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Ground-dwelling mammal and bird diversity in the southern Annamites: Exploring complex habitat associations and the ghost of past hunting pressure

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Abstract
The Langbian Plateau, a biodiversity hotspot in the southern Annamites of Viet Nam, has undergone extensive hunting pressure. However, the limited information on the effects of overexploitation on the current status and community composition of wildlife hinders effective conservation efforts, including the implementation of targeted patrols to reduce snaring. In this study, we conducted a camera-trapping survey across the Langbian Plateau, consisting of a broadleaf evergreen and coniferous habitat mosaic. We recorded 46 ground-dwelling mammals and birds, including several threatened Annamite endemics. Using multi-species Royle-Nichols model and landscape covariates, we found higher richness in broadleaf evergreen forest located in more remote and less rugged areas. We then used species responses to covariates to predict species distribution and identify high-priority areas for conservation. Furthermore, we constructed diversity profiles that indicated higher biodiversity in broadleaf evergreen forest compared to the coniferous forest. Finally, we used a dissimilarity index to assess the level of defaunation, revealing 16% of the community had been lost, with higher levels of defaunation for threatened and larger-sized species. Our findings provide insights into the status, distribution, and occurrence of the ground-dwelling mammal and bird communities in the Langbian Plateau, and can help stakeholders design more effective conservation strategies to protect existing populations.

KEYWORDS
Annamites, camera-trapping, defaunation, diversity profiles, endemic species, multi-species occupancy, Roy-Nichols model, snaring, species richness, unsustainable hunting

1 | INTRODUCTION

Global biodiversity is declining at an alarming rate as a result of anthropogenic pressures (Ceballos et al., 2015; Pievani, 2014). Although habitat loss remains an issue, in recent decades unsustainable hunting has emerged as a major driver of faunal loss in the tropical forests (Ripple et al., 2016). Among tropical regions, wildlife declines have been particularly severe in mainland Southeast Asia (Benítez-López et al., 2019), and as a consequence, the region has an especially high number of threatened mammal and bird species (Schipper et al., 2008; Sodhi et al., 2010; Wolff et al., 2023). Overexploitation through the use of wire snares is the primary driver of wildlife declines, both because of the low cost and high effectiveness of snaring, and the high commercial demand for wildlife products in mainland Southeast Asia (Gray et al., 2021; Harrison et al., 2016). There are an estimated 12.3 million wire snares within the protected areas of Viet Nam, Laos, and Cambodia alone (Belecky & Gray, 2020), and not surprisingly, this level of unsustainable hunting pressure has emptied forests across the region.

Within mainland Southeast Asia, the Annamite mountains harbor exceptionally high levels of biodiversity (Baltzer et al., 2001), but are also an epicenter for defaunation (Gray et al., 2021; Tilker et al., 2019). The region contains a number of endemic and evolutionarily distinct species that are facing extinction (Gray et al., 2021). Among Annamite endemic flagship species, the Vietnam pheasant *Lophura edwardsi* is likely extinct in the wild (Grainger et al., 2018), and the saola *Pseudoryx nghetinhensis* and large-antlered muntjac *Muntiacus vuquangensis* are close to extinction (Timmins et al., 2020; Timmins, Hedges, & Robichaud, 2016). Populations of non-endemic ground-dwelling mammal and bird species have also undergone severe declines, and although many of these species are not threatened with global extinction, their loss from Annamite forests may have unforeseen ecological consequences that jeopardizes the health of these ecosystems (Belecky & Gray, 2020). For example, research has shown that defaunation can reduce seed dispersal and forest regeneration, disrupt nutrient cycling, and negatively impact ecosystem services linked to carbon storage, clean air, and water (Gardner et al., 2019; Krause & Tilker, 2022; Young et al., 2016).

The southern Annamites are biogeographically distinct from the central and northern Annamites, harboring several species that appear to be absent from the wider ecoregion (Bain & Hurley, 2011; Sterling & Hurley, 2005). Furthermore, unlike forest areas in the northern and central Annamites, the forests in the core area of the southern Annamites—known as the Langbian Plateau—consist of a complex mosaic of broadleaf evergreen and large expanses of coniferous forest habitat (Baltzer et al., 2001; Critchfield & Little, 1966). It is likely that this habitat diversity has contributed to the high levels of species diversity and endemism that characterize the southern Annamites region. Little is known about patterns of biodiversity within these two major habitat types, following extensive wildlife overexploitation. In other parts of the world, broadleaf evergreen forests have been shown to have higher levels of overall species richness than coniferous forests, especially for larger vertebrates (Pillay et al., 2022). It is likely that a similar pattern occurs in the forests of the Langbian Plateau, although specific species habitat associations in this area have not been well explored.

The southern Annamite forests have a complex history within the 20th and 21st centuries. As with other tropical regions, big game hunting had become widespread in the Annamites during colonial times (MacKenzie, 1988; Malarney, 2020). Both the broadleaf evergreen and coniferous forests were used extensively during the French colonial period by Vietnamese and foreign hunters who targeted megafaunal species such as tiger *Panthera tigris*, leopard *Panthera pardus*, gaur *Bos gaurus*, and Asian elephant *Elephas maximus* (Bouvard & Millet, 1920; Guérin, 2010; Millet, 1916). There is evidence that this level of hunting had impacts on large mammal populations in the region (Guérin, 2010). Since the 1980s, widespread snaring has become the primary driver of mammal population declines in Viet Nam. Snaring has now reached high levels across the country—with some protected areas removing tens of thousands of snares per year (Save Vietnam's Wildlife, 2019; Tilker et al., 2023)—and has caused widespread wildlife declines and local extirpations (Gray et al., 2021). There is evidence that on the Langbian Plateau, for example, tigers were heavily hunted during the early of 20th century (Guérin, 2010; Guérin & Seveau, 2009), but the species was still reported during 1980s and 1990s (Duckworth & Hedges, 1998), before snaring likely extirpated the last individuals. It is probable that a similar pattern played out for other large mammal species. As a result of this complex history of overexploitation during the colonial era and high levels of snaring in more recent years, the large mammals on the Langbian Plateau—as well as some Annamite endemics such as the large-antlered muntjac, Owston's civet *Chrotogale owstoni*, and Annamite crested argus *Rheinardia ocellata*—are now absent or very rare (BirdLife International, 2010; Southern Institute of Ecology, 2017).

Despite the importance of the southern Annamites for rare and endemic species, little is known about the status of its current terrestrial mammal and bird communities compared to other parts of the region, and especially whether overexploitation had similar effects on community composition and species loss in both forest types. This information gap hinders the development of strategic conservation interventions, including the implementation of targeted patrolling efforts to reduce snaring pressure within protected areas.

To close this knowledge gap, we conducted systematic camera-trapping across four sites and analyzed the data using community occupancy models combined with high resolution remote-sensing data. We also calculated multiple measures of biodiversity using occupancy-based diversity profiles to give additional insights into community composition. We had four main objectives: (1) To understand how environmental and anthropogenic factors impact the occurrence of ground-dwelling mammals and birds in the southern Annamites; we predicted that anthropogenic factors would negatively impact species occurrence, especially for those species that are most susceptible to snaring, and that environmental factors would impact habitat specialist species more than habitat generalists; (2) to compare species occurrence and biodiversity measures between the two main habitats in the region, broadleaf forest and coniferous forest; (3) to understand how past and current hunting has contributed to the defaunation of southern Annamite forests, and which species and functional guilds were most impacted; and (4) to use occupancy prediction maps to identify areas of high conservation importance across the wider landscape.

2 | METHODOLOGY

2.1 | Study site

We surveyed four contiguous protected areas in the core forest area of the southern Annamites: Bidoup—Nui Ba National Park, Phuoc Binh National Park, Da Nhim Protection Forest, and Dran Protection Forest (Figure 1). Historically, Bidoup—Nui Ba and Phuoc Binh National Park were a part of the Thuong Da Nhim Nature Reserve established in 1986 (Eames, 1995), but in 1992 the two areas were split into two forest units and managed separately (Southern Institute of Ecology, 2017). As national parks, both Bidoup Nui Ba and Phuoc Binh areas are assigned complete protection status (Law on Forestry, 2017). Da Nhim and Dran forests were also managed under a single administration authority from 1987 (Eames, 1995), but separated into two protection forests in the late 1990s, in which timber extraction and wildlife exploitation are not completely prohibited (Law on Forestry, 2017). National parks in Viet Nam also do generally receive higher investments and staffing compared to protection forests. The Da Nhim and Dran forests harbor some of the largest areas of natural coniferous forest in the southern Annamites region (Nguyen, 1966).

