar across seasons. We thus created a model that includes both season and site.

```r
#Negative binomial GLM for the effect of season and site on detections (count
) offset by effort (number of active camera trap days)


glm.site.season.nb <- glm.nb(count ~ site + season + offset(log(mat.effort)),
data = mat.anova)

summary(glm.site.season.nb)
```

```
##
## Call:
## glm.nb(formula = count ~ site + season + offset(log(mat.effort)),
##     data = mat.anova, init.theta = 0.1455718947, link = log)
##
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -0.8583  -0.7536  -0.6623  -0.4843   2.7252
##
## Coefficients:
```

```
##                      Estimate Std. Error z value Pr(>|z|)
## (Intercept)           -6.5302     0.1054 -61.938  < 2e-16 ***
## siteTerrestrial_19     1.2831     0.1341   9.565  < 2e-16 ***
## siteTerrestrial_20     1.4130     0.1381  10.234  < 2e-16 ***
## seasonWet.19           0.4016     0.1320   3.042  0.00235 **
## seasonWet.20          -0.2136     0.1397  -1.529  0.12619
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for Negative Binomial(0.1456) family taken to be 1)
##
##     Null deviance: 1745.3  on 3058  degrees of freedom
## Residual deviance: 1573.1  on 3054  degrees of freedom
## AIC: 5819.7
##
## Number of Fisher Scoring iterations: 1
##
##
##                Theta:  0.14557
##            Std. Err.:  0.00818
##
##  2 x log-likelihood:  -5807.68500
```

We accounted for inter-species variation in responses by adding species as a random variable in a GLMM with the site-only and site + season models.

```
#Site only


glmm.site <- glmer.nb(count ~ site + offset(log(mat.effort)) + (1|species), d
ata = mat.anova)


#Site + season


glmm.site.season <- glmer.nb(count ~ site + season + offset(log(mat.effort))
+ (1|species), data = mat.anova)
```

Compare AIC for model selection

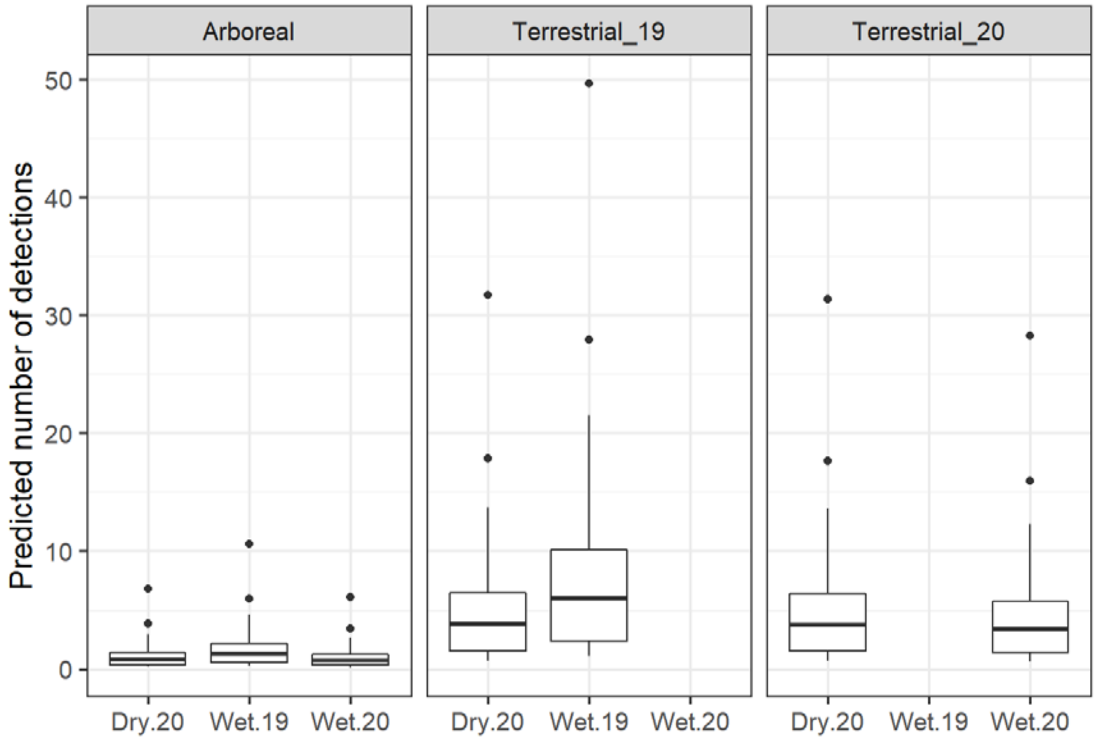
```
##                      df      AIC
## glmm.site.season      7 5472.111
## glmm.site             5 5484.460
## glm.site.season.nb    6 5819.685
## glm.site.nb           4 5829.665
```

The GLMM models performed significantly better than the GLM models, with the site + season GLMM model performing best.

Predicted rate of new detections at a fixed effort of 1000 camera trap days

Examining site and season in the top model (glmm.site.season) by fixing effort at 1000 camera trap days:

```
##   count     site season species station effort count.effort
## 1     2 Arboreal Wet.19    BSDL    A100    440  0.004545455
## 2     9 Arboreal Wet.19    BSDL    A101    292  0.030821918
## 3     6 Arboreal Wet.19    BSDL    A102    146  0.041095890
## 4    16 Arboreal Wet.19    BSDL    A103    412  0.038834951
## 5     1 Arboreal Wet.19    BSDL    A104    403  0.002481390
## 6     3 Arboreal Wet.19    BSDL    A105    439  0.006833713
```



The site + season model appears to best account for naive differences in detection. However, there is no significant difference between terrestrial sampling methods, and the boxplot shows a lot of overlap outside of outliers in predicted number of detections. The difference between arboreal and terrestrial methods is greater and known differences in detection rate between these sampling methods merits separation. Differences across seasons were statistically significant between all seasons, however the unit of difference between seasons is not large with a lot of overlap in the plots. We thus decided to combine wet season data to minimize overparameterization for a single categorical dry-season covariate and separate only by arboreal and terrestrial stations.

4 Covariates

Detection

- CC Canopy connections
- FBS Focal branch slope
- FBD Focal branch diameter
- DBH Tree DBH
- CAM Camera height
- CD Canopy level

Occurrence

- CAN Canopy height
- AC Absolute cover
- GRA Distance to grassland
- WA Distance to water
- RO Distance to road

See Arboreal candidate models excel file for a description of all the covariates (Appendix S1).

In a few cases, missing covariate values were assigned the mean value, which has little effect on estimated coefficients, but does decrease the associated variances.

Checking correlation

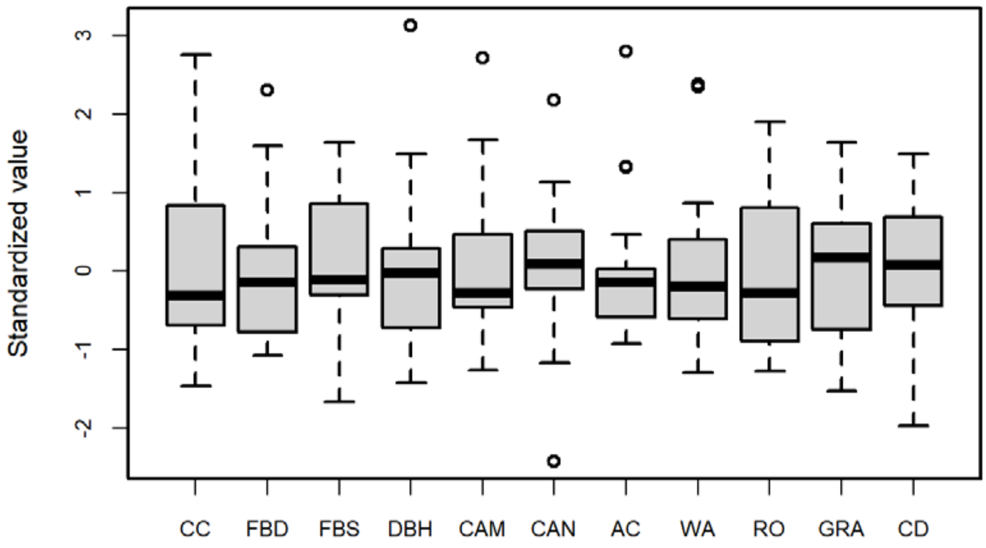
```
##      var          R
## [1,] "WA vs FBD"  "0.618"
## [2,] "GRA vs FBD" "0.537"
## [3,] "WA vs DBH"  "0.509"
## [4,] "CD vs CAM"  "-0.557"
```

- Tree DBH is correlated with focal branch diameter (r = 0.51), which makes sense, but due to the relatively low correlation value I have decided to keep both and not use them in the same models

- Camera height is correlated with canopy level. We opted to keep both covariates as they may potentially explain detection and site use differently, but will not include the covariates in the same model.

