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

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## Abstract

Tropical forests are the most species-rich biomes in the world but suffer high rates of logging and conversion. Tropical tree-dwelling (arboreal and semi-arboreal) mesomammals reliant on old-growth forest structures are especially vulnerable. The degree of behavioral arboreality of semi-arboreal mammals can be related to forest structure and perceived terrestrial threats. Paired arboreal and terrestrial camera traps are a promising new method for estimating the arboreality of cryptic and nocturnal species. Our study aimed to (1) model the effects of forest structure and anthropogenic disturbance on the detection and occurrence of arboreal and semi-arboreal mesomammals and (2) evaluate differences in occurrence and detection between paired arboreal and terrestrial camera trap sites for semi-arboreal mammals while estimating the degree of arboreality. We set 20 terrestrial and arboreal camera trap pairs in eastern Cat Tien National Park (Nam Cat Tien), Vietnam, from June 2019 to September 2020. We evaluated the effects of forest structure and proximity to roads on nine arboreal mesomammal species using single-season occupancy models. We used multi-scale occupancy modeling to estimate the degree of arboreality for four semi-arboreal mammals. All models were fit using hierarchical Bayesian modeling and compared using WAIC. We detected most arboreal and terrestrial mesomammal species currently known to inhabit Nam Cat Tien, including rare and cryptic species. Canopy connectivity and other mature forest characteristics were important for explaining the detection and occurrence of highly arboreal species, while the effect of a tree and focal limb characteristics on detection was species-specific. All semi-arboreal species had a greater probability of terrestrial station use than arboreal, suggesting a greater vulnerability to terrestrial threats, though the degree of arboreality varied by species. Using one sampling method underestimated occupancy for most semi-arboreal species. Multi-method sampling designs with multi-scale occupancy modeling can improve estimates of species distribution and habitat use for guiding management and conservation decisions.

## 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 (Laurance et al., 2008; Brodie et al., 2014), and results in homogenized forests composed largely of habitat generalists and edge-adapted species (Tabarelli, Peres & Melo, 2012).

Tropical tree-dwelling (arboreal and semi-arboreal) mammals are especially vulnerable to forest conversion (Laurance, 1990; Laurance et al., 2008; Whitworth et al., 2019), particularly when reliant on old-growth forest characteristics, such as canopy height, complexity, and connectivity (Cannon & Leighton, 1994). Ecological traits, such as the degree of arboreality, which we define as the probability of a species occurring in the canopy, can also affect species-level responses to forest degradation. Populations of specialized, strictly arboreal species are more vulnerable to changes in forest structure (Laurance & Laurance, 1996; Villaseñor

*et al.*, 2014) while terrestrial species are likely to be more vulnerable to hunting and snaring (Harrison *et al.*, 2016). The increasing number of 'empty forests' (Wilkie *et al.*, 2011; Sreekar *et al.*, 2015) 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 (e.g. Nekaris, Blackham & Nijman, 2008), which often fail to detect species that 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; Gregory *et al.*, 2014), but novel studies have shown that arboreal camera traps can also be useful in detecting species not observed by traditional ground-based techniques (e.g. Whitworth *et al.*, 2016; Bowler *et al.*, 2017; Moore & Niyigaba, 2018; Moore *et al.*, 2020). However, there is still much to be learned on how to appropriately design arboreal camera trapping studies for maximizing detections (Moore *et al.*, 2021). Furthermore, jointly sampling the terrestrial and arboreal environments via camera traps also 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 the perceived presence of terrestrial threats (e.g. humans, predators; McGraw & Bshary, 2002; Makin *et al.*, 2012). Estimating the degree of arboreality has traditionally been based on capture methods (e.g. Camargo *et al.*, 2016) using the proportion of captured individuals trapped within the canopy, or by following semi-arboreal species, mostly habituated diurnal primates, and estimating the proportion of time spent on the ground vs. in the trees (e.g. Makin *et al.*, 2012; Mekonnen *et al.*, 2018). 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 non-invasively expand these types of studies to rarer and nocturnal species while accounting for differences in detectability between terrestrial and arboreal camera stations.

Our study objectives were to (1) assess the effects of forest structure and anthropogenic disturbance on the detection and occurrence of arboreal and semi-arboreal tropical meso-mammals within a historically disturbed protected forest and (2) evaluate differences in occurrence and detection between paired arboreal and terrestrial camera trap sites for semi-arboreal mammals while also estimating the degree of arboreality. We hypothesized that site-level arboreal and semi-arboreal species occurrence would be driven by land-cover features (e.g. proximity to water and grasslands), forest structure (e.g. absolute cover and canopy height) or proximity to roads (a proxy for human accessibility). Furthermore, we hypothesized species detection probability would differ between terrestrial and arboreal camera traps and would vary by focal tree characteristics (e.g. focal branch diameter) and accessibility (e.g. canopy connectivity). Hypotheses were evaluated via specific variable combinations described in Table 1. 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 to these disturbances. Finally, due to the absence of large predators and moderate current human presence in the protected area (Supporting Information Appendix S1, Figure A.1) we hypothesized most semi-arboreal species would display high levels of terrestrial activity.

# Materials and methods

## Study area

Our study was conducted in the eastern core region of Cat Tien National Park, Nam Cat Tien (Fig. 1a) in Dong Nai Province, 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 (https://whc.unesco.org) and Ramsar Site (https://rsis.ramsar.org).