The total surveyed area covered approximately 1100 km^2, with an elevational range from 200 to 2400 m and an annual temperature range between 14.3 and 38.8°C. The survey sites have a typical tropical monsoon climate, with a rainy season occurring from May to October and an average annual precipitation of over 2000 mm (Hoang et al., 2011; Southern Institute of Ecology, 2017). However, precipitation is unevenly distributed within the study sites due to the rain shadow effect, and this, combined with differences in soil type, contribute to two major habitat types: broadleaf evergreen forest and coniferous forest (Nguyen, 1966; Rundel, 1999). While broadleaf evergreen forest is distributed across a broad elevational range, coniferous forest, which is primarily dominated by *Pinus kesiya*, is mainly found between 1100 and 1700 m in the southern Annamites (Champsoloix, 1958). The eastern and western slopes of Bidoup Nui Ba National Park, and the majority of Phuoc Binh National Park, receive high levels of rainfall and are dominated by evergreen broadleaf forests. In contrast, the central and southern parts of Bidoup Nui Ba National Park, as well as the majority of Da Nhim and Dran Protection Forests, receive less rainfall and are predominately coniferous. Within these coniferous forests, small patches of broadleaf evergreen forests may be found along rivers and streams.

2.2 | Camera-trapping and data management

We carried out three camera-trap surveys from September 2019 to April 2021. In total, we set up 157 stations spanning all four protected areas and both main habitat types (Table 1, Figure 1). At each station, two white flash Panthera V6 cameras were set and oriented in different directions to increase detection probabilities (Wong et al., 2019). The two cameras were set a maximum of 20 m apart. Cameras were attached to trees 20–40 cm from the ground and left in the forest for a minimum of 60 days. To avoid spatial autocorrelation, stations were spaced 2–3 km apart from each other, representing a distance larger than the home-range diameter of most species in the study areas. The overall study design followed earlier studies conducted in the northern and central Annamites (Alexiou et al., 2022; Nguyen et al., 2022; Tilker et al., 2019).

Camera-trap images were identified to species level by at least two observers. We discarded low quality

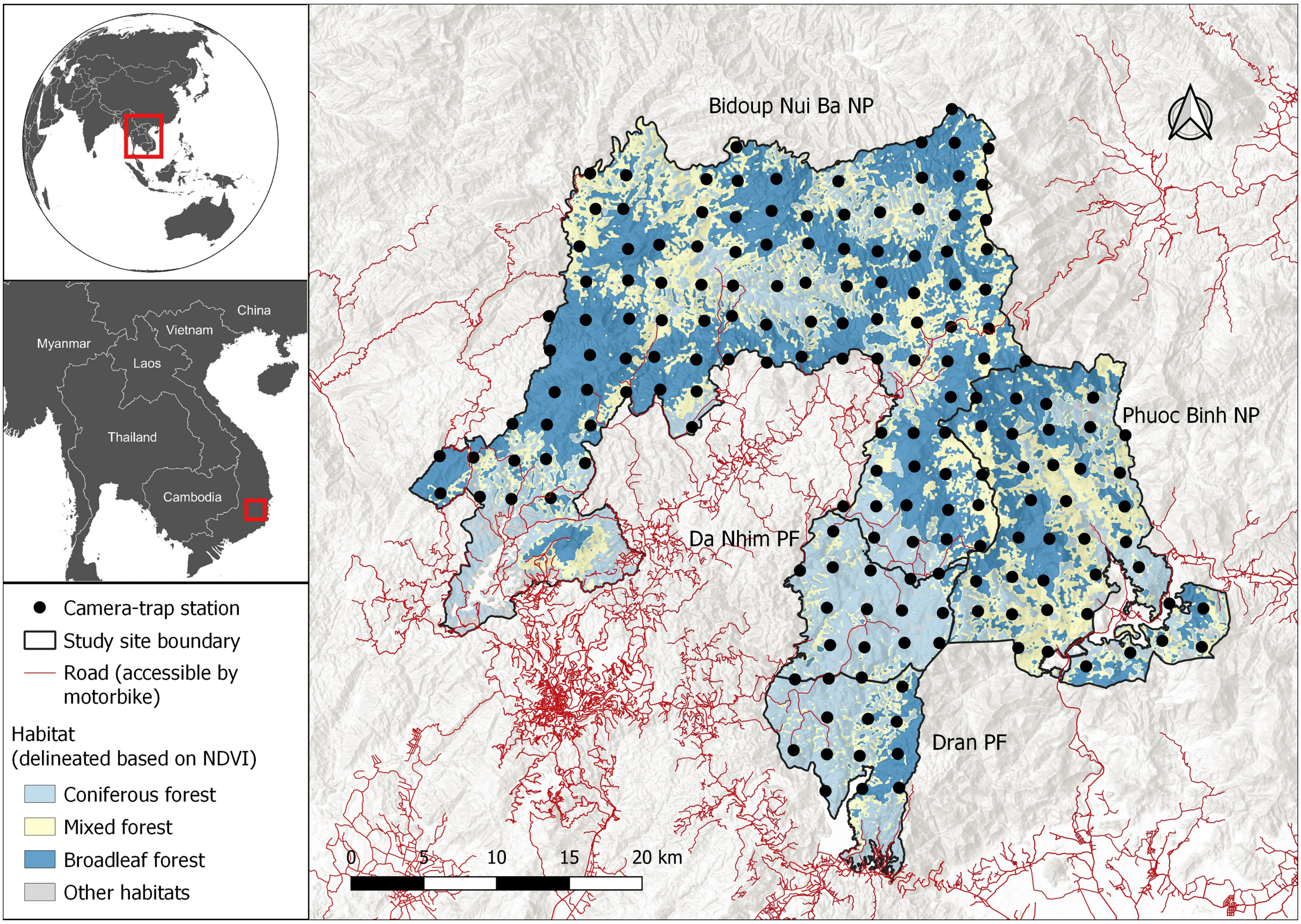

FIGURE 1 Camera-trap stations in the study sites in the southern Annamites. The habitat classes are only for visualization purposes, as they were delineated based on station-based normalized difference vegetation index interquartile ranges of coniferous and broadleaf evergreen forests.

TABLE 1 Summary of camera-trap surveys in the southern Annamites with number of camera-trap stations in each type of habitat.

Survey	Study site	Size (km^2)	Coniferous forest	Broadleaf evergreen forest	Timeframe
1	Bidoup—Nui Ba National Park	~360	13	37	09.2019–03.2020
2	Bidoup—Nui Ba National Park	~360	15	37	04.2020–10.2020
3	Phuoc Binh National Park	~250	04	29	11.2020–04.2021
3	Da Nhim Protection Forest	~90	11	1	11.2020–04.2021
3	Dran Protection Forest	~90	06	4	11.2020–04.2021

photographs for which no consensus could be reached. We excluded images of squirrels and murids because of the difficulty of identifying these species using camera-trap images. Because of similar morphologies, pangolins *Manis* spp. and ferret badgers *Melogale* spp. were only identified to genus level. Species that were primarily arboreal, including black-shanked douc *Pygathrix nigripes* and small-toothed palm civet *Arctogalidia trivirgata*, were also excluded, as ground-level camera-trapping is unlikely to reliably detect these species even if they are present. For birds, we included the mainly terrestrial galliforms and pittas, as well as other species that are known to forage on the forest floor and thus detectable by camera-trapping (O'Brien & Kinnaird, 2008). Because we analyzed data at the station (not camera) level, we combined photographs from both cameras within a station and used the threshold of 60 min to treat a photographic event as an independent record. All camera-trap data were managed using the package *camtrapR* 2.1.1.0 (Niedballa et al., 2016) in R software 4.0.5 (R Core team, 2022).

2.3 | Occupancy modeling

We used a community Royle-Nichols (RN) model to investigate the response of the ground-dwelling mammal and bird communities to both environmental and anthropogenic factors (see Supporting information S1 for model description) (Royle & Nichols, 2003; Yamaura et al., 2011). Like regular occupancy models, the RN model uses species detection/non-detection data to account for imperfect species detection. Instead of estimating species-level detection probability p directly, it assumes that p is a function of individual detection probability r and the number of individuals N present at a station (Royle & Nichols, 2003). Consequently, the state variable estimated in the RN model is local expected abundance, rather than occurrence. The RN model parameterization of p accounts for spatial variation in detection probability due to variation in abundance and fit our data adequately, whereas a regular occupancy model failed to fit the data (see Table S3). Estimates of local abundance, however, are difficult to interpret in camera-trap studies as the area to which they pertain is undefined (Sollmann, 2018) and, in a community model context, likely varies among species. Therefore, we converted estimates of expected abundance to occupancy probability using the inverse complementary log–log link in the defaunation and diversity profile analysis (see below).