- FBD is correlated with distance to water and grassland, suggesting that trees selected closer to water were generally smaller. This is likely due to chance selection of trees, given that absolute cover, a more robust index of overall site-level basal area, was not correlated with distance to water or grassland. Thus we elected to keep all covariates.
- Understory cover was highly correlated with absolute cover (r = 0.93) so we elected to keep AC and use it as a terrestrial detection covariate in place of understory cover.

Plot of variation within covariates



APPENDIX S12

Table S1. Hypotheses and predictions of candidate variables describing how vegetation characteristics and anthropogenic disturbance affects detection and occurrence of mesomammals in Cat Tien National Park, Vietnam. Detection and occupancy variables were combined for GLMM analyses.

Variable	**Name**	**Hypothesis**	**Prediction**
Detection			
CC	Canopy connections	Canopy connectedness can increase accessibility and movement within the canopy for arboreal mammals, thereby affecting likelihood of detection on the focal branch	Detection will increase with higher number of canopy connections
FBS	Focal branch slope	Depending on vertical and horizontal movement patterns, species may prefer particular limb slopes which can affect detection rates	Detection will increase with higher branch slope
FBD	Focal branch diameter	Focal branch size may affect time spent on a particular branch, or behavior, which can affect use (and thereby detection) patterns	Detection will increase with larger focal branch diameter
DBH	Tree DBH	Larger trees are more likely to provide access to canopy resources, and animals may spend more time resting in larger trees; larger trees may also hold more individuals, thereby increasing detection probability	Detections will increase with larger tree DBH
CAM	Camera height	Camera height is correlated with position in the canopy. Different parts of the canopy have different levels of access to resources, forage, and connectedness to other trees for horizontal movement	Detection will increase at higher camera height
CD	Canopy difference	Position of the focal limb in relation to the rest of the canopy is an index of canopy access and thus use of the focal tree and limb	Detection will decrease as the difference between the focal branch and canopy increases

SE	Dry season	Rainfall can reduce species detections by cameras simply due to technical errors such as mud and humidity obscuring the lens, but also by reducing movement of individuals. However, seasonal flooding may also increase utilization of trees for movement through the landscape, and seasonal availability of fruit during the wet season may alter movement rates between resource patches.	Detection will increase in the dry season as high quality forage is more sparsely distributed
AC	Absolute cover	(Terrestrial only). Absolute cover was strongly (r ~ 0.96) correlated with understory cover, a metric of underbrush density which may constrain a species' movement through a landscape as well as the detection distance of the terrestrial camera trap.	Terrestrial detection will declined with greater absolute cover.
Occurrence			
CAN	Canopy height	Canopy height may be a measure of tree type and resource availability, such as fruit and insects, refuge from predators, den availability, etc.	Occurrence will increase with canopy height
AC	Absolute cover	Absolute cover is a measure of basal area per hectare, or a combination of tree size and density within the landscape Species reliant on tree cover and spatial complexity, especially semi-arboreal species, are more likely to use sites with high absolute cover	Occurrence will increase as absolute cover increases
WA	Distance to water	Reliable water sources, such as rivers and wetlands, are important for wildlife especially during the dry season when seasonal water sources dry up	Occurrence will increase with proximity to water
GR	Distance to grassland	Seasonally inundated grasslands and wetlands can provide important resources for many species of wildlife, and have proven to be and important determinant of species occurrence in previous studies	Occurrence will increase with proximity to grassland

RO	Distance to road	Roads facilitate accessibility to the forest by humans and can proximity to roads can thus act as a metric for perceived and real levels of human risk and other disturbances (eg. vehicles, anthropogenic noise, etc.)	Occurrence will decrease at sites closer to roads

Table S2. Variable information and estimation methods used for all covariates included in the mesomammal GLMM and occupancy models

Covariate	**Data type**	**Data Source**	**Resolution**	**Estimation method**
Canopy connectivity	Continuous	Vegetation survey	Station	Canopy connectivity was measured as the number of branches and trunks from proximate trees within 2m (easily traversable for most focal mesomammals) of the focal tree.
Focal branch slope	Continuous	Vegetation survey	Station	Focal branch slope was estimated by eye as the angle difference from a straight vertical line (0 degrees) to a straight horizontal line (90 degrees).
Focal branch diameter	Continuous	Vegetation survey	Station	Focal branch diameter was collected by measuring the circumference of the largest branch facing the camera and converting to diameter by dividing by π. If the focal branch was out of reach, diameter was estimated by eye to the nearest 5cm.
Tree DBH	Continuous	Vegetation survey	Station	Tree diameter was collected by measuring the circumference of the focal tree at approximately 150 cm and converted to diameter by dividing by π. For trees with wide buttresses, diameter of the main trunk was estimated by eye using a horizontal measuring tape.
Camera height	Continuous	Vegetation survey	Station	Arboreal camera height was measured as the straight-line distance from the camera trap sensor to the ground using a 50m measuring tape

Canopy height	Continuous	Vegetation survey	Station	Canopy height was estimated with a rangefinder by measuring the heights of five trees whose crowns were at height with the contiguous site-level canopy and were within 20 meters of the focal tree. The mean across all estimates was used for the site-level covariate.
Canopy level	Continuous	Vegetation survey	Station	The position of the focal limb in relation to the rest of the canopy was measured by calculating the absolute value of the difference between camera height and canopy height.
Understory cover	Continuous	Vegetation survey	50m x 50m	A Photograph of a red 2x1-meter tarp was taken five meters from each PCQ interval point (0m, 17m, 35m) for a total of 9 photos per site. For each photo, we estimated the proportion of vegetation obstructing the red tarp by using the CountColors package in R to calculate the proportion of green color pixels (Weller 2019). The mode across all photos at a site was used for site-level covariate.
Absolute cover	Continuous	Vegetation survey	50m x 50m	We measured nearest tree distances, height, and diameter at breast height (DBH >30 cm) at each PCQ interval location to estimate absolute cover (basal area/ha) and used Mitchell 2007's PCQ method to correct for missing values where trees were inaccessible or >200m away
Distance to grassland	Continuous	Remote sensing	10m	Proximity to grassland was measured from high-resolution remote-sensing Geographic Information Systems data (Phan 2018) and geospatial vectors using the Near tool in ArcGIS and constrained to within park boundaries to reduce confounding with crop or grazing land
Distance to water	Continuous	Remote sensing	10m	Proximity to water was measured from high-resolution remote-sensing Geographic Information Systems data (Phan 2018) and geospatial vectors using the Near tool in ArcGIS

Distance to road	Continuous	Remote sensing	10m	Proximity to road was measured from high-resolution remote-sensing Geographic Information Systems data (Phan 2018) and geospatial vectors using the Near tool in ArcGIS. All roads were at least 5m across and created significant canopy gaps though traffic levels vary from high (road bisecting the park) to low (road following the eastern park boundary; Figure 2).
Season	Categorical	Online historical database		Seasons were determined from changes in daily precipitation in Ho Chi Minh City (from World Weather Online). This was calculated from monthly rainfall divided by number of rain days, whereby the wet season had higher average daily precipitation (12.7-15.2 cm) and dry season had lower average daily precipitation (0.3-8.3 cm). We used one seasonal categorical covariate which encompassed two seasons; the intercept (wet season, June-November 2019 and June-September 2020) and SE (dry season, December-May 2020).

Citations: Hannah Weller (2019). countcolors: Locates and Counts Pixels Within Color Range(s) in Images. R package version 0.9.1.

https://CRAN.R-project.org/package=countcolors

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APPENDIX S13

Table S1. Hypotheses and predictions of candidate GLMM models describing how metrics of forest structure and anthropogenic disturbance affect count of detections of arboreal mesomammals in Cat Tien National Park, Vietnam. Models with variables as fixed effects denoted by the letter a and models with variables described as varying by species denoted by the letter b. AC = absolute cover, CAM = camera height, CAN = canopy height, CC = Canopy connectivity, CD = canopy difference, DBH = focal tree DBH, FBD = focal branch diameter, FBS = focal branch slope, GRA = distance to grassland, RO = distance to road, WA = distance to water.