The Nam Cat Tien region is composed of secondary mixed evergreen and deciduous lowland dipterocarp forest, bamboo forest, wetland, and grassland. The wide distribution of secondary and bamboo-dominated forests is due to a legacy of anthropogenic disturbance (herbicide spraying during the U.S. Vietnam war and logging) 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). In addition, hunting for subsistence and the urban wildlife trade is a serious threat to the remaining wildlife within the park (Polet & Ling, 2004; Nguyen, 2009; Le, Hoang & Covert, 2019), though the frequency of illegal use remains low.

Seventy-six mammal species, including 29 mesomammals, were confirmed to inhabit Cat Tien National Park during surveys conducted between 1993 and 2001, comprising 30% of Vietnam's known mammal species (Polet & Ling, 2004). Of these, 13 can be classified as native arboreal or semi-arboreal mesomammals (<50 kg; Supporting Information Appendix S1, Table A.1), of which 10 (83%) are listed as

**Table 1** 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 eastern Cat Tien National Park (Nam Cat Tien), Vietnam

| Model | Hypothesis | Prediction |
|---|---|---|
| **Detection** | | |
| $p$ (CAM + CC + FBS + SE) | Canopy connectedness can increase accessibility and movement within the canopy, thereby affecting the probability 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 the type and length of use (resting vs. foraging vs. movement). | Detection will increase with higher camera height, canopy connectedness, and branch slope. |
| $p$ (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. |
| $p$ (CC + CD + SE) | Distance from the canopy is a quantitative measure of the relative position and accessibility of the camera to the surrounding canopy. Low canopy distance (little distance between the canopy and camera height) and high canopy connectivity suggest a high level of accessibility of the focal tree and thereby detection. | Detection will increase with a higher number of canopy connections and lower distance to 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 the surrounding canopy and thus the probability of use of the focal branch for arboreal travel and use. | Detection will increase with a 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 the accessibility of the focal branch for use and detection. | Detection will increase with a higher focal branch diameter, branch slope, and a lower distance to the canopy level. |
| **Occupancy** | | |
| $\psi$ (CAN) | Canopy height may be a measure of forest maturity and indicate the availability of resources dependent on taller and more mature trees, such as fruit and insects, a refuge from predators, den availability, etc. | Occurrence will increase with canopy height. |
| $\psi$ (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. |
| $\psi$ (DBH) | (Arboreal only) Larger trees are more likely to provide access to canopy resources, including tree hollows, dens, and refuge from predators, and can indicate a more mature forest. | Occurrence will increase with tree DBH |
| $\psi$ (CC) | (Arboreal only) Canopy connectedness is a measure of canopy integrity and cover. Areas of the forest with more connectivity are likely to provide arboreal pathways which facilitate movement through the canopy between resource patches, while canopy gaps and areas of low connectivity are likely to impede movement and thus be avoided. | Occurrence will increase as canopy connectivity increases. |

**Table 1** Continued

| Model | Hypothesis | Prediction |
|---|---|---|
| $\psi$ (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 decrease with distance to water. |
| $\psi$ (GRA) | Distance to grassland can act as a proxy for the linear effect of forest succession and thereby maturity. Forest edges and grasslands may conversely 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. |
| $\psi$ (RO) | Roads facilitate accessibility to the forest by humans and 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 increase with distance to road. |

AC, absolute cover; CAM, camera height; CAN, canopy height; CC, Canopy connectivity; CD, canopy distance; DBH, focal tree DBH; FBD, focal branch diameter; FBS, focal branch slope; GRA, distance to grassland; RO, distance to road; SE, dry season, and WA, distance to water. A categorical off-trail covariate (TR) was added to terrestrial detection for all multi-scale models. Additional summary statistics and details on covariate hypotheses are in Supporting Information Appendix S2.

threatened under IUCN, including Sunda pangolin *Manis javanicus* and Elliot's silver langur *Trachypithecus margarita* (IUCN, 2021).