Covariates on local abundance included elevation, remoteness, terrain ruggedness index (TRI), normalized difference vegetation index (NDVI), and vegetation homogeneity (Table S4). Elevation has been shown to be an important driver of species distribution in multiple areas within the Annamites (Alexiou et al., 2022; Nguyen et al., 2022; Tilker, Abrams, et al., 2020). TRI can affect the locomotion, foraging, predation, and prey-avoidance behavior, and therefore can shape habitat-use and species occurrence (Ironside et al., 2018; Riley et al., 1999). NDVI is linked to plant density and primary productivity, and therefore reflects habitat characteristics (Borowik et al., 2013; Pettorelli et al., 2011). In our study we used NDVI to distinguish between the two main habitat types, with broadleaf evergreen forests having higher NDVI values, and coniferous forests having lower values (Figure S5d). NDVI values were obtained from Landsat 8 images at 30 m resolution and averaged across the survey period. The median values of all adjacent pixels within 100 m buffer of each pixel were calculated and used for the RN model and predictions. Habitat homogeneity was calculated from NDVI using a Grey Level Co-occurrence Matrix (Haralick et al., 1973) for 33×33 pixels (approximately 1 km^2 grid). Because homogeneity was based on NDVI, this measure indicates how homogeneous (low vegetation variation) or heterogeneous (high vegetation variation) broadleaf evergreen or the coniferous forests patches are within the landscape. We expected that habitat specialist species would prefer more homogenous areas, while habitat generalists would either show no preference or be positively associated with more heterogeneous habitats. In addition to these environmental factors, wildlife is directly impacted by hunting. Because spatial data on the past and current hunting activities were not available, we used human population density and remoteness as a proxy for hunting pressure. Various studies in the Annamites have found the links between population density and species or snare occurrence, suggesting forest areas around high population villages or towns usually have high snaring level and high defaunation (Nguyen et al., 2022; Tilker, Abrams, et al., 2020; Tilker et al., 2023). We also expected that more remote areas are harder for hunters to access, and as a result, would have experienced less hunting pressure (Benítez-López et al., 2019) and thus have higher species occupancies. We created the human population density layer by extracting the population grid from ESA's Global Human Settlement Layer Data Package 2022 (Schiavina et al., 2023) and using focal statistics to obtain the density estimate for each pixel. We constructed the remoteness layer by using access points every 100 meters along the roads—defined as villages and points spaced every 100 m along roads—and applying the Rees' hiking function (Rees, 2004) to calculate the minimum time needed to walk from an access point to a pixel, considering the different walking speeds on slopes. We modeled both community and species-specific coefficients for all covariates. Further details on how the covariates were calculated are given in Table S4.

We also included survey effort as a covariate on detection, measured as the number of active camera-trap nights within one occasion. As the camera-traps were facing in different directions, we accounted for an effort of 2 per trap night if both camera-traps were operating. Furthermore, we accounted for the different survey periods in the model by including a categorical "survey" covariate on detection probability. We modeled coefficients of both covariates on detection as species-level random effects.

All continuous covariates were scaled to have mean = 0 and standard deviation = 1 before they were included in the analysis. We used Spearman's rank correlation coefficient *rho* to test if the covariates were correlated. The test showed that there was no strong correlation ($|rho| < 0.7$) among covariates (Figure S5g).

We used 20-days occasion lengths to create station-level species detection/non-detection matrices as inputs for the community RN model. We estimated the parameters using Bayesian inference, specifically the program JAGS 4.3.0 (Plummer, 2003) via the *rjags* 4–13 package (Plummer, 2022) in R software 4.0.5 (R Core team, 2022). We used vague normal priors on coefficients and vague gamma priors on precision parameters (for details, see model code in Supporting information S2). We ran three parallel Markov chains with 250,000 iterations, of which 50,000 iterations were discarded as burn-in, and thinned remaining iterations by a factor of 20 to make the output more manageable. To assess chain convergences, we calculated the Gelman-Rubin statistic, with values under 1.1 indicating convergence (Shirley, 2011). Model fit was assessed using Bayesian p-values obtained by calculating the Freeman-Tukey residual for species and location-level observations aggregated over sampling occasions (Gelman et al., 1996).

We report the covariate coefficients as posterior means and standard deviations. We infer the certainty, or evidence in favor, of the species and community responses to covariates based on the Bayesian Credible Intervals (BCIs). We consider that evidence for an effect is strong if the 95% BCI does not overlap zero, and moderate if the 75% BCI does not overlap zero. In addition, the effect sizes are provided in the Supporting information S10. At the species level, we are aware that coefficients of species with very few independent records cannot be reliably estimated. We set the thresholds of five independent records and three stations to consider species that are rare. Although we retained these species in the analysis to calculate species richness and biodiversity, we interpret the covariate effects for these species with care. In addition, the rare definitions are only applicable for our study site in the Langbian Plateau, as some of these species may be more common in other landscapes.

2.4 | Diversity profiles

We calculated biodiversity profiles to better understand the structure of the ground-dwelling mammal and bird communities in our study sites, and assess how these communities differ between habitat types. A biodiversity profile is a plotted series of Hill numbers that capture most of the commonly used diversity indices including species richness (R), Shannon index (H′), and Simpson index (D) (Chao et al., 2014; Leinster & Cobbold, 2012). We constructed diversity profiles based on average estimated occupancy probability (see Abrams et al., 2021). Camera-trap stations were classified as coniferous and broadleaf evergreen forest based on information collected in the field and biodiversity profiles were constructed for both habitat types.

2.5 | Historical defaunation

We used a defaunation index to investigate levels of defaunation within our sites. Although many species occur or historically occurred in both coniferous and broadleaf evergreen forest, we split the analysis between the two main habitat types to evaluate if one habitat had undergone higher levels of defaunation than the other. The defaunation index uses a Bray–Curtis dissimilarity index to assess differences in community composition (Giacomini & Galetti, 2013), and can be used to measure changes between current and historical species assemblages (Bogoni et al., 2018; Pereira et al., 2021). We defined the current assemblage as all ground-dwelling mammal and bird species recorded in this study, and which were included in the occupancy model. The historical assemblage was compiled from known historical records of species in the southern Annamites (see Table S7 for details on the literature review). The defaunation index was calculated for the entire study landscape and separated by the two habitat types using the equation:

$$D(r,f) = \frac{\sum_{k=1}^{S} \omega_k \left(N_{k,r} - N_{k,f}\right)}{\sum_{k=1}^{S} \omega_k \left(N_{k,r} + N_{k,f}\right)}$$

where D is the defaunation index of the current assemblage f with the respect to the historical assemblage r, S is the total number of species in both current and historical assemblages, $N_{k,r}$ is presence or absence of species k in the historical assemblage r, $N_{k,f}$ is presence or absence of species k in the current assemblage f, ω is the weight assigned to each species (Giacomini & Galetti, 2013; Tilker et al., 2019). Defaunation indices were calculated separately using three different species weighting options: no weight, body size as measured in kilograms, and IUCN Red List status. IUCN Red List weighting followed Tilker et al. (2019) and body size information was obtained from both Tilker et al. (2019) and Smith et al. (2011) (see Table S7 for details). Assuming that there are no invasive or reintroduced species in the current assemblage (i.e., the current assemblage cannot have more species than the reference assemblage), the defaunation index values range from 0 to 1 with a higher value indicating greater defaunation.

2.6 | Mapping priority areas

We predicted species richness across the entire study area using species responses to covariates. We first extracted covariate layers at a 200 × 200 m resolution. To avoid overextrapolation, we masked out covariate values that fell outside the minimum and maximum range of each covariate layer for our camera-trap stations. To predict species richness, we then used 250 posterior samples of coefficients from the RN model to calculate species-specific occupancy probabilities for each 200 × 200 m pixel. From these, we generated presence/absence states for all species, summed over species to obtain pixel-level richness, and plotted the mean richness over the 250 samples for each pixel. These prediction maps were generated for both total species richness and richness of threatened and Annamites endemic species. Priority areas were identified as those with high concentrations of high-value pixels, representing high species richness.

3 | RESULTS

In total, the 157 camera-trap stations were operational for 18,433 camera-trap nights. We photographed at least 46 ground-dwelling mammal and bird species (Table S6). We recorded several threatened and endemic species, including Annamite striped rabbit *Nesolagus timminsi*, large-antlered muntjac, Owston's civet, Annamite crested argus, and collared laughingthrush *Trochalopteron yersini*. We also recorded a number of large mammals that are rare in the region, including gaur, sambar *Rusa unicolor*, and sun bear *Helarctos malayanus*, although the number of records was low (Table S6). We failed to detect large and medium size canids and felids.

3.1 | Community RN model results

The Gelman-Rubin statistic for all chains was <1.1, indicating convergence for all parameters. The Bayesian *p*-value was .75, suggesting that model fit to the data was adequate.