Name	**Model**	**Hypothesis**	**Prediction**
Model 1a	count ~ CC + FBD + FBS + (1 | species)	Focal branch characteristics such as the slope and size of the focal branch as well as connectedness to nearby trees can affect type and length of use (resting vs. foraging vs. movement) and thereby detection rates.	Count of species detections will increase with higher canopy connectivity, focal branch diameter, and focal branch slope.
Model 1b	count ~ CC + (FBD + FBS | species)	The effect of branch slope and branch diameter will vary by species depending largely on the preferred mode of locomotion.	Count of species detections will increase with lower branch slope and branch diameter for brachiators, gliders, and climbers while detections will increase with higher branch slope and diameter for arboreal quadrupeds.
Model 2a	count ~ CC + CAM + FBS + (1 | species)	Different heights within the canopy can vary in access to resources. Branch slope and canopy connectedness can increase accessibility and movement within the canopy and use of that particular tree by arboreal mammals.	Count of species detections will increase with higher canopy connections, focal branch slope, and camera height.
Model 2b	count ~ CC + (FBS + CAM | species)	The effect of branch slope and camera height will vary by species depending largely on the preferred mode of locomotion and resource niche.	Detections of canopy-crown foraging species will increase with focal branch slope and camera height.

Model 3a	count ~ CC + DBH + CAM + (1 | species)	Larger trees are more likely to provide access to canopy resources, and animals may spend more time resting in larger trees; larger trees may also hold more individuals, and in combination with canopy connectivity to proximate trees may increase detection probability.	Count of species detections will increase with higher canopy connectivity, tree DBH, and camera height.
Model 3b	count ~ DBH + (CC + CAM| species)	The effect of canopy connectivity and camera height will vary by species based on reliance on horizontal arboreal movement and spatial niche.	The effect of canopy connectivity and camera height on detection rate will be greater on more specialized arboreal species while the effect will be smaller for semi-arboreal species.
Model 4a	count ~ CC + CD + CAN + (1 | species)	Canopy difference is a quantitative measure of relative position of the camera in the canopy and an index of accessibility to the surrounding mid-canopy. Low canopy difference (little difference between the canopy and camera height) and high canopy connectivity suggests a high level of accessibility of the focal tree and thereby detection.	Count of species detections will increase at sites with lower canopy difference, higher canopy connectivity, and greater canopy height.
Model 4b	count ~ CAN + CD + (CC | species)	The effect of canopy connectivity will vary by species.	The effect of canopy connectivity on detection rate will be greater on more specialized arboreal species while the effect will be smaller for semi-arboreal species.
Model 5a	count ~ CC + WA + CAN + (1 | species)	In combination with forest maturity, reliable water sources, such as rivers and wetlands, are important for wildlife especially during the dry season when seasonal water sources dry up.	Count of species detections will increase in more mature forest with high connectivity, high canopy, higher DBH, and close to water.
Model 5b	count ~ WA + CAN + (CC | species)	The effect of canopy connectivity will vary by species.	The effect of canopy connectivity on detection rate will be greater on more specialized arboreal species while the effect will be smaller for semi-arboreal species.
Model 6a	count ~ CC + GRA + DBH + (1 | species)	Distance to grassland can act as a proxy for the linear effect of forest succession and maturity, which may affect the likelihood and frequency of use of that site by a species.	Count of species detections will increase with canopy connectivity, absolute cover, distance to grassland, and canopy height.

Model 6b	count ~ DBH + (CC + GRA | species)	The effect of canopy connectivity and distance to grassland will vary by species.	Grasslands can be an important resource for some species, especially semi-arboreal species, but the edge effects of early successional habitat may deter more arboreal species.
Model 7a	count ~ AC + CC + CAN + (1 | species)	Absolute cover, canopy connectivity, and canopy height are all metrics of forest integrity and maturity which are likely to affect site-level use and detections of arboreal species.	Count of species detections will increase with absolute cover, canopy connectivity, and canopy height.
Model 7b	count ~ AC + (CC + CAN | species)	Thus, proximity to roads can act as a metric for perceived and real levels of human risk and other disturbances (i.e. vehicles, anthropogenic noise). Grasslands may also indicate degraded or edge forest which can affect species' use of a site.	Count of species detections will decline with proximity to roads and grassland.
Model 8a	count ~ CC + GRA + RO + (1 | species)	Roads can act as barriers to movement for highly arboreal species and facilitate accessibility to the forest by humans. Thus, proximity to roads can act as a metric for perceived and real levels of human risk and other disturbances (i.e. vehicles, anthropogenic noise). Grasslands may also indicate degraded or edge forest which can affect species' use of a site.	Count of species detections will decline with proximity to roads and grassland and increase with canopy connectivity
Model 8b	count ~ GRA + (CC + RO | species)	The effect of canopy connectivity and distance to road will vary by species.	The effect of roads on count of species detections will be higher for more disturbance sensitive and arboreal species whose movement and thus range may be limited by large roads and who may be more sensitive to anthropogenic disturbance.
Model 9a	count ~ AC + CAN + RO + (1 | species)	Absolute cover and canopy connectivity are metrics for forest maturity which may influence species' use of and activity levels at a particular site in combination with proximity to human disturbance.	Count of species detections will increase at sites with high canopy connectivity, higher canopy, and further from roads.
Model 9b	count ~ CAN + (AC + RO | species)	The effect of absolute cover and distance to road will vary by species.	The effect of roads on count of species detections will be negative for more disturbance sensitive and arboreal species while the effect of absolute cover will be positive for those species.

Table S2. Hypotheses and predictions of candidate occupancy models describing how metrics of forest structure and anthropogenic disturbance affect detection and occupancy (site use) of arboreal and semi-arboreal mesomammals in Cat Tien National Park, Vietnam. AC = absolute cover, CAM = camera height, CAN = canopy height, CC = Canopy connectivity, CD = canopy difference, DBH = focal tree DBH, FBD = focal branch diameter, FBS = focal branch slope, GRA = distance to grassland, RO = distance to road, WA = distance to water.

Model	**Hypothesis**	**Prediction**
Detection		
p(CAM + CC + FBS + SE)	Canopy connectedness can increase accessibility and movement within the canopy, thereby affecting likelihood of detection on the focal branch. Camera height is correlated with position in the canopy. Different parts of the canopy have different levels of access to resources, forage, and connectedness to other trees for horizontal movement, so individuals may utilize different parts of the canopy at different rates; the slope of the focal branch can also affect type and length of use (resting vs. foraging vs. movement).	Detection will increase with higher camera height, canopy connectedness, and branch slope
p(CC + CD + SE)	Canopy difference is a quantitative measure of relative position of the camera in the canopy and would coarsely indicate accessibility to the surrounding mid-canopy. Low canopy level (little difference between the canopy and camera height) and high canopy connectivity suggests a high level of accessibility of the focal tree and thereby detection.	Detection will increase with higher number of canopy connections and canopy level
p(FBD + CC + SE)	Focal branch size (diameter) may affect time spent on a particular branch, or behavior, which can affect use (and thereby detection) patterns; Canopy connectedness can increase accessibility to surrounding canopy and thus likelihood of use of the focal branch for arboreal travel and use.	Detection will increase with higher number of canopy connections and branch diameter.

p(FBD + FBS + CD + SE)	The size and slope of the focal branch can affect whether an animal decides to use it for resting/foraging/movement as well as the length of time spent on that branch, thus affecting detection. Position relative to the canopy may also affect accessibility of the focal branch for use and detection.	Detection will increase with higher focal branch diameter, branch slope, and lower canopy difference
p(CAM + FBD + SE)	The size and height of the focal branch may affect whether a species uses the focal branch for movement through the canopy and thus detection.	Detections will increase at higher camera height, larger tree DBH, and higher focal branch slope.
Occupancy		
ψ(CAN)	Canopy height may be a measure of tree type and resource availability, such as fruit and insects, refuge from predators, den availability, etc. Seasonal flooding may push semi-arboreal species out of inundated areas, especially close to water and where canopy connectedness is poor	Occurrence will increase with canopy height.
ψ(AC)	Absolute cover is a measure of basal area per hectare, or a combination of tree size and density within the landscape. Species reliant on tree cover and spatial complexity, especially semi-arboreal species, are more likely to use sites with high absolute cover	Occurrence will increase as absolute cover increases.
ψ(WA)	Reliable water sources, such as rivers and wetlands, are important for wildlife especially during the dry season when seasonal water sources dry up	Occurrence will increase with proximity to water.

ψ(GRA)	Distance to grassland can act as a proxy for the linear effect of forest succession and thereby maturity. Forest edges and grasslands may also provide resources such as fruiting pioneer trees and fast growing, young vegetation consumed by many omnivores and herbivores.	Occurrence will decrease with distance from grassland for more adaptable and semi-arboreal species, and will increase for more specialist, arboreal species.
ψ(RO)	Roads facilitate accessibility to the forest by humans and can proximity to roads can thus act as a metric for perceived and real levels of human risk and other disturbances (i.e. vehicles, anthropogenic noise).	Occurrence will decrease at sites closer to road

APPENDIX S14

Table S1. Table of expected log predictive density values (eldp) for the GLMM candidate models derived using approximate leave-one-out cross validation. AC = absolute cover, CAM = camera height, CAN = canopy height, CC = Canopy connectivity, CD = canopy difference, DBH = focal tree DBH, FBD = focal branch diameter, FBS = focal branch slope, GRA = distance to grassland, RO = distance to road, WA = distance to water.