## Camera trapping

We set 20 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 (Fig. 1b). Sites were selected at varying proximity to anthropogenic disturbance (urban areas, park edge, roads), with minimum proximity between adjacent sites of 500 m. Cameras were active 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 set approximately 30–70 cm off the ground on or near human trails (within 5 m) from June 2019 to January 2020 as part of a larger terrestrial occupancy study (Masseloux *et al.*, 2022) but were moved off-trail (within 50 m 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 via double-rope tree climbing on a horizontal limb or facing a vertical trunk at a height between 7 and 28 m. The median canopy height at all our sites was 26 m with a range of 14–36 m, capturing the range of available canopy types. However, most cameras were set in mid- and sub-canopy where we hypothesized most species would occur due to higher canopy connectivity which facilitates 'arboreal pathways' (Hopkins, 2011). Safety, feasibility of climbing, location in the canopy relative to other trees (canopy connectivity), and presence of an ideal focal tree limb were all considered prior to setting an arboreal camera. All cameras were set to take five successive photographs with a delay period of 1 s 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 which also 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 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 were focal branch slope, canopy connections, focal branch diameter, camera height, canopy distance (position of the focal limb in relation to the canopy) 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 a 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. Fruits were rarely detected during vegetation surveys and revisits, precluding inclusion as a variable. Hypotheses, predictions, data source, and summary statistics (median and range) for all variables are summarized in Supporting Information Appendix S2. We tested for pair-wise correlation among covariates and highly correlated variables ($r > 0.5$) were removed or not included within the same model (Supporting Information Appendix S3). All covariates were standardized at a mean of zero and a standard deviation of 1.
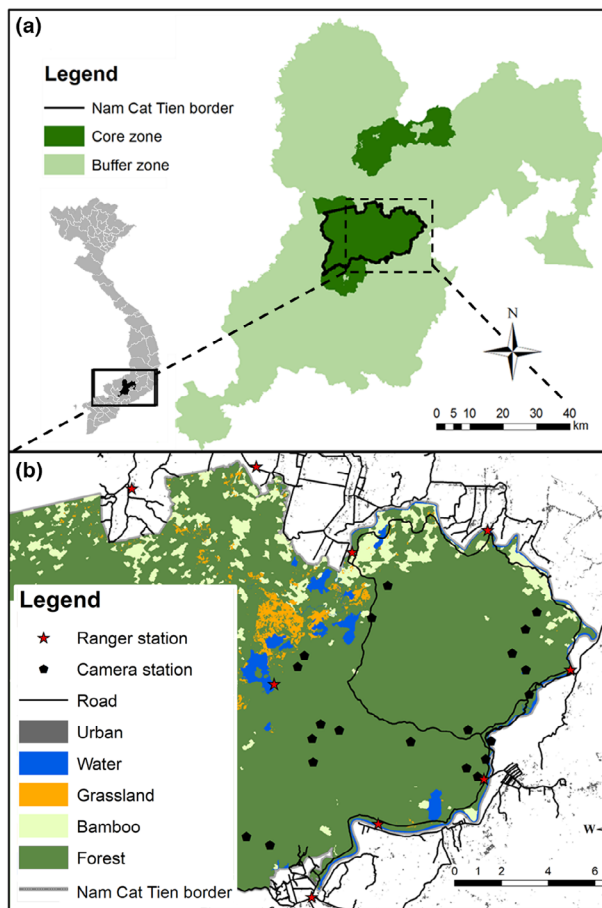
**Figure 1** (a) Dong Nai Biosphere reserve (as delineated by UNESCO; light green) and core protected area (dark green) zones of Cat Tien National Park, Vietnam. Our study was conducted in the eastern Nam Cat Tien (black outline) region of the park. (b) Layout of camera trap sites within the forests of Nam Cat Tien, Vietnam.

## Modeling framework

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 our objectives, we used occupancy modeling (MacKenzie *et al.*, 2017) for all species.

## Single-species occupancy models

We used single-season occupancy modeling (MacKenzie *et al.*, 2002) to assess the effects of forest structure and anthropogenic disturbance on detection ($p$) and occupancy probability ($\psi$) of arboreal and semi-arboreal tropical mesomammals (objective 1) using detection/non-detection data from our arboreal camera traps. 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 outline specific model hypotheses and predictions in Table 1. Models include several factors on $p$, but only a single variable on $\psi$ to not overparameterize this submodel, given the few sampled sites. We considered differences in species detection across the dry and wet season using a stacked modeling approach, where data for each season is stacked as subsequent rows and season is included as a site-level categorical variable (see Monterroso *et al.*, 2020); our single-species detection history matrix, therefore, was composed of three stacked matrices of 20-sites by 27-occasions (7 days per occasion). Due to data sparsity, we did not include season as a covariate on the occurrence and 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. Sites with no active sampling sessions (due to theft or malfunction) were removed. We used a Bayesian framework to fit and compare models for each arboreal species and estimated parameter effects on $p$ and $\psi$ using the software program MARK (White & Burnham, 1999).

## Multi-scale occupancy models

To evaluate differences in occupancy and detection between terrestrial and arboreal methods for semi-arboreal mammals (objective 2), 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, the 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, $\psi$ is the probability that the site is occupied, $p^s$ is the probability of detection at station $s$, given that the site is occupied and the species is present at the sample station and $\theta^s$ is the probability that the species is present at the sample station given that the site is occupied. Model parameters can be functions of site-specific covariates, and $p^s$ and $\theta^s$ can be modeled as a function of station-specific covariates.

We further used the multi-scale model to evaluate the degree of arboreality (objective 2), which can be accomplished in several different ways (Supporting Information Appendix S4, Table D.1). Since our inference is spatial, we can consider arboreality at all sites or occupied sites only. For example, the degree of arboreality could be understood by examining the ratio of the probability of arboreal station use to the probability of terrestrial station use at occupied sites ($\alpha$), the ratio of the probability of only using the arboreal station to the probability of only using the terrestrial station at occupied sites ($\beta$), and the probability an occupied site is used at the terrestrial and arboreal station among all sites used terrestrial or arboreal ($\gamma$; Table 2b). While these

differ from traditional definitions of arboreality (e.g. proportion of time or detections in the canopy; Mekonnen *et al.*, 2018; Estrada & Coates-Estrada, 1985), we believe that these interpretations are informative about the likelihood of a species utilizing the canopy at a given site.