Model results showed strong evidence of positive responses of mammal and bird communities to remoteness and NDVI, indicating that the majority of species had higher occupancies in more remote areas (seven species showed strong evidence of positive responses, 17 species showed moderate evidence of positive responses; Figure 2) and in forests with higher NDVI (five species showed strong evidence of positive responses, 30 species had moderate evidence of positive responses; Figure 2). At the same time, both communities showed a strong support for negative response to TRI, indicating that species occurred more often in flatter, less rugged terrain (39 species showed moderate to strong evidence of negative responses; Figure 2). The communities also showed moderate evidence of negative response to the human population density with 16 species (two species showed strong evidence and 14 species showed moderate evidence; Figure 2) preferring areas of low human density and only four species had the tendency to have higher occupancies (moderate evidence of positive response) in high human density areas. Species responses to elevation and homogeneity varied in direction, and thus there was no effect at the community level (Figure 2). For elevation, 11 species had strong or moderate evidence of negative responses, while 18 species had strong or moderate evidence of positive responses (Figure 2). For homogeneity, 13 species had strong or moderate evidence of negative responses, indicating that these species prefer more heterogeneous habitats, while 10 species had a strong or moderate evidence of positive responses and thus higher occupancies in more homogeneous forests (Figure 2).

3.2 | Diversity profiles and historical defaunation

Diversity profiles showed strong evidence of higher diversity in the broadleaf evergreen forest compared to the coniferous forest (Figure 3a, 95% BCIs of the diversity profiles did not overlap). Diversity profiles started with higher species richness in broadleaf evergreen forest and the profiles declined less steeply than in coniferous forest, indicating a higher level of community evenness within broadleaf evergreen compared to coniferous forest.

The defaunation index indicated that approximately 16% of species that historically occurred within the southern Annamites are now likely extinct in the study areas (Figure 3b; Table S7). The defaunation index showed higher levels of dissimilarity between current and historical assemblages when species were weighted by threatened status and body size. Defaunation indices were slightly higher in coniferous forest compared to evergreen forest, indicating that, proportionally, this habitat has lost a higher percentage of its ground-dwelling mammal and bird species (Figure 3b).

3.3 | Mapping priority areas

Overall, the species richness maps showed similar patterns for all species (Figure 4a), threatened species (Figure 4b), and endemic species (Figure 4c). Three areas of high species richness stand out. Two of these hotspots are located in the higher mountains in the west and east of Bidoup Nui Ba National Park, and are particularly important for endemic species (Figure 4c). The third area is located in a remote area in the north of Bidoup Nui Ba National Park (Figure 4a). The prediction map of threatened species also showed a higher richness in Phuoc Binh National Park compared to the Dran and Da Nhim Protection Forest areas (Figure 4b).

FIGURE 2 The responses of ground-dwelling mammal and bird communities and each species in the community. The light blue bar indicates there is weak or no evidence for a response (75% Bayesian Credible Intervals [BCI] overlaps zero); the dark blue bar indicates moderate evidence for a response (75% BCI does not overlap zero and 95% BCI overlaps zero); the red bar indicates the high evidence for a response (95% BCI does not overlap zero).The black vertical lines represent the zero value, the red vertical lines are community covariate coefficients. Rare species in our study sites are shown in brackets.

4 | DISCUSSION

Our study is the first comprehensive camera-trapping assessment of the ground-dwelling mammal and bird communities in the southern Annamites. Notably, we recorded a number of highly threatened and endemic species that are rare in other parts of the Annamites. Our findings highlight the importance of the broadleaf evergreen forests in this region for ground-dwelling mammal and bird communities. At the same time, our results suggest that past and current hunting has contributed to high levels of defaunation, including the loss of larger herbivores and predators from these sites, resulting in a shift toward small and medium sized species within the communities.

Our analysis indicates that the distribution of ground-dwelling mammals and birds—with the exception of the rare species whose responses to covariates we interpreted with caution—is influenced by a number of complex factors (Figure 2). We found positive responses to NDVI for all Annamite endemics with moderate evidence, indicating that these species are predominantly found in broadleaf evergreen forest. Our findings support earlier studies from other parts of the Annamites suggesting that these species are associated with broadleaf evergreen forest habitat (Brickle et al., 2008; Mahood & Eames, 2012; Tilker, Nguyen, et al., 2020; Timmins et al., 2020; Timmins, Coudrat, et al., 2016). At the community level, NDVI also certainly had a positive effect on occupancy. Only four species—Chinese francolin *Francolinus pintadeanus*, Eurasian jay *Garrulus glandarius*, Burmese hare *Lepus peguensis*, and Northern red muntjac *Muntiacus vaginalis*—showed a negative response to NDVI, indicating a tendency of association with coniferous forest. These species are known to prefer open forests, in which a scrubby understory vegetation—as it is also found in the coniferous forest—may provide important food resources (Brickle et al., 2008; Eames, 1995; Habiba et al., 2022; Johnston & Smith, 2019).

Several species showed responses to habitat homogeneity with moderate to high evidence. As expected, known habitat generalists—masked palm civet *Paguma larvata*, leopard cat *Prionailurus bengalensis*, Northern red muntjac, and Malayan porcupine *Hystrix brachyura* (Lunde et al., 2016; Timmins, Duckworth, et al., 2016; Timmins, Steinmetz, et al., 2016; Willcox et al., 2014)—showed strong evidence of negative responses to homogeneity, indicating these species could occur in multiple habitat types (Figure 2). On the other hand, some Annamite endemics—including Annamite striped rabbit, Owston's civet, and collared laughingthrush—showed positive responses to homogeneous habitat with moderate evidence, suggesting an association with homogeneous broadleaf evergreen forests. Of the Annamite endemics, the large-antlered muntjac did not respond to homogeneity, a finding that is consistent with a study from Nakai Nam Theun National Park in Laos (Alexiou et al., 2022). Taken together, the responses to homogeneity and NDVI highlight the importance of large and continuous evergreen forests for conservation priority ground-dwelling mammals and birds, especially the Annamites endemic species.

There was strong evidence that the mammal and bird community showed a preference for flatter areas (strong evidence of negative response to TRI, Figure 2); none of the species was associated with more rugged terrains. It is possible that our findings reflect a preference for flatter terrain to reduce energy expenditure for locomotion and foraging (Ganskopp et al., 2000; Killeen et al., 2014), though we acknowledge that this remains speculative.

Elevation had strong evidence of positive effect on the occurrence of many of the mammal and bird species, though there was no response at the community level. It is likely that elevational responses capture changes in habitat, which varies along elevational gradients (Rundel, 1999), and aspects of accessibility, with higher elevation areas being more difficult for hunters to reach. Accordingly, it remains unknown if some of the Annamite endemics that showed a positive response to elevation with moderate evidence—including Annamite striped rabbit, large-antlered muntjac, Owston's civet, and collared laughingthrush—are predominantly associated more with the highland broadleaf evergreen forests or if these distributions are shaped by potentially lower hunting pressure in these areas.

The fact that both the ground-dwelling mammal and bird communities showed strong evidence of positive responses to remoteness, that is, a tendency for higher occupancies in more remote areas, supports the notion that past hunting pressure has shaped wildlife occurrence within the study sites (Figure 2). We interpret the response to remoteness to indicate that faunal communities have been depleted in easier-to-access areas where hunting levels are likely higher, and are more intact in more remote areas where hunting pressure has been less intense. Our findings reflect previous studies in the Annamites that show a depletion of wildlife communities across a remoteness gradient with more intact communities in more remote areas (Alexiou et al., 2022; Tilker et al., 2019). It is interesting that large Indian civet *Viverra zibetha* and sun bear, two species that are highly susceptible to snaring and are now rare in the Annamites (Scotson et al., 2017; Timmins, Duckworth, et al., 2016), have higher occupancies in remote areas. Our findings also indicate that even common species—Malayan porcupine, masked palm civet, Northern red muntjac, Eurasian wild pig *Sus scrofa*, yellow-throated marten *Martes flavigula* (see Table S6)—are probably being impacted by hunting pressure in more accessible parts of the landscape.