Model	**Model**	**eldp**	**Δelpd**
Model 8b	count ~ GRA + (CC + RO | species)	-775.05	0.00
Model 2b	count ~ CC + (FBS + CAM | species)	-775.66	-0.61
Model 8a	count ~ GRA + CC + RO + (1 | species)	-778.00	-2.95
Model 3b	count ~ DBH + (CC + CAM| species)	-778.51	-3.46
Model 1b	count ~ CC + (FBD + FBS | species)	-780.41	-5.37
Model 6b	count ~ DBH + (CC + GRA | species)	-780.82	-5.78
Model 6a	count ~ CC + GRA + DBH + (1 | species)	-783.92	-8.87
Model 7b	count ~ AC + (CC + CAN | species)	-784.61	-9.56
Model 4b	count ~ CAN + CD + (CC | species)	-787.65	-12.60
Model 5b	count ~ WA + CAN + (CC | species)	-787.81	-12.76
Model 4a	count ~ CC + CD + CAN + (1 | species)	-791.82	-16.77
Model 5a	count ~ CC + WA + CAN + (1 | species)	-793.00	-17.96
Model 7a	count ~ AC + CC + CAN + (1 | species)	-793.09	-18.05
Model 1a	count ~ CC + FBD + FBS + (1 | species)	-793.45	-18.41
Model 2a	count ~ CC + CAM + FBS + (1 | species)	-794.12	-19.07
Model 3a	count ~ CC + DBH + CAM + (1 | species)	-794.64	-19.60
Model 9a	count ~ AC + CAN + RO + (1 | species)	-808.44	-33.40
Model 9b	count ~ CAN + (AC + RO | species)	-809.03	-33.99

Table S2 WAIC table from single-species arboreal occupancy models for nine arboreal species. AC = absolute cover, CAM = camera height, CAN = canopy height, CC = Canopy connectivity, CD = canopy difference, DBH = focal tree DBH, FBD = focal branch diameter, FBS = focal branch slope, RO = distance to road, WA = distance to water. Distance to grass not included as an occupancy covariate due to moderate correlation with distance to water (see Appendix S11).

(a) Black-shanked douc-langur

Number	Model	WAIC	ΔWAIC
mod1	psi(AC) p(CAM + CC + FBS + SE)	745.26	0.00
mod15	psi(AC) p(CC + CD + SE)	747.33	2.07
mod2	psi(CAN) p(CAM + CC + FBS + SE)	748.14	2.88
mod29	psi(AC) p(FBD + FBS + CD + SE)	749.96	4.71
mod16	psi(CAN) p(CC + CD + SE)	750.50	5.24
mod5	psi(DBH) p(CAM + CC + FBS + SE)	750.80	5.54
mod6	psi(RO) p(CAM + CC + FBS + SE)	751.22	5.97
mod3	psi(CC) p(CAM + CC + FBS + SE)	751.48	6.22
mod4	psi(CD) p(CAM + CC + FBS + SE)	752.00	6.74
mod7	psi(WA) p(CAM + CC + FBS + SE)	752.39	7.14
mod19	psi(DBH) p(CC + CD + SE)	752.61	7.36
mod17	psi(CC) p(CC + CD + SE)	753.18	7.92
mod18	psi(CD) p(CC + CD + SE)	753.44	8.19
mod20	psi(RO) p(CC + CD + SE)	753.57	8.32
mod21	psi(WA) p(CC + CD + SE)	754.04	8.78
mod30	psi(CAN) p(FBD + FBS + CD + SE)	754.04	8.79
mod31	psi(CC) p(FBD + FBS + CD + SE)	754.72	9.46
mod34	psi(RO) p(FBD + FBS + CD + SE)	755.01	9.75
mod33	psi(DBH) p(FBD + FBS + CD + SE)	755.73	10.48
mod22	psi(AC) p(FBD + CC + SE)	755.96	10.70
mod32	psi(CD) p(FBD + FBS + CD + SE)	756.09	10.83
mod35	psi(WA) p(FBD + FBS + CD + SE)	757.54	12.28
mod8	psi(AC) p(CAM + FBD + SE)	757.82	12.56
mod23	psi(CAN) p(FBD + CC + SE)	758.51	13.25
mod25	psi(CD) p(FBD + CC + SE)	759.63	14.38
mod24	psi(CC) p(FBD + CC + SE)	759.75	14.49
mod27	psi(RO) p(FBD + CC + SE)	760.82	15.56

mod9	psi(CAN) p(CAM + FBD + SE)	760.88	15.62
mod28	psi(WA) p(FBD + CC + SE)	762.20	16.95
mod26	psi(DBH) p(FBD + CC + SE)	762.30	17.05
mod13	psi(RO) p(CAM + FBD + SE)	762.49	17.23
mod10	psi(CC) p(CAM + FBD + SE)	762.57	17.32
mod11	psi(CD) p(CAM + FBD + SE)	764.05	18.80
mod12	psi(DBH) p(CAM + FBD + SE)	764.66	19.40
mod14	psi(WA) p(CAM + FBD + SE)	764.95	19.70

(b) Yellow-cheeked gibbon

Number	Model	WAIC	ΔWAIC
mod2	psi(CAN) p(CAM + CC + FBS + SE)	168.45	0.00
mod4	psi(CD) p(CAM + CC + FBS + SE)	170.85	2.40
mod1	psi(AC) p(CAM + CC + FBS + SE)	172.58	4.13
mod7	psi(WA) p(CAM + CC + FBS + SE)	173.41	4.96
mod5	psi(DBH) p(CAM + CC + FBS + SE)	173.46	5.01
mod3	psi(CC) p(CAM + CC + FBS + SE)	173.58	5.13
mod6	psi(RO) p(CAM + CC + FBS + SE)	173.71	5.26
mod30	psi(CAN) p(FBD + FBS + CD + SE)	174.98	6.53
mod32	psi(CD) p(FBD + FBS + CD + SE)	178.86	10.41
mod29	psi(AC) p(FBD + FBS + CD + SE)	179.40	10.95
mod33	psi(DBH) p(FBD + FBS + CD + SE)	179.79	11.34
mod35	psi(WA) p(FBD + FBS + CD + SE)	180.19	11.74
mod31	psi(CC) p(FBD + FBS + CD + SE)	180.47	12.02
mod34	psi(RO) p(FBD + FBS + CD + SE)	180.59	12.13
mod16	psi(CAN) p(CC + CD + SE)	188.58	20.13
mod9	psi(CAN) p(CAM + FBD + SE)	188.99	20.53
mod23	psi(CAN) p(FBD + CC + SE)	190.25	21.80
mod11	psi(CD) p(CAM + FBD + SE)	191.44	22.99
mod10	psi(CC) p(CAM + FBD + SE)	192.52	24.07
mod12	psi(DBH) p(CAM + FBD + SE)	192.86	24.41
mod13	psi(RO) p(CAM + FBD + SE)	192.90	24.45
mod8	psi(AC) p(CAM + FBD + SE)	193.11	24.66
mod14	psi(WA) p(CAM + FBD + SE)	193.55	25.10
mod17	psi(CC) p(CC + CD + SE)	193.58	25.12
mod21	psi(WA) p(CC + CD + SE)	193.59	25.14
mod15	psi(AC) p(CC + CD + SE)	193.83	25.38
mod19	psi(DBH) p(CC + CD + SE)	193.88	25.43
mod20	psi(RO) p(CC + CD + SE)	194.54	26.09
mod18	psi(CD) p(CC + CD + SE)	195.19	26.74
mod24	psi(CC) p(FBD + CC + SE)	196.84	28.39
mod22	psi(AC) p(FBD + CC + SE)	197.08	28.63
mod28	psi(WA) p(FBD + CC + SE)	197.10	28.65
mod26	psi(DBH) p(FBD + CC + SE)	197.41	28.96
mod25	psi(CD) p(FBD + CC + SE)	197.61	29.16
mod27	psi(RO) p(FBD + CC + SE)	197.61	29.16