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 (Table 1). We also considered a categorical covariate for dry vs. wet season across both arboreal and terrestrial detection and a categorical covariate for on vs. off trail on terrestrial detection as the effect of the trail has been documented to have variable effects on mammal detection (Harmsen *et al.*, 2010; Sollmann *et al.*, 2013; Kolowski & Forrester, 2017). The sample station parameter ($\theta^s$) was always modeled with a difference in arboreal and terrestrial station occurrence. Lastly, we included one of five possible covariates on $\psi$ (canopy height, distance to road, absolute cover, distance to water, and distance to grassland; Table 1) for species with naïve multi-scale occupancy estimates <0.80 (Supporting Information Appendix S1, Table A.2). 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 Gaussian priors on all logit-scaled effects on detection and site-level occupancy ($\mu = 0$, $\sigma = 1.75$; Cooch & White, 2020). For each model, we fit two parallel Markov-chain Monte Carlo chains of 10 000 iterations with tuning of 4000 and a burn in of 2000. 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

**Table 2** Estimates of (a) site-level occupancy ($\psi$) and detection ($p$) from the most supported single-species model for nine arboreal species (only arboreal data) at the mean covariate value, and (b) site-level occupancy, station-level occupancy ($\theta$) and station-level detection ($p$) from the most supported multi-scale model for four semi-arboreal species (arboreal and terrestrial data) at the mean covariate value. $\alpha = 1$ indicates no difference in the probability of use of the tree or ground, $\alpha < 1$ indicates a greater probability of use of the ground and $\alpha > 1$ indicates a greater probability of use of the trees. $\beta = 0$ indicates the species never strictly uses occupied sites arboreally, $\beta = 1$ indicates even use of occupied sites terrestrially and arboreally, and $\beta > 1$ indicates more strict use of occupied sites arboreally than terrestrially. $\gamma = 1$ indicates occupied sites are only used both arboreally and terrestrially and $\gamma = 0$ indicates occupied sites are never used both arboreally and terrestrially

(a)

| Species | Species abbreviation | $\psi$ Mean | $\psi$ SE | $p$ Mean | $p$ SE |
|---|---|---|---|---|---|
| Black-shanked douc-langur | BSDL | 0.65 | 0.07 | 0.19 | 0.02 |
| Yellow-cheeked gibbon | YCGI | 0.27 | 0.09 | 0.05 | 0.02 |
| Northern pig-tailed macaque | PTMA | 0.76 | 0.06 | 0.26 | 0.02 |
| Long-tailed macaque | LTMA | 0.29 | 0.08 | 0.12 | 0.03 |
| Common palm civet | CPCI | 0.53 | 0.11 | 0.10 | 0.02 |
| Small-toothed palm civet | STPC | 0.48 | 0.09 | 0.11 | 0.02 |
| Yellow-throated marten | YTMA | 0.54 | 0.11 | 0.06 | 0.01 |
| Black giant squirrel | BGSQ | 0.36 | 0.07 | 0.18 | 0.02 |
| Indian giant flying squirrel | IGFS | 0.44 | 0.08 | 0.13 | 0.02 |

(b)

| Notation | Description | Equation | PTMA | LTMA | CPCI | YTMA |
|---|---|---|---|---|---|---|
| $\psi$ | Site-level occupancy | $\psi$ | 0.98 | 0.85 | 0.98 | 0.89 |
| $\theta^{Terr}$ | Station-level terrestrial occupancy | $\theta^{Terr}$ | 0.98 | 0.61 | 0.97 | 0.79 |
| $\theta^{Arb}$ | Station-level arboreal occupancy | $\theta^{Arb}$ | 0.76 | 0.31 | 0.47 | 0.64 |
| $p^{Terr}$ | Station-level terrestrial detection | $p^{Terr}$ | 0.43 | 0.17 | 0.33 | 0.07 |
| $p^{Arb}$ | Station-level arboreal detection | $p^{Arb}$ | 0.27 | 0.19 | 0.13 | 0.06 |
| $\Phi^{A}$ | Probability of arboreal station use | $\psi \times \theta^{Arb}$ | 0.74 | 0.26 | 0.46 | 0.57 |
| $\Phi^{T}$ | Probability of terrestrial station use | $\psi \times \theta^{Terr}$ | 0.96 | 0.52 | 0.95 | 0.70 |
| $\Phi^{AT}$ | Probability of both arboreal and terrestrial station use | $\psi \times \theta^{Arb} \times \theta^{Terr}$ | 0.73 | 0.16 | 0.45 | 0.45 |
| $\alpha$ | Ratio of the probability of arboreal to terrestrial station use (given site occupied) | $\theta^{Arb} / \theta^{Terr}$ | 0.78 | 0.51 | 0.48 | 0.81 |
| $\beta$ | Ratio of the probability of only using the arboreal station to the probability of only using the terrestrial station (given site occupied) | $\dfrac{\theta^{Arb} - (\theta^{Arb} \times \theta^{Terr})}{\theta^{Terr} - (\theta^{Arb} \times \theta^{Terr})}$ | 0.06 | 0.29 | 0.03 | 0.47 |
| $\gamma$ | Probability an occupied site is used at both the terrestrial and arboreal station among all occupied sites used terrestrially or arboreally | $\dfrac{\theta^{Terr} \times \theta^{Arb}}{(\theta^{Terr} + \theta^{Arb}) - (\theta^{Terr} \times \theta^{Arb})}$ | 0.75 | 0.26 | 0.46 | 0.55 |

make inferences using estimated mean effects and 95% Bayesian credible intervals (BCI) from the top supported model. We quantify support for estimated species 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 25 unique species, 13 on the arboreal cameras and 19 on the terrestrial cameras (Supporting Information Appendix S1, Table A.1). Six species were only detected arboreally (e.g., yellow-cheeked gibbon *Nomascus gabriellae*, small-toothed palm civet *Arctogalidia trivirgata*), 12 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*, northern pig-tailed macaque *Macaca nemestrina*; Supporting Information Appendix S1, Table A.1). The species accumulation curves suggest all or almost all species were detected, although we have greater confidence for terrestrial species richness (Fig. 2; Supporting Information Appendix S3). In addition, according to the Murphy & Phan (2002) and Polet & Ling (2004) 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 & Phan, 2002). In contrast, we detected only 19 out of 23 (83%) terrestrial mesomammals (for additional details see Masseloux *et al.*, 2022). In the following analyses, we did not include Elliot's silver langur, Sunda pangolin, pygmy slow loris *Nycticebus pygmaeus*, and stump-tailed macaque *Macaca arctoides* due to the sparsity of detections (naïve occupancy <0.1) leading to model convergence issues. Low terrestrial detection rates also precluded multi-scale modeling of black-shanked douc langur *Pygathrix nigripes*.