Although the evidence of the community response to human population density was not strong, we found that some endemic species—large-antlered muntjac, Owston's civet, and Annamite crested argus—as well as non-endemic but snare-sensitive species—large Indian civet, sun bear, Malayan porcupine, masked palm civet, and

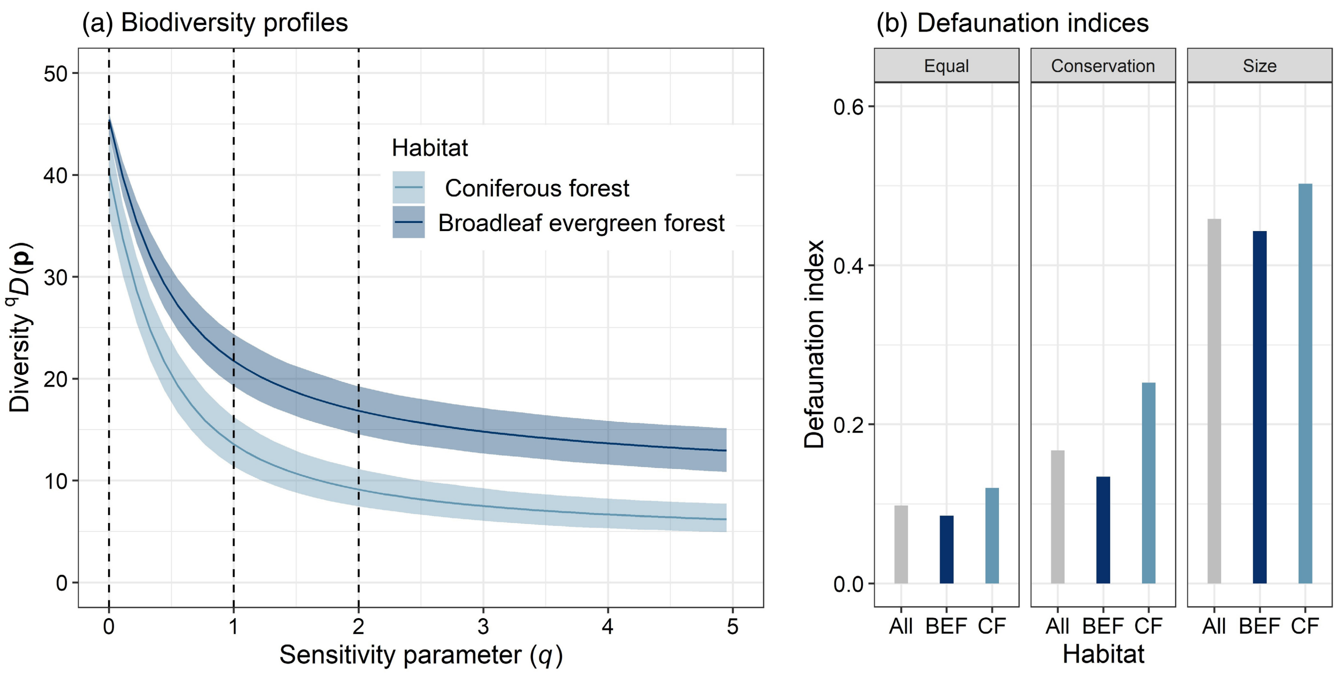

FIGURE 3 Biodiversity profiles and defaunation indices of ground-dwelling mammal and bird communities in coniferous forest (CF) and broadleaf evergreen forests (BEF) of southern Annamites. In the biodiversity profiles, the q parameter indicates the sensitive of the measure to occupancy estimate of species. Higher q means a higher weight is placed on the more common species thereby incorporating evenness into the diversity measure. The defaunation indices were calculated considering all species with equal weighting (equal), with weighting based on IUCN Red List threatened category (conservation), and with weighting based on body size (size).

Eurasian wild pig—had high occupancies in areas characterized by low surrounding human population density. This suggests that remoteness alone might be not enough to capture the hunting gradient in our landscape, and that including human population density helps to produce a better hunting proxy layer. In the central Annamites, snare occupancy has been found to be strongly associated with human density (Tilker et al., 2023), and the Langbian Plateau is likely facing a similar situation in which areas near settlements have been heavily hunted in the last decades, and continue to be impacted by snaring. We also do not exclude other disturbances such as collecting non-timber products, cattle grazing, or illegal logging, all of which may also be captured in the human population density layer. However, we refrain from speculating on the extent of these disturbances and their impact on the occurrence of ground-dwelling mammals and birds without information or research in our study sites.

4.1 | Diversity and defaunation in broadleaf evergreen and coniferous forests

As expected, species richness and evenness were found to be higher in broadleaf evergreen forest compared to coniferous forests in the southern Annamites (Figure 3a). Such a finding is consistent with the high diversity that is often ascribed to broadleaf wet evergreen forest, and the lower diversity of coniferous forest (Pillay et al., 2022). Similar patterns between coniferous and broadleaf evergreen forest have been shown for other taxonomic groups, including amphibians (Southern Institute of Ecology, 2017) and birds (Eames, 1995), in the southern Annamites. Given the higher structural diversity and primary productivity of broadleaf forests compared to coniferous forests, such a pattern is not surprising.

The defaunation index showed that broadleaf and coniferous forest have lost eight and six ground-dwelling mammal and bird species, respectively. Because of the inherently lower species richness in coniferous forest, this resulted in higher defaunation index values in coniferous forest compared to the broadleaf evergreen forest. Furthermore, our results show that larger and more threatened species have been disproportionately lost from our study sites; these findings are similar to those from Tilker et al. (2019) in the central Annamites and reflect the broader trend of declining populations of the megafauna worldwide (Ripple et al., 2014, 2015). Several studies have shown body mass to be linked to extinction risk (Cardillo et al., 2005, 2008). The tendency for larger species to be lost from the faunal community is also

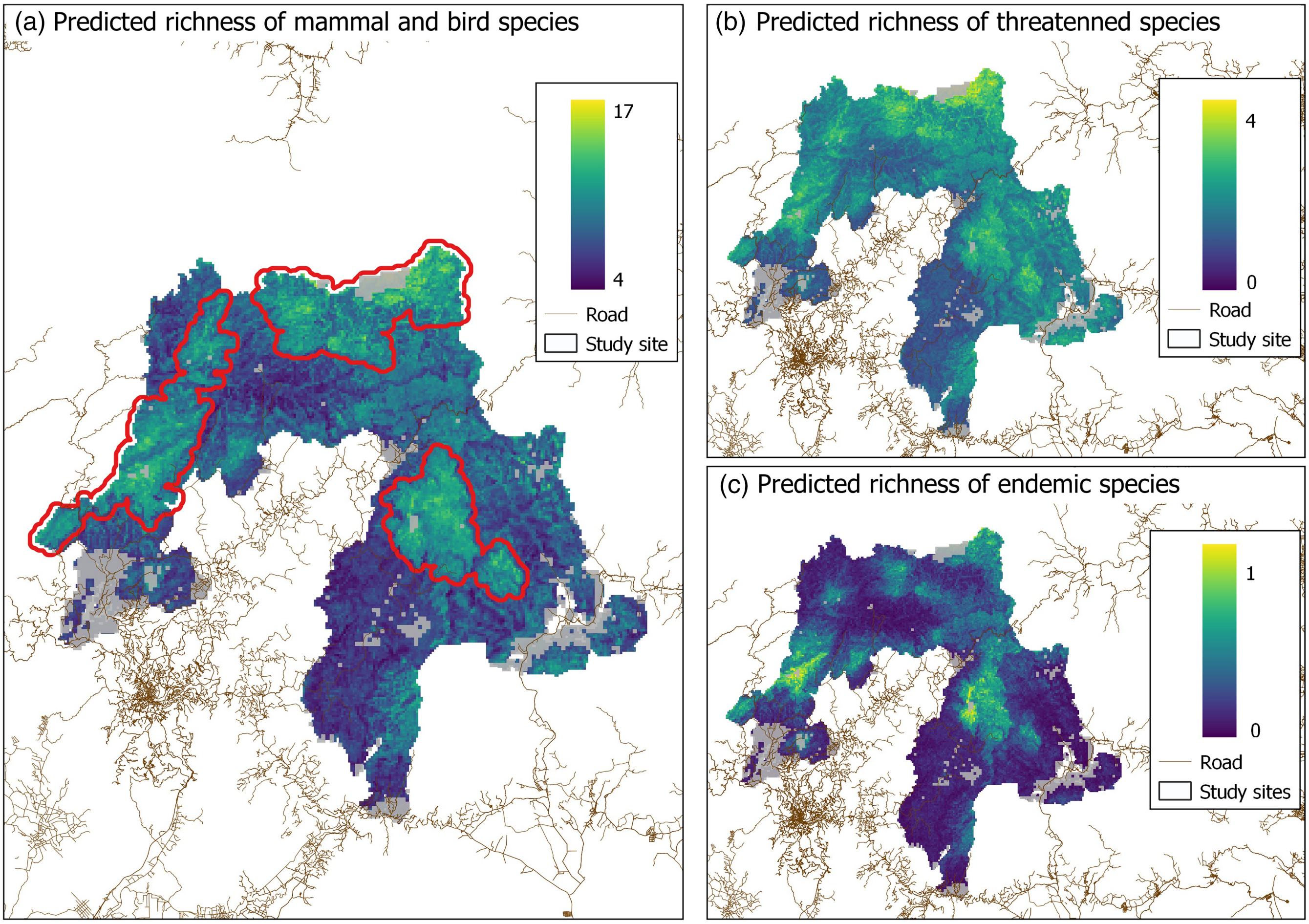

FIGURE 4 Richness predictions of (a) ground-dwelling mammal and bird species, (b) threatened species, and (c) Annamite endemic species. The priority areas are highlighted with the red boundaries. The gray areas within our study sites are pixels where the values of covariates are outside of the station-based covariate ranges and therefore the predictions are not available for these areas.

shown by the fact that we failed to record any medium- or large-sized carnivores—including tiger, leopard, mainland clouded leopard *Neofelis nebulosa*, Asiatic golden cat *Catopuma temminckii*, and dhole *Cuon alpinus*—all of which would have been present in the southern Annamites. The loss of the large mammalian carnivore guild will almost certainly have impacts on the ecosystem. In other tropical regions, the loss of larger carnivores has triggered an increase in abundance of mesopredators (Prugh et al., 2009; Ritchie & Johnson, 2009) and smaller herbivores (Colman et al., 2015; Flagel et al., 2016). Such an increase in mesopredator and herbivore populations can have significant impacts on forest regeneration, and in turn, long-term ecosystem stability (Ripple et al., 2014). We also failed to record large herbivores that would have been historically present, including elephant and Eld's deer *Rucervus eldii*, and only documented gaur at a single camera-trap station, indicating that the species is extremely rare. Large herbivores fulfill important ecosystem functions—including the regulation of vegetation structure, seed dispersal, and nutrient cycling (Ong, 2020; Ripple et al., 2015)—and it is possible that their extirpation will have cascading effects that could fundamentally impact the southern Annamites ecosystem.