(c) Pig-tailed macaque

Number	Model	WAIC	ΔWAIC
mod27	psi(RO) p(FBD + CC + SE)	926.41	0.00
mod25	psi(CD) p(FBD + CC + SE)	927.42	1.01
mod22	psi(AC) p(FBD + CC + SE)	928.22	1.81
mod26	psi(DBH) p(FBD + CC + SE)	928.85	2.44
mod23	psi(CAN) p(FBD + CC + SE)	929.18	2.77
mod24	psi(CC) p(FBD + CC + SE)	929.75	3.34
mod28	psi(WA) p(FBD + CC + SE)	929.82	3.41
mod20	psi(RO) p(CC + CD + SE)	933.77	7.36
mod18	psi(CD) p(CC + CD + SE)	934.85	8.44
mod6	psi(RO) p(CAM + CC + FBS + SE)	935.12	8.71
mod4	psi(CD) p(CAM + CC + FBS + SE)	935.84	9.43
mod15	psi(AC) p(CC + CD + SE)	936.12	9.71
mod19	psi(DBH) p(CC + CD + SE)	936.20	9.79
mod16	psi(CAN) p(CC + CD + SE)	936.44	10.03
mod17	psi(CC) p(CC + CD + SE)	936.48	10.07
mod21	psi(WA) p(CC + CD + SE)	936.63	10.22
mod3	psi(CC) p(CAM + CC + FBS + SE)	937.07	10.66
mod5	psi(DBH) p(CAM + CC + FBS + SE)	937.14	10.73
mod1	psi(AC) p(CAM + CC + FBS + SE)	937.36	10.95
mod7	psi(WA) p(CAM + CC + FBS + SE)	937.88	11.47
mod2	psi(CAN) p(CAM + CC + FBS + SE)	938.49	12.08
mod13	psi(RO) p(CAM + FBD + SE)	944.31	17.90
mod11	psi(CD) p(CAM + FBD + SE)	945.17	18.76
mod34	psi(RO) p(FBD + FBS + CD + SE)	945.35	18.94
mod8	psi(AC) p(CAM + FBD + SE)	946.17	19.76
mod32	psi(CD) p(FBD + FBS + CD + SE)	946.60	20.19
mod10	psi(CC) p(CAM + FBD + SE)	946.71	20.30
mod12	psi(DBH) p(CAM + FBD + SE)	946.78	20.37
mod9	psi(CAN) p(CAM + FBD + SE)	946.88	20.47
mod31	psi(CC) p(FBD + FBS + CD + SE)	947.32	20.91
mod14	psi(WA) p(CAM + FBD + SE)	947.34	20.94
mod29	psi(AC) p(FBD + FBS + CD + SE)	947.39	20.98
mod33	psi(DBH) p(FBD + FBS + CD + SE)	947.52	21.11
mod30	psi(CAN) p(FBD + FBS + CD + SE)	948.17	21.76
mod35	psi(WA) p(FBD + FBS + CD + SE)	948.49	22.08

(d) Long-tailed macaque

Number	Model	WAIC	ΔWAIC
mod21	psi(WA) p(CC + CD + SE)	218.28	0.00
mod7	psi(WA) p(CAM + CC + FBS + SE)	221.15	2.87
mod35	psi(WA) p(FBD + FBS + CD + SE)	224.46	6.18
mod14	psi(WA) p(CAM + FBD + SE)	224.55	6.27
mod32	psi(CD) p(FBD + FBS + CD + SE)	228.08	9.80
mod19	psi(DBH) p(CC + CD + SE)	229.16	10.87
mod18	psi(CD) p(CC + CD + SE)	229.87	11.59
mod31	psi(CC) p(FBD + FBS + CD + SE)	233.08	14.80
mod33	psi(DBH) p(FBD + FBS + CD + SE)	233.64	15.36
mod5	psi(DBH) p(CAM + CC + FBS + SE)	234.12	15.84
mod17	psi(CC) p(CC + CD + SE)	234.90	16.61
mod15	psi(AC) p(CC + CD + SE)	235.83	17.55
mod30	psi(CAN) p(FBD + FBS + CD + SE)	237.01	18.72
mod12	psi(DBH) p(CAM + FBD + SE)	237.11	18.83
mod16	psi(CAN) p(CC + CD + SE)	237.29	19.00
mod2	psi(CAN) p(CAM + CC + FBS + SE)	237.71	19.43
mod3	psi(CC) p(CAM + CC + FBS + SE)	238.22	19.94
mod4	psi(CD) p(CAM + CC + FBS + SE)	238.22	19.94
mod20	psi(RO) p(CC + CD + SE)	238.28	20.00
mod29	psi(AC) p(FBD + FBS + CD + SE)	238.63	20.35
mod1	psi(AC) p(CAM + CC + FBS + SE)	239.92	21.64
mod34	psi(RO) p(FBD + FBS + CD + SE)	240.29	22.01
mod10	psi(CC) p(CAM + FBD + SE)	240.96	22.68
mod6	psi(RO) p(CAM + CC + FBS + SE)	240.98	22.70
mod9	psi(CAN) p(CAM + FBD + SE)	241.36	23.07
mod8	psi(AC) p(CAM + FBD + SE)	243.07	24.78
mod13	psi(RO) p(CAM + FBD + SE)	243.45	25.17
mod11	psi(CD) p(CAM + FBD + SE)	244.75	26.47
mod26	psi(DBH) p(FBD + CC + SE)	293.17	74.89
mod28	psi(WA) p(FBD + CC + SE)	293.66	75.38
mod22	psi(AC) p(FBD + CC + SE)	293.87	75.59
mod24	psi(CC) p(FBD + CC + SE)	295.68	77.39
mod23	psi(CAN) p(FBD + CC + SE)	297.02	78.73
mod27	psi(RO) p(FBD + CC + SE)	297.30	79.01
mod25	psi(CD) p(FBD + CC + SE)	297.30	79.02

(e) Common palm civet

Number	Model	WAIC	ΔWAIC
mod27	psi(RO) p(FBD + CC + SE)	382.12	0.00
mod22	psi(AC) p(FBD + CC + SE)	392.18	10.06
mod23	psi(CAN) p(FBD + CC + SE)	394.21	12.09
mod24	psi(CC) p(FBD + CC + SE)	394.24	12.12
mod26	psi(DBH) p(FBD + CC + SE)	395.14	13.02
mod28	psi(WA) p(FBD + CC + SE)	395.30	13.19
mod25	psi(CD) p(FBD + CC + SE)	395.32	13.21
mod20	psi(RO) p(CC + CD + SE)	398.25	16.14
mod34	psi(RO) p(FBD + FBS + CD + SE)	399.14	17.02
mod6	psi(RO) p(CAM + CC + FBS + SE)	402.08	19.97
mod15	psi(AC) p(CC + CD + SE)	404.63	22.51
mod16	psi(CAN) p(CC + CD + SE)	406.36	24.25
mod21	psi(WA) p(CC + CD + SE)	407.16	25.04
mod17	psi(CC) p(CC + CD + SE)	407.44	25.33
mod18	psi(CD) p(CC + CD + SE)	407.92	25.81
mod19	psi(DBH) p(CC + CD + SE)	408.15	26.03
mod1	psi(AC) p(CAM + CC + FBS + SE)	409.24	27.13
mod29	psi(AC) p(FBD + FBS + CD + SE)	409.35	27.23
mod13	psi(RO) p(CAM + FBD + SE)	409.84	27.72
mod31	psi(CC) p(FBD + FBS + CD + SE)	409.86	27.74
mod2	psi(CAN) p(CAM + CC + FBS + SE)	410.01	27.90
mod5	psi(DBH) p(CAM + CC + FBS + SE)	410.71	28.59
mod33	psi(DBH) p(FBD + FBS + CD + SE)	410.75	28.63
mod7	psi(WA) p(CAM + CC + FBS + SE)	410.76	28.65
mod3	psi(CC) p(CAM + CC + FBS + SE)	411.03	28.92
mod32	psi(CD) p(FBD + FBS + CD + SE)	411.16	29.04
mod30	psi(CAN) p(FBD + FBS + CD + SE)	411.42	29.30
mod35	psi(WA) p(FBD + FBS + CD + SE)	411.43	29.31
mod4	psi(CD) p(CAM + CC + FBS + SE)	411.68	29.57
mod8	psi(AC) p(CAM + FBD + SE)	416.35	34.24
mod10	psi(CC) p(CAM + FBD + SE)	418.04	35.92
mod9	psi(CAN) p(CAM + FBD + SE)	418.52	36.40
mod14	psi(WA) p(CAM + FBD + SE)	419.29	37.18
mod11	psi(CD) p(CAM + FBD + SE)	419.36	37.25
mod12	psi(DBH) p(CAM + FBD + SE)	419.75	37.64