### Single-species arboreal occupancy models

We fit and compared 35 candidate models for each arboreal and semi-arboreal species (*n* = 9, arboreal data only; Supporting Information Appendix S5, Table E.1). Estimated mean occupancy probabilities over all sampled sites for arboreal species varied from 0.27 (yellow-cheeked gibbon) to 0.76 (pig-tailed macaque; Table 2a). The most supported model varied by species, but recurring detection covariates were canopy connectivity, camera height and focal branch diameter (Fig. 3; Supporting Information Appendix S5: Table E.1). Canopy connectivity and camera height had medium positive effects on most species except black giant squirrel *Ratufa bicolor*, for which camera height had no effect (mean = −0.05; 95% BCI = −0.50, −0.39; Pr < 0 = 0.6), and yellow-throated marten, for which canopy connectivity had no effect (mean = −0.05, BCI = −0.46, 0.33, Pr < 0 = 0.6; Fig. 3). Larger branch size increased detection for most species except pig-tailed macaque, small-toothed palm civet, and flying squirrel. Detection of long-tailed macaque *Macaca fascicularis* was strongly associated with increasing distance from the canopy (mean = 2.62, BCI = 1.87, 3.42, Pr > 0 = 1), and a negative effect of camera height (mean = −2.75, BCI = −3.67, −1.83, Pr < 0 = 1) from the next most supported model that included the
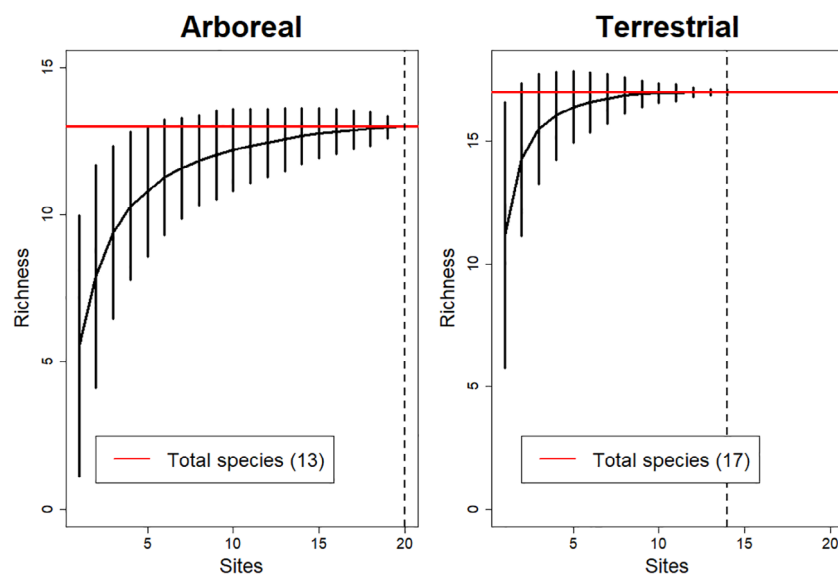