Over the last 30 years, habitat loss and degradation has been minimal inside protected areas of the southern Annamites (Graham et al., 2021; Vogelmann et al., 2017), and large areas of structurally intact forest remain in our study sites. The loss of large carnivores and herbivores from our sites is therefore unlikely to be related to ecological factors. Instead, it is likely a result of the long and complex history of hunting activities in these areas, starting with sport hunting during the French colonial times, and intensifying in the last three decades with the widespread use of indiscriminate wire snares (Harrison et al., 2016; Milner-Gulland & Bennett, 2003). There are numerous reports that trophy hunting of large carnivores and herbivores was common during the colonial periods; our study sites in the southern Annamites were especially famous for hunting of tiger and gaur (Bouvard &

Millet, 1920; Guérin & Seveau, 2009; Millet, 1916). It is thus likely that historical trophy hunting during the colonial period had already depleted large mammal populations, and that with increasing snaring levels in more recent decades, these species were locally extirpated.

4.2 | Conservation priority areas

Hunting is forbidden in our study sites, but due to their large size, rugged terrain, and the large number of people who are currently engaged in hunting activities, it is difficult to stop hunting in the landscape. To prevent snaring, a multi-faced approach will be required that addresses the underlying drivers of hunting and strengthens on-site protection (Gray et al., 2021; Tilker et al., 2023). However, such a holistic approach requires enormous resources and also takes time. Unfortunately, all of the highly threatened and Annamite endemic species in our study sites are at such low occupancies that, without urgent and targeted conservation efforts, it is possible that they will disappear from the landscape in the near future. To protect remaining populations of rare species, conservation activities such as snare removal should, in the short term, focus on those areas in the landscape where we find the highest concentration of conservation-priority species. Our data indicate that there are three main hotspots for endemic species within the southern Annamites forest complex and the majority of these areas are located within the broadleaf evergreen forests of Bidoup Nui Ba National Park (Figure 4c). For threatened but non-endemic species (Table S6), large parts of Phuoc Binh National Park were also identified as a priority area (Figure 4b). Da Nhim and Dran Protection Forests and the southwest area of Bidoup Nui Ba National Park have overall lower richness of ground-dwelling mammal and bird species, reflecting that these areas are comprised of coniferous forests, and are also easier to access (Figure 4). In general, to ensure the survival of threatened species and Annamite endemics, we recommend that intensive snare removal efforts should focus on these three areas.

5 | CONCLUSION

Our findings highlight the importance of remote, large, and continuous broadleaf evergreen forests in the southern Annamites for both Annamite endemic and non-endemic but threatened species; indeed, the broadleaf evergreen forests of this region are among the only areas in the wider Annamites ecoregion to support populations of large-antlered muntjac, Annamite crested argus, Owston's civet, and Annamite striped rabbit. Nonetheless, our study also indicates that hunting has been a major driver of faunal loss in these forests, resulting in severe defaunation and low occupancies for conservation priority species. The spatial prediction maps that we present are the first produced for the southern Annamites, and can be used by conservation stakeholders to target conservation actions in priority areas that are of particular relevance for Annamite endemic and threatened species.

AUTHOR CONTRIBUTIONS

AN, AT, and AW conceived and designed the study. AN, DL, and XHP conducted the field work. AN and LP processed satellite images and generated covariates layers. AN conducted analysis; RS and JN provided expertise in statistical analysis. AN, AT, and AW wrote the first draft of the manuscript; all authors contributed to the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest regarding the publication of this manuscript.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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REFERENCES

Abrams, J. F., Sollmann, R., Mitchell, S. L., Struebig, M. J., & Wilting, A. (2021). Occupancy-based diversity profiles: Capturing biodiversity complexities while accounting for imperfect detection. *Ecography*, *44*(7), 975–986. https://doi.org/10.1111/ecog.05577

Alexiou, I., Abrams, J. F., Coudrat, C. N. Z., Nanthavong, C., Nguyen, A., Niedballa, J., Wilting, A., & Tilker, A. (2022). Camera-trapping reveals new insights in the ecology of three sympatric muntjacs in an overhunted biodiversity hotspot. *Mammalian Biology*, *102*(2), 489–500. https://doi.org/10.1007/s42991-022-00248-0

Bain, R. H., & Hurley, M. M. (2011). A biogeographic synthesis of the amphibians and reptiles of Indochina. *Bulletin of the American Museum of Natural History*, *360*(360), 1–138. https://doi.org/10.1206/360.1

Baltzer, M. C., Nguyen, T. D., & Shore, R. (2001). Towards a vision for the biodiversity conservation in the forests of the lower Mekong ecoregion complex. In *Summary of the biological assessment for the ecoregion biodiversity conservation program in the forests of the lower Mekong ecoregion complex*. WWF Indochina/WWF-US.

Belecky, M., & Gray, T. (2020). *Silence of the snares: Southeast Asia's snaring crisis*. WWF International. https://www.worldwildlife.org/publications/silence-of-the-snares-southeast-asia-s-snaring-crisis

Benítez-López, A., Santini, L., Schipper, A. M., Busana, M., & Huijbregts, M. A. J. (2019). Intact but empty forests? Patterns of huntinginduced mammal defaunation in the tropics. *PLoS Biology*, *17*(5), e3000247. https://doi.org/10.1371/journal.pbio.3000247

BirdLife International. (2010). The biodiversity of Chu Yang sin National Park, Dak Lak Province, Vietnam.

Bogoni, J. A., Pires, J. S. R., Graipel, M. E., Peroni, N., & Peres, C. A. (2018). Wish you were here: How defaunated is the Atlantic Forest biome of its medium- to large-bodied mammal fauna? *PLoS One*, *13*(9), e0204515. https://doi.org/10.1371/journal.pone.0204515

Borowik, T., Pettorelli, N., Sönnichsen, L., & Jędrzejewska, B. (2013). Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. *European Journal of Wildlife Research*, *59*(5), 675–682. https://doi.org/10.1007/s10344-013-0720-0

Bouvard, P., & Millet, F. (1920). Dalat, sanatorium de l'Indochine française: La chasse au Lang-Bian. https://gallica.bnf.fr/ark:/12148/bpt6k5844492w.texteImage

Brickle, N. W., Duckworth, J. W., Tordoff, A. W., Poole, C. M., Timmins, R., & McGowan, P. J. K. (2008). The status and conservation of Galliformes in Cambodia, Laos and Vietnam. *Biodiversity and Conservation*, *17*(6), 1393–1427. https://doi.org/10.1007/s10531-008-9346-z

Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J., & Purvis, A. (2008). The predictability of extinction: Biological and external correlates of decline in mammals. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1641), 1441–1448. https://doi.org/10.1098/rspb.2008.0179

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L., & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, *309*(5738), 1239–1241. https://doi.org/10.1126/science.1116030

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), e1400253. https://doi.org/10.1126/sciadv.1400253

Champsoloix, R. (1958). Le pin à trois feuilles du Lang Bian (*Pinus khasya* Royle). *Bios & Forets Des Tropiques*, *57*, 3–11. doi:10.19182/bft1958.57.a18733

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Colman, N. J., Crowther, M. S., & Letnic, M. (2015). Macroecological patterns in mammal abundances provide evidence that an apex predator shapes forest ecosystems by suppressing herbivore and mesopredator abundance. *Journal of Biogeography*, *42*(10), 1975–1985. https://doi.org/10.1111/jbi.12563

Critchfield, W. B., & Little, E. L. (1966). *Geographic distribution of the pines of the world*. US Department of Agriculture, Forest Service. https://doi.org/10.5962/bhl.title.66393

Duckworth, W., & Hedges, S. (1998). Tracking Tigers: A review of the status of tiger, Asian elephant, gaur, and banteng in Vietnam, Lao, Cambodia, and Yunnan (China). https://agris.fao.org/agris-search/search.do?recordID=GB2021419936

Eames, J. C. (1995). Endemic birds and protected area development on the Da Lat plateau, Vietnam. *Bird Conservation International*, *5*(4), 491–523. https://doi.org/10.1017/S0959270900001209