(f) Small-toothed palm civet

Number	Model	WAIC	ΔWAIC
mod24	psi(CC) p(FBD + CC + SE)	447.91	0.00
mod26	psi(DBH) p(FBD + CC + SE)	447.93	0.02
mod22	psi(AC) p(FBD + CC + SE)	448.15	0.24
mod27	psi(RO) p(FBD + CC + SE)	448.38	0.47
mod23	psi(CAN) p(FBD + CC + SE)	448.62	0.71
mod28	psi(WA) p(FBD + CC + SE)	449.24	1.33
mod25	psi(CD) p(FBD + CC + SE)	449.73	1.82
mod17	psi(CC) p(CC + CD + SE)	454.75	6.84
mod15	psi(AC) p(CC + CD + SE)	454.88	6.97
mod19	psi(DBH) p(CC + CD + SE)	455.06	7.15
mod18	psi(CD) p(CC + CD + SE)	455.65	7.74
mod20	psi(RO) p(CC + CD + SE)	455.72	7.81
mod21	psi(WA) p(CC + CD + SE)	455.82	7.91
mod3	psi(CC) p(CAM + CC + FBS + SE)	455.99	8.08
mod16	psi(CAN) p(CC + CD + SE)	456.13	8.22
mod7	psi(WA) p(CAM + CC + FBS + SE)	456.53	8.61
mod4	psi(CD) p(CAM + CC + FBS + SE)	456.64	8.73
mod6	psi(RO) p(CAM + CC + FBS + SE)	456.84	8.93
mod1	psi(AC) p(CAM + CC + FBS + SE)	456.94	9.03
mod2	psi(CAN) p(CAM + CC + FBS + SE)	457.12	9.21
mod5	psi(DBH) p(CAM + CC + FBS + SE)	457.18	9.27
mod31	psi(CC) p(FBD + FBS + CD + SE)	469.54	21.63
mod33	psi(DBH) p(FBD + FBS + CD + SE)	470.72	22.81
mod34	psi(RO) p(FBD + FBS + CD + SE)	471.29	23.38
mod10	psi(CC) p(CAM + FBD + SE)	471.98	24.07
mod35	psi(WA) p(FBD + FBS + CD + SE)	472.44	24.53
mod29	psi(AC) p(FBD + FBS + CD + SE)	472.54	24.63
mod12	psi(DBH) p(CAM + FBD + SE)	472.72	24.81
mod30	psi(CAN) p(FBD + FBS + CD + SE)	473.10	25.19
mod13	psi(RO) p(CAM + FBD + SE)	474.03	26.12
mod11	psi(CD) p(CAM + FBD + SE)	474.75	26.84
mod32	psi(CD) p(FBD + FBS + CD + SE)	475.06	27.15
mod14	psi(WA) p(CAM + FBD + SE)	475.44	27.53
mod9	psi(CAN) p(CAM + FBD + SE)	475.55	27.64
mod8	psi(AC) p(CAM + FBD + SE)	476.27	28.36

(g) Yellow-throated marten

Number	Model	WAIC	ΔWAIC
mod22	psi(AC) p(FBD + CC + SE)	299.42	0.00
mod8	psi(AC) p(CAM + FBD + SE)	300.05	0.63
mod29	psi(AC) p(FBD + FBS + CD + SE)	302.61	3.19
mod15	psi(AC) p(CC + CD + SE)	303.68	4.26
mod16	psi(CAN) p(CC + CD + SE)	304.61	5.19
mod23	psi(CAN) p(FBD + CC + SE)	305.18	5.76
mod28	psi(WA) p(FBD + CC + SE)	305.23	5.81
mod9	psi(CAN) p(CAM + FBD + SE)	305.71	6.29
mod1	psi(AC) p(CAM + CC + FBS + SE)	305.74	6.32
mod14	psi(WA) p(CAM + FBD + SE)	305.88	6.46
mod21	psi(WA) p(CC + CD + SE)	306.64	7.22
mod26	psi(DBH) p(FBD + CC + SE)	306.76	7.34
mod12	psi(DBH) p(CAM + FBD + SE)	307.13	7.71
mod30	psi(CAN) p(FBD + FBS + CD + SE)	307.41	7.99
mod2	psi(CAN) p(CAM + CC + FBS + SE)	307.50	8.08
mod27	psi(RO) p(FBD + CC + SE)	307.58	8.16
mod24	psi(CC) p(FBD + CC + SE)	307.77	8.35
mod25	psi(CD) p(FBD + CC + SE)	307.82	8.40
mod35	psi(WA) p(FBD + FBS + CD + SE)	308.09	8.67
mod18	psi(CD) p(CC + CD + SE)	308.14	8.72
mod11	psi(CD) p(CAM + FBD + SE)	308.14	8.72
mod19	psi(DBH) p(CC + CD + SE)	308.29	8.87
mod7	psi(WA) p(CAM + CC + FBS + SE)	308.32	8.90
mod10	psi(CC) p(CAM + FBD + SE)	308.50	9.08
mod13	psi(RO) p(CAM + FBD + SE)	308.55	9.13
mod34	psi(RO) p(FBD + FBS + CD + SE)	309.15	9.73
mod33	psi(DBH) p(FBD + FBS + CD + SE)	309.26	9.84
mod31	psi(CC) p(FBD + FBS + CD + SE)	310.06	10.64
mod17	psi(CC) p(CC + CD + SE)	310.34	10.92
mod5	psi(DBH) p(CAM + CC + FBS + SE)	310.39	10.97
mod32	psi(CD) p(FBD + FBS + CD + SE)	310.52	11.10
mod20	psi(RO) p(CC + CD + SE)	310.64	11.22
mod3	psi(CC) p(CAM + CC + FBS + SE)	311.17	11.76
mod4	psi(CD) p(CAM + CC + FBS + SE)	311.84	12.42
mod6	psi(RO) p(CAM + CC + FBS + SE)	312.32	12.90

(h) Black giant squirrel

Number	Model	WAIC	ΔWAIC
mod13	psi(RO) p(CAM + FBD + SE)	415.11	0.00
mod27	psi(RO) p(FBD + CC + SE)	415.18	0.07
mod22	psi(AC) p(FBD + CC + SE)	415.40	0.29
mod8	psi(AC) p(CAM + FBD + SE)	415.44	0.33
mod12	psi(DBH) p(CAM + FBD + SE)	415.49	0.38
mod14	psi(WA) p(CAM + FBD + SE)	415.61	0.50
mod28	psi(WA) p(FBD + CC + SE)	415.79	0.68
mod26	psi(DBH) p(FBD + CC + SE)	415.84	0.73
mod25	psi(CD) p(FBD + CC + SE)	416.27	1.16
mod11	psi(CD) p(CAM + FBD + SE)	416.27	1.16
mod9	psi(CAN) p(CAM + FBD + SE)	416.29	1.19
mod10	psi(CC) p(CAM + FBD + SE)	416.30	1.19
mod24	psi(CC) p(FBD + CC + SE)	416.82	1.71
mod23	psi(CAN) p(FBD + CC + SE)	416.85	1.74
mod34	psi(RO) p(FBD + FBS + CD + SE)	419.39	4.29
mod29	psi(AC) p(FBD + FBS + CD + SE)	419.45	4.34
mod35	psi(WA) p(FBD + FBS + CD + SE)	419.76	4.65
mod33	psi(DBH) p(FBD + FBS + CD + SE)	420.19	5.08
mod30	psi(CAN) p(FBD + FBS + CD + SE)	420.29	5.18
mod32	psi(CD) p(FBD + FBS + CD + SE)	420.78	5.67
mod31	psi(CC) p(FBD + FBS + CD + SE)	420.99	5.88
mod1	psi(AC) p(CAM + CC + FBS + SE)	424.79	9.68
mod6	psi(RO) p(CAM + CC + FBS + SE)	427.05	11.94
mod7	psi(WA) p(CAM + CC + FBS + SE)	427.64	12.53
mod5	psi(DBH) p(CAM + CC + FBS + SE)	427.67	12.56
mod4	psi(CD) p(CAM + CC + FBS + SE)	427.68	12.57
mod3	psi(CC) p(CAM + CC + FBS + SE)	427.69	12.58
mod2	psi(CAN) p(CAM + CC + FBS + SE)	428.51	13.40
mod15	psi(AC) p(CC + CD + SE)	434.42	19.31
mod20	psi(RO) p(CC + CD + SE)	435.50	20.39
mod19	psi(DBH) p(CC + CD + SE)	436.80	21.69
mod18	psi(CD) p(CC + CD + SE)	437.09	21.98
mod16	psi(CAN) p(CC + CD + SE)	437.22	22.11
mod17	psi(CC) p(CC + CD + SE)	437.25	22.15
mod21	psi(WA) p(CC + CD + SE)	437.64	22.53