**Figure 2** Species accumulation curves resampled at site level for arboreal and terrestrial camera trapping stations (*n* = 20 paired sites) set in eastern Cat Tien National Park (Nam Cat Tien) from June 2019 to September 2020. Uncertainty estimates of 95% confidence intervals are based on random permutations of the site-level data. Survey-level resampling showed similar results (Supporting Information Appendix S3).
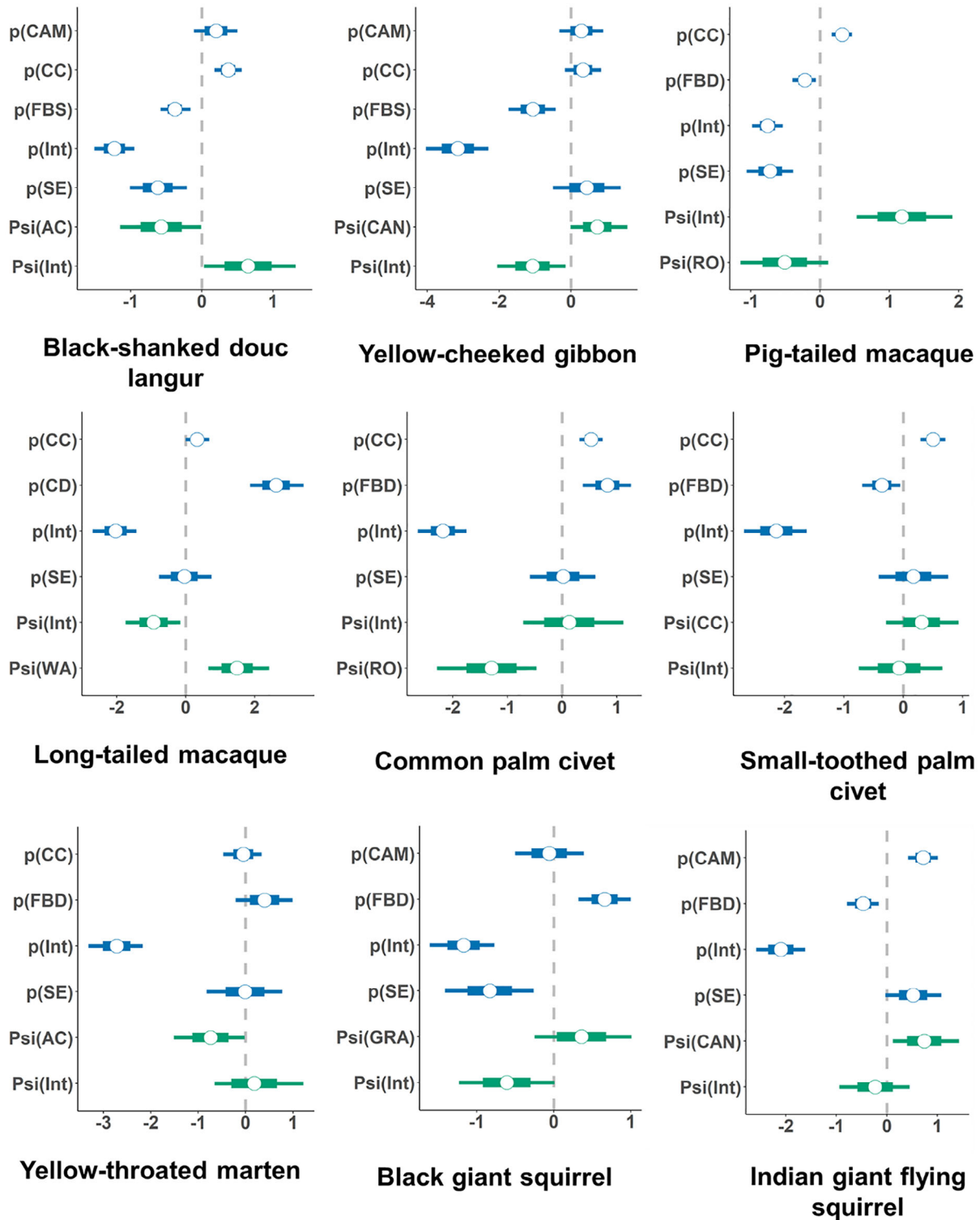
**Figure 3** Parameter estimates for covariate effects on detection (*p*; blue) and occurrence (*ψ*; green) probability from the most supported single-species occupancy model for nine arboreal species on the logit-scale from arboreal camera trap data (*n* = 20 stations) collected in eastern Cat Tien National Park (Nam Cat Tien), Vietnam, from June 2019 to September 2020. The mean is indicated by the circle, 70% and 95% Bayesian credible intervals are indicated by the thick and thin lines, respectively. The gray dashed line indicates 0 or no effect. AC, absolute cover; CAN, canopy height; CAM, camera height; CC, canopy connectivity; CD, canopy distance; FBD, focal branch diameter; GRA, distance to grassland; RO, distance to road; SE, dry season; WA, distance to water.

covariate (Supporting Information Appendix S6: Table F.1) suggests that long-tailed macaque detections increase in the sub-canopy. The dry season had a small to moderate effect ($|\beta| < 1$) on the detection of most species. Some species' model sets included several parsimonious occupancy covariates, possibly due to a low number of sampled sites or poor explanatory power of our selected covariates for that species. There was strong support for the positive effect of distance to water on occurrence of long-tailed macaque (mean = 1.49, BCI = 0.66, 2.42, Pr > 0 = 1) and moderate support for the positive effect of canopy height on occurrence of gibbon (mean = 0.73, BCI = −0.01, 1.57, Pr > 0 = 0.97) and flying squirrel (mean = 0.74, BCI = 0.12, 1.43, Pr > 0 = 0.99). There was also moderate support for the negative effect of absolute cover on occurrence of black-shanked douc-langur (mean = −0.57, BCI = −1.15, −0.01, Pr < 0 = 0.98) and yellow-throated marten (mean = −0.76, BCI = −1.55, −0.01, Pr < 0 = 0.98), and distance to road on the occurrence of common palm civet (mean = −1.29, BCI = −2.29, −0.47, Pr < 0 = 1; Fig. 3; Supporting Information Appendix S6, Table F.1).

## Single-species multi-scale occupancy models

We fit 5 candidate models to four semi-arboreal species for which we had enough terrestrial and arboreal data to fit models with $\theta$ (Supporting Information Appendix S5, Table E.2). Arboreal detection probability ($p^{Arb}$) was higher than terrestrial ($p^{Terr}$) for long-tailed macaque, but lower for all other species (Table 2b; Fig. 4). However, there was strong support for lower arboreal occupancy ($\theta^{Arb}$) compared to terrestrial occupancy ($\theta^{Terr}$) for all species (Table 2b; Fig. 4). Differences in arboreal and terrestrial occupancy probability also varied widely by species (Table 2b). We found that all semi-arboreal species had a greater probability of terrestrial station use than arboreal ($\alpha < 1$), however, the degree of arboreality varied by species. Pig-tailed macaque had a high probability of independent arboreal and terrestrial station use (Table 2b) and had a high ($\gamma = 0.75$) probability of using both arboreal and terrestrial stations at occupied sites (Supporting Information Appendix S6, Table F.2). Long-tailed macaque was twice as terrestrial as arboreal (Table 2b; $\alpha = 0.51$) and more likely to use either an arboreal or terrestrial station at a given site but not both ($\gamma = 0.26$). The common palm civet had a high probability of terrestrial station use ($\Phi^T = 0.95$), was half as likely to use an arboreal station ($\alpha = 0.48$), and had a low probability of only using an arboreal station to move through a site ($\beta = 0.03$). Lastly, yellow-throated marten had a high probability of independent arboreal and terrestrial station use ($\alpha = 0.82$), but a lower ($\Phi^{AT} = 0.45$) likelihood of using both stations at a site.