Flagel, D. G., Belovsky, G. E., & Beyer, D. E. (2016). Natural and experimental tests of trophic cascades: Gray wolves and white-tailed deer in a Great Lakes forest. *Oecologia*, *180*(4), 1183–1194. https://doi.org/10.1007/s00442-015-3515-z

Ganskopp, D., Cruz, R., & Johnson, D. E. (2000). Least-effort pathways?: A GIS analysis of livestock trails in rugged terrain. *Applied Animal Behaviour Science*, *68*(3), 179–190. https://doi.org/10.1016/S0168-1591(00)00101-5

Gardner, C. J., Bicknell, J. E., Baldwin-Cantello, W., Struebig, M. J., & Davies, Z. G. (2019). Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. *Nature Communications*, *10*(1), 4590. https://doi.org/10.1038/s41467-019-12539-1

Gelman, A., Meng, X.-L., & Stern, H. (1996). Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica*, *6*(4), 733–807. http://www.stat.columbia.edu/~gelman/research/published/A6n41.pdf

Giacomini, H. C., & Galetti, M. (2013). An index for defaunation. *Biological Conservation*, *163*, 33–41. https://doi.org/10.1016/j.biocon.2013.04.007

Graham, V., Geldmann, J., Adams, V. M., Negret, P. J., Sinovas, P., & Chang, H. C. (2021). Southeast Asian protected areas are effective in conserving forest cover and forest carbon stocks compared to unprotected areas. *Scientific Reports*, *11*(1), 23760. https://doi.org/10.1038/s41598-021-03188-w

Grainger, M. J., Garson, P. J., Browne, S. J., McGowan, P. J. K., & Savini, T. (2018). Conservation status of Phasianidae in Southeast Asia. *Biological Conservation*, *220*, 60–66. https://doi.org/10.1016/j.biocon.2018.02.005

Gray, T. N. E., Belecky, M., O'Kelly, H. J., Rao, M., Roberts, O., Tilker, A., Signs, M., & Yoganand, K. (2021). Understanding and solving the south-east Asian snaring crisis. *Ecological Citizen*, *4*(2), 129–141. https://www.ecologicalcitizen.net/pdfs/v04n2-09.pdf

Guérin, M. (2010). Européens et prédateurs exotiques en Indochine, le cas du tigre. https://hal.science/hal-00492359/

Guérin, M., & Seveau, A. (2009). Auprès du Tigre sur les hauts plateaux de l'Indochine. Les mémoires de Pierre Dru, garde principal sur la route du Lang Bian en 1904. *Outre-Mers*, *96*(362), 155–192. https://doi.org/10.3406/outre.2009.4387

Habiba, U., Anwar, M., Hussain, M., Khatoon, R., Khan, K. A., Bano, S. A., Hussain, A., Khalil, S., Akhter, A., & Akhter, A. (2022). Seasonal distribution and habitat use preference of barking deer (Muntiacus vaginalis) in murree-kotli sattian-kahuta national park, Punjab Pakistan. *Brazilian Journal of Biology*, *82,* e242334. https://doi.org/10.1590/1519-6984.242334

Haralick, R. M., Shanmugam, K., & Dinstein, I. (1973). Textural features for image classification. *IEEE Transactions on Systems, Man, and Cybernetics*, *SMC-3*(6), 610–621. https://doi.org/10.1109/TSMC.1973.4309314

Harrison, R. D., Sreekar, R., Brodie, J. F., Brook, S., Luskin, M., O'Kelly, H., Rao, M., Scheffers, B., & Velho, N. (2016). Impacts of hunting on tropical forests in Southeast Asia. *Conservation Biology*, *30*(5), 972–981. https://doi.org/10.1111/cobi.12785

Hoang, M. D., Baxter, G. S., & Page, M. (2011). Preliminary results on food selection of the black-shanked douc (Pygathrix nigripes) in Southern Vietnam. *Vietnamese Journal of Primatology*, *1*(5), 29–39. http://www.primate-sg.org/storage/pdf/VJP_1-5_pp29-39.pdf

Ironside, K. E., Mattson, D. J., Arundel, T., Theimer, T., Holton, B., Peters, M., Edwards, T. C., Jr., & Hansen, J. (2018). Geomorphometry in landscape ecology: Issues of scale, physiography, and application. *Environment and Ecology Research*, *6*(5), 397–412. https://doi.org/10.13189/eer.2018.060501

Johnston, C. H., & Smith, A. T. (2019). Lepus peguensis, The IUCN Red List of Threatened Species 2019. https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T41284A45188632.en

Killeen, J., Thurfjell, H., Ciuti, S., Paton, D., Musiani, M., & Boyce, M. S. (2014). Habitat selection during ungulate dispersal and exploratory movement at broad and fine scale with implications for conservation management. *Movement Ecology*, *2*(1), 15. https://doi.org/10.1186/s40462-014-0015-4

Krause, T., & Tilker, A. (2022). How the loss of forest fauna undermines the achievement of the SDGs. *Ambio*, *51*(1), 103–113. https://doi.org/10.1007/s13280-021-01547-5

Law on Forestry No. 16/2017/QH14, Chapter VI. National Assembly of Viet Nam.

Leinster, T., & Cobbold, C. A. (2012). Measuring diversity: The importance of species similarity. *Ecology*, *93*(3), 477–489. https://doi.org/10.1890/10-2402.1

Lunde, D., Aplin, K., & Molur, S. (2016). *Hystrix brachyura* (Vol. 2016, e.T10749A115099298). The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T10749A22232129.en

MacKenzie, J. M. (1988). *The empire of nature: Hunting, conservation and British imperialism*. Manchester University Press.

Mahood, S. P., & Eames, J. C. (2012). A review of the status of Collared Laughingthrush Garrulax yersini and Grey-crowned Crocias Crocias langbianis. *Forktail*, *28*(2012), 44–48.

Malarney, S. K. (2020). Defining the true hunter: Big game hunting, moral distinction, and virtuosity in French colonial Indochina. *Comparative Studies in Society and History*, *62*(3), 651–680.

Millet, F. (1916). *La chasse sur les hauts plateaux moïs du Langbian*. La Revue Indochinoise.

Milner-Gulland, E. J., & Bennett, E. L. (2003). Wild meat: The bigger picture. *Trends in Ecology & Evolution*, *18*(7), 351–357. https://doi.org/10.1016/S0169-5347(03)00123-X

Nguyen, K. (1966). Les forêts de Pinus khasya et de Pinus merkusii du Centre-Vietnam : Étude de la dynamique des sols en liaison avec celle de la végétation. *Annales des Sciences Forestières*, *23*(2), 219–372. https://doi.org/10.1051/forest/19660201

Nguyen, T. V., Wilting, A., Niedballa, J., Nguyen, A., Rawson, B. M., Nguyen, A. Q. H., Cao, T. T., Wearn, O. R., Dao, A. C., & Tilker, A. (2022). Getting the big picture: Landscape-scale occupancy patterns of two Annamite endemics among multiple protected areas. *Conservation Science and Practice*, *4*(3), e620. https://doi.org/10.1111/csp2.620

Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. (2016). camtrapR: An R package for efficient camera trap data management. *Methods in Ecology and Evolution*, *7*(12), 1457–1462. https://doi.org/10.1111/2041-210X.12600

O'Brien, T. G., & Kinnaird, M. F. (2008). A picture is worth a thousand words: The application of camera trapping to the study of birds. *Bird Conservation International*, *18*(S1), S144–S162. https://doi.org/10.1017/S0959270908000348

Ong, L. (2020). *The ecological functions of Asian elephants in the Sundaic rainforest: Herbivory and seed dispersal*. University of Nottingham. http://eprints.nottingham.ac.uk/63904

Pereira, A. D., Bogoni, J. A., Bazilio, S., & Orsi, M. L. (2021). Mammalian defaunation across the Devonian kniferidges and meridional plateaus of the Brazilian Atlantic Forest. *Biodiversity and Conservation*, *30*(13), 4005–4022. https://doi.org/10.1007/s10531-021-02288-3

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., & Kausrud, K. (2011). The normalized difference vegetation index (NDVI): Unforeseen successes in animal ecology. *Climate Research*, *46*(1), 15–27. https://doi.org/10.3354/cr00936

Pievani, T. (2014). The sixth mass extinction: Anthropocene and the human impact on biodiversity. *Rendiconti Lincei*, *25*(1), 85–93. https://doi.org/10.1007/s12210-013-0258-9

Pillay, R., Venter, M., Aragon-Osejo, J., González-del-Pliego, P., Hansen, A. J., Watson, J. E. M., & Venter, O. (2022). Tropical forests are home to over half of the world's vertebrate species. *Frontiers in Ecology and the Environment*, *20*(1), 10–15. https://doi.org/10.1002/fee.2420

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, *124*(125.10), 1–10.