(i) Indian giant flying squirrel

Number	Model	WAIC	ΔWAIC
mod9	psi(CAN) p(CAM + FBD + SE)	437.19	0.00
mod14	psi(WA) p(CAM + FBD + SE)	440.63	3.44
mod12	psi(DBH) p(CAM + FBD + SE)	441.81	4.62
mod10	psi(CC) p(CAM + FBD + SE)	441.98	4.79
mod8	psi(AC) p(CAM + FBD + SE)	443.83	6.64
mod11	psi(CD) p(CAM + FBD + SE)	444.19	7.00
mod13	psi(RO) p(CAM + FBD + SE)	444.70	7.51
mod2	psi(CAN) p(CAM + CC + FBS + SE)	447.31	10.12
mod3	psi(CC) p(CAM + CC + FBS + SE)	451.75	14.56
mod5	psi(DBH) p(CAM + CC + FBS + SE)	452.17	14.97
mod7	psi(WA) p(CAM + CC + FBS + SE)	452.35	15.16
mod30	psi(CAN) p(FBD + FBS + CD + SE)	452.98	15.79
mod4	psi(CD) p(CAM + CC + FBS + SE)	453.40	16.21
mod1	psi(AC) p(CAM + CC + FBS + SE)	454.35	17.16
mod6	psi(RO) p(CAM + CC + FBS + SE)	454.47	17.28
mod35	psi(WA) p(FBD + FBS + CD + SE)	457.47	20.28
mod33	psi(DBH) p(FBD + FBS + CD + SE)	458.60	21.41
mod31	psi(CC) p(FBD + FBS + CD + SE)	459.30	22.11
mod34	psi(RO) p(FBD + FBS + CD + SE)	460.50	23.31
mod32	psi(CD) p(FBD + FBS + CD + SE)	460.51	23.32
mod29	psi(AC) p(FBD + FBS + CD + SE)	460.70	23.51
mod23	psi(CAN) p(FBD + CC + SE)	460.84	23.65
mod28	psi(WA) p(FBD + CC + SE)	464.86	27.66
mod24	psi(CC) p(FBD + CC + SE)	466.10	28.91
mod26	psi(DBH) p(FBD + CC + SE)	466.12	28.93
mod16	psi(CAN) p(CC + CD + SE)	467.62	30.43
mod25	psi(CD) p(FBD + CC + SE)	468.42	31.23
mod22	psi(AC) p(FBD + CC + SE)	468.67	31.47
mod27	psi(RO) p(FBD + CC + SE)	469.25	32.06
mod21	psi(WA) p(CC + CD + SE)	471.61	34.42
mod17	psi(CC) p(CC + CD + SE)	472.53	35.34
mod19	psi(DBH) p(CC + CD + SE)	472.80	35.60
mod15	psi(AC) p(CC + CD + SE)	474.08	36.88
mod20	psi(RO) p(CC + CD + SE)	474.53	37.34
mod18	psi(CD) p(CC + CD + SE)	475.62	38.43

Table S3. WAIC table from multi-scale arboreal occupancy models for four semi-arboreal species. AC = absolute cover, CAN = canopy height, CC = Canopy connectivity, CD = canopy difference, FBD = focal branch diameter, GRA = distance to grassland, RO = distance to road, WA = distance to water.

(a) Pig-tailed macaque

Number	Model	WAIC	ΔWAIC
mod2	psi(CAN) theta(method) p(method + arb:FBD + arb:CC + Terr:AC + SE)	4061.21	0.00
mod3	Psi(GRA) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	4061.60	0.38
mod5	psi(RO) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	4061.68	0.46
mod4	psi(WA) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	4061.75	0.54
mod1	psi(AC) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	4062.17	0.95

(b) Long-tailed macaque

Number	Model	WAIC	ΔWAIC
mod2	psi(CAN) theta(method) p(method + Arb:CC + Arb:CD + Terr:AC + SE)	1350.71	0.00
mod5	psi(RO) theta(method) p(method + Arb:CC + Arb:CD + Terr:AC + SE)	1352.24	1.54
mod1	psi(AC) theta(method) p(method + Arb:CC + Arb:CD + Terr:AC + SE)	1358.12	7.42
mod4	psi(WA) theta(method) p(method + Arb:CC + Arb:CD + Terr:AC + SE)	1358.47	7.77
mod3	Psi(GRA) theta(method) p(method + Arb:CC + Arb:CD + Terr:AC + SE)	1358.59	7.89

(c) Common palm civet

Number	Model	WAIC	ΔWAIC

mod5	psi(RO) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	2871.60	0.00
mod2	psi(CAN) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	2872.58	0.98
mod1	psi(AC) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	2872.67	1.07
mod4	psi(WA) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	2873.02	1.43
mod3	psi(GRA) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	2873.52	1.92

(c) Yellow-throated marten

Number	**Model**	**WAIC**	**ΔWAIC**
mod3	psi(GRA) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	1272.45	0.00
mod1	psi(AC) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	1272.67	0.22
mod4	psi(WA) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	1272.87	0.42
mod5	psi(RO) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	1273.06	0.61
mod2	psi(CAN) theta(method) p(method + Arb:FBD + Arb:CC + Terr:AC + SE)	1273.38	0.93

APPENDIX S15

Table S1. Mean, 95% BCI, and Prob. Effect for the random slope effects by species for two competing top arboreal GLMM models (a) count ~ GR + (CC + RO | species) and (b) count ~ CC + (FBS + CAM | Species). Prob. Effect indicates the probability an effect is different from zero; Bolded values indicate a strong effect (>0.9).

(a)		***Canopy connectivity***			***Distance to road***	
Species	Mean	95% BCI	Prob. Effect	Mean	95% BCI	Prob. Effect
Black-shanked douc-langur	0.38	(0.00, 0.79)	**0.95**	-0.34	(-0.69, 0.01)	**0.94**
Yellow-cheeked gibbon	0.10	(-0.36, 0.59)	0.62	-0.35	(-0.89, 0.13)	0.88
Pig-tailed macaque	0.41	(-0.01, 0.86)	**0.95**	-0.64	(-1.06, -0.23)	**0.99**
Long-tailed macaque	1.19	(0.62, 1.84)	**1.00**	-0.65	(-1.13, -0.18)	**0.99**
Common palm civet	0.91	(0.45, 1.40)	**1.00**	-0.62	(-1.08, -0.18)	**0.99**
Small-toothed palm civet	0.76	(0.34, 1.23)	**1.00**	0.09	(-0.40, 0.64)	0.59
Yellow-throated marten	0.30	(-0.15, 0.77)	0.87	0.10	(-0.32, 0.55)	0.63
Black giant squirrel	0.51	(0.12, 0.93)	**0.99**	-0.49	(-0.94, -0.08)	**0.97**
Indian giant flying squirrel	0.20	(-0.20, 0.58)	0.80	-0.27	(-0.64, 0.10)	0.88

(b)		***Focal branch slope***			***Camera height***	
Species	Mean	95% BCI	Prob. Effect	Mean	95% BCI	Prob. Effect
Black-shanked douc-langur	-0.49	(-0.88, -0.12)	**0.98**	-0.04	(-0.64, 0.60)	0.55
Yellow-cheeked gibbon	-0.40	(-0.97, 0.10)	0.89	0.68	(0.01, 1.36)	**0.95**
Pig-tailed macaque	-0.01	(-0.42, 0.39)	0.51	-0.40	(-0.90, 0.13)	**0.90**
Long-tailed macaque	-0.05	(-0.62, 0.49)	0.55	-0.79	(-1.55, -0.14)	**0.98**
Common palm civet	0.25	(-0.21, 0.74)	0.81	-0.60	(-1.22, -0.07)	**0.97**
Small-toothed palm civet	0.38	(-0.04, 0.87)	**0.92**	0.14	(-0.42, 0.73)	0.65
Yellow-throated marten	0.32	(-0.14, 0.82)	0.86	-0.14	(-0.68, 0.40)	0.66
Black giant squirrel	0.01	(-0.43, 0.49)	0.51	0.80	(0.15, 1.47)	**0.98**
Indian giant flying squirrel	-0.42	(-0.87, 0.00)	**0.95**	1.15	(0.52, 1.86)	**1.00**

Table S2. Coefficient estimates (Mean and 95% BCI) from the top multi-scale model for four semi-arboreal mesomammal species. Int = intercept, Arb = arboreal, Terr = terrestrial, AC = absolute cover, CAM = camera height, CAN = canopy height, CC = Canopy connectivity, CD = canopy difference, DBH = focal tree DBH, FBD = focal branch diameter, FBS = focal branch slope, GRA = distance to grassland, RO = distance to road, WA = distance to water.