There was substantial model selection uncertainty for $\psi$ for yellow-throated marten (all WAIC values were within a difference of 2). For long-tailed macaque, canopy height had a large negative effect on occurrence (mean = −1.18, 95% BCI = −2.26, 0.28, Pr < 0 = 0.96) and a parsimonious

model suggested distance to road had a large positive effect on occurrence (mean = 0.82, 95% BCI = 0.14, 1.66, Pr > 0 = 0.99). The absolute cover had a small negative effect on terrestrial detection (Fig. 4; Supporting Information Appendix S6, Table F.2). 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 and trail on terrestrial detection was small and had low support for all species (Fig. 4; Supporting Information Appendix S6, Table F.2). Mean occupancy estimates using the multi-scale models were significantly higher than occupancy estimates from the single-species arboreal models for all species and higher than terrestrial station only occurrence ($\theta^{Terr}$) for yellow-throated marten and long-tailed macaque (Table 2a and b; Supporting Information Appendix S6, Table F.2).

## Discussion

Environmental and anthropogenic spatial and structural characteristics can affect species' use of and distribution within a landscape (Gehring & Swihart, 2003; Grelle, 2003). Due to cryptic, small-bodied, nocturnal and rare species often being missed during surveys or forgotten (Whitworth *et al.*, 2016; Bowler *et al.*, 2017), results in data deficiencies that may endanger conservation efforts for threatened species. Our study supports arboreal camera trapping as a promising 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 the 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. We detected 6 species in the canopy that were not detected by terrestrial cameras, suggesting that combining methods can improve mammal biodiversity inventories (see also Haysom *et al.*, 2021). Our study also 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.

We found support for several structural forest characteristics which can affect the detections of mesomammals by arboreal cameras. Canopy connectivity was a recurring determinant of species detection, as trees with more connections to proximate trees can act as arboreal highways, facilitating movement through the canopy. Studies in other tropical regions have also found tree connectivity to be a strong predictor of the use and occurrence of arboreal mammals in the canopy (Gregory *et al.*, 2017; Whitworth *et al.*, 2019). Arboreal mammals generally prefer to move through the canopy along established routes that maximize revisits to known
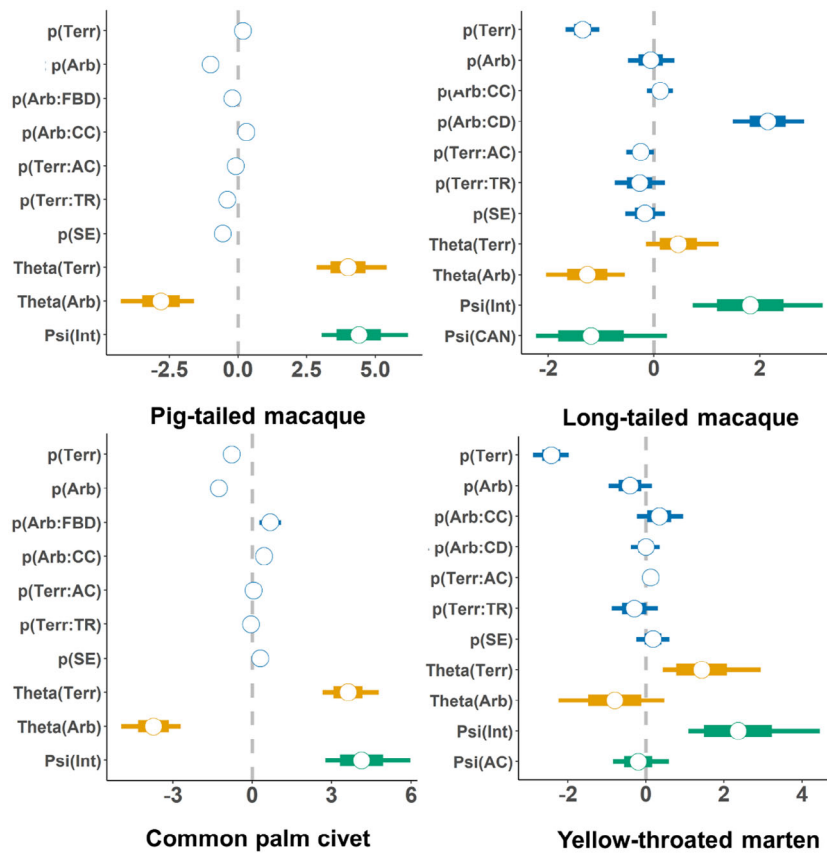
**Figure 4** Parameter estimates for covariate effects on site-level occurrence ($\psi$, green), station-level occurrence ($\theta$, yellow) and detection ($p$, blue) from the most supported multi-scale occupancy model for four semi-arboreal species on the logit-scale from arboreal and terrestrial camera trap data ($n = 20$ paired sites) collected in eastern Cat Tien National Park (Nam Cat Tien), Vietnam, from June 2019 to September 2020. The posterior mean is indicated by the circle, 70% and 95% Bayesian credible intervals are indicated by the thick and thin lines, respectively; intervals that are not visible are too small for plotting. The dashed gray line indicates 0 or no effect from the intercept. AC, absolute cover; CAN, canopy height; CC, Canopy connectivity; CD, canopy distance; FBD, focal branch diameter; GRA, distance to grassland; RO, distance to road; SE, dry season; TR, off-trail; WA, distance to water. Colons indicate the covariate only applies to terrestrial (Terr) or arboreal (Arb) stations.