Plummer, M. (2022). rjags: Bayesian graphical models using MCMC. https://cran.r-project.org/web/packages/rjags/rjags.pdf

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The rise of the mesopredator. *Bioscience*, *59*(9), 779–791. https://doi.org/10.1525/bio.2009.59.9.9

R Core team. (2022). R: A language and environment for statistical computing.

Rees, W. G. (2004). Least-cost paths in mountainous terrain. *Computers & Geosciences*, *30*(3), 203–209.

Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). A terrain ruggedness index that qauntifies topographic heterogeneity.

Intermountain Journal of Sciences, *5*(1-4), 23–27. http://download.osgeo.org/qgis/doc/reference-docs/Terrain_Ruggedness_Index.pdf

Ripple, W. J., Abernethy, K., Betts, M. G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P. A., Macdonald, D. W., Machovina, B., Newsome, T. M., Peres, C. A., Wallach, A. D., Wolf, C., & Young, H. (2016). Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science*, *3*(10), 160498. https://doi.org/10.1098/rsos.160498

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the World's largest carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terborgh, J., & Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, *1*(4), e1400103. https://doi.org/10.1126/sciadv.1400103

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, *12*(9), 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Royle, J. A., & Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology*, *84*(3), 777–790. https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2

Rundel, P. W. (1999). Forest Habitats and Flora in Laos PDR, Cambodia and Vietnam. hinnamno.org, https://www.researchgate.net/publication/259623025

Save Vietnam's Wildlife. (2019). 5-year report 2014–2019.

Schiavina, M., Freire, S., & MacManus, K. (2023). GHS-POP R2023A—GHS population grid multitemporal (1975–2030). *European Commission, Joint Research Centre (JRC)*. https://doi.org/10.2905/2FF68A52-5B5B-4A22-8F40-C41DA8332CFE

Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A. S., Stuart, S. N., Temple, H. J., Baillie, J., BoitanI, L., Lacher, T. E., Jr., Mittermeier, R. A., Smith, A. T., Absolon, D., Aguiar, J. M., Amori, G., Bakkour, N., … Young, B. E. (2008). The status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science*, *322*(5899), 225–230. https://doi.org/10.1126/science.1165115

Scotson, L., Fredriksson, G., Augeri, D., Cheah, C., Ngoprasert, D. & Wai-Ming, W. (2017). Helarctos malayanus. *The IUCN Red List of Threatened Species 2017*, e.T9760A123798233. https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T9760A45033547.en

Shirley, K. (2011). Inference from simulations and monitoring convergence. In *Handbook of markov chain monte carlo* (pp. 163–174). CRC Press. https://doi.org/10.1201/b10905-7

Smith, F. A., Lyons, S. K., Ernest, S. K., Jones, K. E., Kaufman, D. M., Dayan, T., Marquet, P. A., Brown, J. H., & Haskell, J. P. (2011). Macroecological database of mammalian body mass. MOM v3.3. https://opendata.eol.org/dataset/smithbodysize

Sodhi, N. S., Posa, M. R. C., Lee, T. M., Bickford, D., Koh, L. P., & Brook, B. W. (2010). The state and conservation of southeast Asian biodiversity. *Biodiversity and Conservation*, *19*(2), 317–328. https://doi.org/10.1007/s10531-009-9607-5

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *Wiley Online Library*, *56*(4), 740–749. https://doi.org/10.1111/aje.12557

Southern Institute of Ecology. (2017). *Biodiversity baseline survey for sustainable natural*. Final report to JICA/SNRM. https://www.jica.go.jp/project/vietnam/037/materials/index.html

Sterling, E., & Hurley, M. M. (2005). Conserving biodiversity in Vietnam: Applying biogeography to conservation research. *Proceedings of the California Academy of Sciences*, *56*(I9), 98–118. https://www.academia.edu/download/85713186/proccas_v56_SuppI.pdf#page=98

Tilker, A., Abrams, J. F., Mohamed, A., Nguyen, A., Wong, S. T., Sollmann, R., Niedballa, J., Bhagwat, T., Gray, T. N. E., Rawson, B. M., Guegan, F., Kissing, J., Wegmann, M., & Wilting, A. (2019). Habitat degradation and indiscriminate hunting differentially impact faunal communities in the southeast Asian tropical biodiversity hotspot. *Communications Biology*, *2*(1), 396. https://doi.org/10.1038/s42003-019-0640-y

Tilker, A., Abrams, J. F., Nguyen, A. N., Hörig, L., Axtner, J., Louvrier, J., Rawson, B. M., Nguyen, H. A., Guegan, F., Nguyen, T. V., Le, M., Sollmann, R., & Wilting, A. (2020). Identifying conservation priorities in a defaunated tropical biodiversity hotspot. *Diversity and Distributions*, *26*(4), 426–440. https://doi.org/10.1111/ddi.13029

Tilker, A., Nguyen, A., Abrams, J. F., Bhagwat, T., Le, M., Van Nguyen, T., Nguyen, A. T., Niedballa, J., Sollmann, R., & Wilting, A. (2020). A little-known endemic caught in the southeast Asian extinction crisis: The Annamite striped rabbit *Nesolagus timminsi*. *Oryx*, *54*(2), 178–187. https://doi.org/10.1017/S0030605318000534

Tilker, A., Niedballa, J., Viet, H. L., Abrams, J. F., Marescot, L., Wilkinson, N., Rawson, B. M., Sollmann, R., & Wilting, A. (2023). Can snare removal safeguard protected areas caught in the southeast Asian snaring crisis? Promises and perspectives. *bioRxiv*, *2023*, 01.26.525728. https://doi.org/10.1101/2023.01.26.525728

Timmins, R. J., Coudrat, C. N. Z., Duckworth, J. W., Gray, T. N. E., Robichaud, W., Willcox, D. H. A., Long, B. & Roberton, S. (2016). Chrotogale owstoni. *The IUCN Red List of Threatened Species 2016*, e.T4806A45196929. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T4806A45196929.en

Timmins, R. J., Duckworth, J. W., Chutipong, W., Ghimirey, Y., Willcox, D. H. A., Rahman, H., Long, B. & Choudhury, A. (2016). Viverra zibetha. *The IUCN Red List of Threatened Species 2016*, e.T41709A45220429. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41709A45220429.en

Timmins, R. J., Hedges, S., & Robichaud, W. (2016). Pseudoryx nghetinhensis. *The IUCN Red List of Threatened Species*, e.T18597A166485696. https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T18597A46364962.en

Timmins, R. J., Steinmetz, R., et al. (2016). Muntiacus vaginalis. *The IUCN Red List of Threatened Species 2016*, e.T136551A22165292. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T136551A22165292.en

Timmins, R. J., Duckworth, J. W., Robichaud, W., Long, B., Gray, T. N. E., & Tilker, A. (2016). Muntiacus vuquangensis. *The IUCN Red List of Threatened Species 2016*, e.T44703A22153828. https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T44703A22153828.en

Vogelmann, J., Khoa, P., Lan, D., Shermeyer, J., Shi, H., Wimberly, M., Duong, H., & Huong, L. (2017). Assessment of

Forest degradation in Vietnam using Landsat time series data. *Forests*, *8*(7), 238. https://doi.org/10.3390/f8070238

Willcox, D. H. A., Tran, Q. P., Hoang, M. D., & Nguyen, T. T. A. (2014). The decline of non-Panthera cat species in Vietnam. *Cat News*, *8*, 53–61.

Wolff, N. H., Visconti, P., Kujala, H., Santini, L., Hilbers, J. P., Possingham, H. P., Oakleaf, J. R., Kennedy, C. M., Kiesecker, J., Fargione, J., & Game, E. T. (2023). Prioritizing global land protection for population persistence can double the efficiency of habitat protection for reducing mammal extinction risk. *One Earth*, *6*(11), 1564–1575. https://doi.org/10.1016/j.oneear.2023.10.001

Wong, S. T., Belant, J. L., Sollmann, R., Mohamed, A., Niedballa, J., Mathai, J., Street, G. M., & Wilting, A. (2019). Influence of body mass, sociality, and movement behavior on improved detection probabilities when using a second camera trap. *Global Ecology and Conservation*, *20*, e00791. https://doi.org/10.1016/j.gecco.2019.e00791

Yamaura, Y., Andrew Royle, J., Kuboi, K., Tada, T., Ikeno, S., & Makino, S. (2011). Modelling community dynamics based on species-level abundance models from detection/nondetection data. *Journal of Applied Ecology*, *48*(1), 67–75. https://doi.org/10.1111/j.1365-2664.2010.01922.x

Young, H. S., McCauley, D. J., Galetti, M., & Dirzo, R. (2016). Patterns, causes, and consequences of Anthropocene Defaunation. *Annual Review of Ecology, Evolution, and Systematics*, *47*(1), 333–358. https://doi.org/10.1146/annurev-ecolsys-112414-054142

SUPPORTING INFORMATION

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

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