Species	**Estimates**						
Black-shanked douc-langur	**P(int)**	**p(CAM)**	**p(CC)**	**p(FBS)**	**p(SE)**	**Psi(Int)**	**Psi(AC)**
Mean	-1.23	0.2	0.37	-0.38	-0.62	0.65	-0.57
95% BCI	(-1.51, -0.95)	(-0.11, 0.5)	(0.18, 0.56)	(-0.58, -0.16)	(-1.01, -0.21)	(0.03, 1.32)	(-1.15, -0.01)
Prob. Effect	1	0.9	1	1	1	0.98	0.98
Yellow-cheeked gibbon	**P(int)**	**p(CAM)**	**p(CC)**	**p(FBS)**	**p(SE)**	**Psi(Int)**	**Psi(CAN)**
Mean	-3.15	0.29	0.33	-1.06	0.44	-1.07	0.73
95% BCI	(-4.04, -2.3)	(-0.32, 0.9)	(-0.17, 0.84)	(-1.74, -0.43)	(-0.5, 1.38)	(-2.05, -0.15)	(-0.01, 1.57)
Prob. Effect	1	0.82	0.9	1	0.81	0.99	0.97
Pig-tailed macaque	**P(int)**	**p(FBD)**	**p(CC)**	**p(SE)**	**Psi(Int)**	**Psi(RO)**	*NA*
Mean	-0.76	-0.22	0.32	-0.72	1.18	-0.51	*NA*
95% BCI	(-0.98, -0.54)	(-0.4, -0.06)	(0.17, 0.46)	(-1.06, -0.39)	(0.53, 1.91)	(-1.15, 0.12)	*NA*
Prob. Effect	1	1	1	1	1	0.94	*NA*
Long-tailed macaque	**P(int)**	**p(CC)**	**p(CD)**	**p(SE)**	**Psi(Int)**	**Psi(WA)**	*NA*
Mean	-2.03	0.33	2.62	-0.04	-0.93	1.49	*NA*
95% BCI	(-2.7, -1.43)	(0, 0.68)	(1.87, 3.42)	(-0.77, 0.75)	(-1.74, -0.15)	(0.66, 2.42)	*NA*
Prob. Effect	1	0.98	1	0.55	0.99	1	*NA*

Common palm civet	**P(int)**	**p(FBD)**	**p(CC)**	**p(SE)**	**Psi(Int)**	**Psi(RO)**	*NA*
Mean	-2.18	0.83	0.53	0.02	0.13	-1.29	*NA*
95% BCI	(-2.64, -1.75)	(0.38, 1.26)	(0.32, 0.74)	(-0.59, 0.61)	(-0.71, 1.12)	(-2.29, -0.47)	*NA*
Prob. Effect	1	1	1	0.53	0.59	1	*NA*

Small-toothed palm civet	**P(int)**	**p(FBD)**	**p(CC)**	**p(SE)**	**Psi(Int)**	**Psi(CC)**	*NA*
Mean	-2.14	-0.36	0.5	0.17	-0.07	0.31	*NA*
95% BCI	(-2.68, -1.63)	(-0.69, -0.05)	(0.29, 0.71)	(-0.41, 0.76)	(-0.75, 0.66)	(-0.29, 0.93)	*NA*
Prob. Effect	1	0.99	1	0.72	0.6	0.85	*NA*

Yellow-throated marten	**P(int)**	**p(FBD)**	**p(CC)**	**p(SE)**	**Psi(Int)**	**Psi(AC)**	*NA*
Mean	-2.72	0.4	-0.05	-0.02	0.18	-0.76	*NA*
95% BCI	(-3.3, -2.15)	(-0.19, 0.99)	(-0.46, 0.33)	(-0.8, 0.75)	(-0.67, 1.21)	(-1.55, -0.01)	*NA*
Prob. Effect	1	0.9	0.6	0.52	0.63	0.98	*NA*

Black giant squirrel	**P(int)**	**p(CAM)**	**p(FBD)**	**p(SE)**	**Psi(Int)**	**Psi(RO)**	*NA*
Mean	-1.2	-0.01	0.68	-0.81	-0.58	-0.36	*NA*
95% BCI	(-1.66, -0.76)	(-0.46, 0.46)	(0.32, 1.04)	(-1.39, -0.22)	(-1.23, 0.03)	(-0.97, 0.23)	*NA*
Prob. Effect	1	0.53	1	1	0.97	0.88	*NA*

Indian giant flying squirrel	**P(int)**	**p(CAM)**	**p(FBD)**	**p(SE)**	**Psi(Int)**	**Psi(CAN)**	*NA*
Mean	-2.1	0.72	-0.47	0.52	-0.23	0.74	*NA*
95% BCI	(-2.59, -1.62)	(0.42, 1.01)	(-0.79, -0.16)	(-0.03, 1.08)	(-0.94, 0.45)	(0.12, 1.43)	*NA*
Prob. Effect	1	1	1	0.97	0.75	0.99	*NA*

Table 3. Beta estimates (Mean and 95% BCI) from the top multi-scale model for four semi-arboreal mesomammal species. Int = intercept, Arb = arboreal, Terr = terrestrial, AC = absolute cover, CAN = canopy height, CC = Canopy connectivity, CD = canopy difference, FBD = focal branch diameter, GRA = distance to grassland, RO = distance to road, WA = distance to water.

Species	**Estimates**					
Pig-tailed macaque	**p(Terr)**	**p(Arb)**	**p(Arb:FBD)**	**p(Arb:CC)**	**p(Terr:AC)**	**p(SE)**
Mean	-0.03	-0.75	-0.22	0.3	-0.1	-0.66
95% BCI	(-0.14, 0.09)	(-0.91, -0.6)	(-0.39, -0.05)	(0.16, 0.44)	(-0.2, 0.01)	(-0.81, -0.51)
Prob. Effect	0.68	1	1	1	0.96	1
Long-tailed macaque	**p(Terr)**	**p(Arb)**	**p(Arb:CC)**	**p(Arb:CD)**	**p(Terr:AC)**	**p(SE)**
Mean	-1.47	0.1	0.11	2.16	-0.28	-0.25
95% BCI	(-1.73, -1.22)	(-0.27, 0.45)	(-0.14, 0.36)	(1.53, 2.82)	(-0.54, -0.03)	(-0.59, 0.07)
Prob. Effect	1	0.71	0.81	1	0.99	0.93
Common palm civet	**p(Terr)**	**p(Arb)**	**p(Arb:FBD)**	**p(Arb:CC)**	**p(Terr:AC)**	**p(SE)**
Mean	-0.79	-1.46	0.75	0.51	0.05	0.26
95% BCI	(-0.93, -0.65)	(-1.77, -1.17)	(0.43, 1.07)	(0.36, 0.67)	(-0.06, 0.16)	(0.07, 0.45)
Prob. Effect	1	1	1	1	0.79	1
Yellow-throated marten	**p(Terr)**	**p(Arb)**	**p(Arb:FBD)**	**p(Arb:CC)**	**p(Terr:AC)**	**p(SE)**
Mean	-2.53	-0.24	0.3	-0.01	0.1	0.04
95% BCI	-2.91, -2.16	-0.68, 0.2	-0.3, 0.92	-0.4, 0.34	-0.13, 0.32	-0.35, 0.43
Prob. Effect	1	0.85	0.83	0.51	0.81	0.59

Species		Estimates			
Pig-tailed macaque		**Theta(Terr)**	**Theta(Arb)**	**Psi(Int)**	**Psi(CAN)**
	Mean	3.96	-2.77	4.53	0.04
	95% BCI	(2.83, 5.36)	(-4.15, -1.5)	(3.13, 6.36)	(-0.97, 1.08)
	Prob. Effect	1	1	1	0.53
Long-tailed macaque		**Theta(Terr)**	**Theta(Arb)**	**Psi(Int)**	**Psi(CAN)**
	Mean	0.45	-1.24	1.83	-1.18
	95% BCI	(-0.17, 1.21)	(-2.02, -0.55)	(0.75, 3.32)	(-2.26, 0.28)
	Prob. Effect	0.92	1	1	0.96
Common palm civet		**Theta(Terr)**	**Theta(Arb)**	**Psi(Int)**	**Psi(RO)**
	Mean	3.7	-3.64	4.14	-0.52
	95% BCI	(2.66, 4.98)	(-4.98, -2.5)	(2.81, 5.93)	(-1.71, 0.86)
	Prob. Effect	1	1	1	0.79
Yellow-throated marten		**Theta(Terr)**	**Theta(Arb)**	**Psi(Int)**	**Psi(GRA)**
	Mean	1.37	-0.74	2.46	0.54
	95% BCI	0.41, 2.78	-2.17, 0.57	1.17, 4.36	-0.63, 1.72
	Prob. Effect	1	0.88	1	0.84

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