resource locations (e.g., fruiting trees) while avoiding large gaps in the canopy (Cannon & Leighton, 1994). Hopkins (2011) similarly found that Howler monkeys selected arboreal paths between forage sites with high levels of resource availability and canopy connectivity over comparable linear pathways. We can thus posit that arboreal species in Nam Cat Tien are more likely to frequent these highly connected areas of the canopy. 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).

In contrast, 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 that were predominantly detected at higher canopy height or

within the emergent canopy level (e.g. yellow-cheeked gibbon, black-shanked douc-langur, Indian giant flying squirrel *Petaurista philippensis*) 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; Cheyne, Thompson & Chivers, 2013). The primary mode of locomotion for Indian giant flying squirrels involves climbing and gliding between tree trunks, which would also explain the effect of vertical slope on detections.

The degree to which a species is arboreal can be a useful metric for assessing the vulnerability of semi-arboreal fauna to specifically terrestrial or arboreal threats. For example, snares, which indiscriminately capture terrestrial 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). Semi-arboreal species which exhibit a high probability of terrestrial occurrence are more likely to be vulnerable to terrestrial threats such as snares while species which are predominantly arboreal are more likely to be vulnerable to changes in forest structure (e.g. logging). Species may also elect to change their degree of arboreality in response to such threats, thereby reducing risk (e.g. Mekonnen *et al.*, 2018). While all four of our semi-arboreal species occurred more terrestrially than arboreally, the degree of difference varied by species. For example, common palm civets were half as likely to occur arboreally than terrestrially at our sites (Table 2b). 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 and snare densities tend to be higher (Clements *et al.*, 2014). Interestingly, while the most parsimonious single-species occupancy model for long-tailed macaque included the positive effect of distance to water on occurrence, the most parsimonious multi-scale model included a negative effect of canopy height on occurrence. This suggests that important variables affecting species' occurrence may be missed if an entire subset of the species' habitat is absent from the analyses. Combining arboreal and terrestrial datasets using multi-scale occupancy modeling is thus likely to provide more robust estimates of the effects of environmental and anthropogenic variables on semi-arboreal species.

Our limited sample size precluded the use of covariates on station-specific occupancy ($\theta^s$), but future research efforts could expand on this application of the multi-scale method by examining changes in the degree of arboreality over more explicit gradients of forest structure and anthropogenic activity. Occupancy modeling does not allow for conclusions about time spent in the canopy, which has been traditionally used to define arboreality (Mekonnen *et al.*, 2018). A species may spend a lot of time foraging on the ground in a small area but display a greater probability of detection and occurrence in the trees if using the canopy for movement. However, examining how these probabilities change over time and space is still informative for studying the effects of anthropogenic disturbance on a species' realized niche. In addition, there is great potential for use of paired camera traps at fruiting trees or key resource areas for studying arboreal-terrestrial behavior, such as giving-up densities in different landscapes or response to a simulated threat (e.g. Makin *et al.*, 2012; Smith *et al.*, 2017; Suraci *et al.*, 2017).

One of the major challenges of arboreal camera trapping is the complex, three-dimensional sampling space of the canopy (Moore *et al.*, 2021). Standardized detection is a key requirement in occupancy modeling. As arboreal detection rates are typically much lower than terrestrial detection rates (Whitworth *et al.*, 2016; Moore *et al.*, 2020; Haysom *et al.*, 2021), arboreal data is likely to be more sparse and thus less conducive to complex models with many covariates. Identifying forest and focal limb characteristics which maximize detections in a particular region or habitat will allow future studies to standardize arboreal camera placement and focus on variables affecting occupancy. Our study provides preliminary suggestions of important metrics for species-specific detection in tropical forests at the canopy level. We hope these will guide future arboreal studies targeting similar 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. 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 forests and mitigate terrestrial threats to ensure the persistence of arboreal and semi-arboreal mesomammals.

## Acknowledgments

## Author contributions

Juliana Masseloux and Brian Gerber conceived ideas, designed the methodology, analyzed the data and led the writing of the manuscript. Jessica Burr and Quy Tan Le contributed significantly to data collection and manuscript revisions and gave the final approval for publication.

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## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Mesomammal species list, naive occupancy estimates, and anthropogenic risk map.

**Appendix S2.** Covariate summary statistics and hypotheses.

**Appendix S3.** Preliminary and exploratory analyses.

**Appendix S4.** Derived probabilities of site occupancy and conditional occupancy to compare terrestrial and arboreal activity.

**Appendix S5.** WAIC tables for model selection for single-species and multi-scale occupancy models.

**Appendix S6.** Mean, 95% BCI, and probability of an effect from the top single-species and multi-scale occupancy models.