

ORIGINAL ARTICLE

Changes in tropical terrestrial vertebrate communities along two anthropogenic gradients: Forest degradation and accessibility

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Abstract

Forest degradation and hunting are two major drivers of species declines in tropical forests, often associated with forest production activities and infrastructure. To assess how the medium-to-large bodied terrestrial vertebrate community varied across these two main gradients of anthropogenic impact, we conducted a camera-trap survey across three production forest reserves in central Sabah, Malaysian Borneo, each with different past and current logging regimes. We analyzed data from a 32-species community using a Bayesian community occupancy model, investigating the response of occurrence, diversity, and composition to forest degradation and accessibility (a proxy for hunting pressure). We found forest degradation to be a strong driver of occurrence of individual species. Such responses led to declines in diversity and shifts in community composition, where forest-dependent species decreased while disturbance-tolerant species increased in occupancy probability with increasing forest degradation. Accessibility had a weaker effect on community diversity and species occupancy, and low-level hunting pressure and management of access to our study sites likely played an important role in mitigating accessibility effects. Nonetheless, our results showed accessibility had compounding effects on a wildlife community already affected negatively by forest degradation. Despite the impacts of forest degradation and accessibility on the terrestrial vertebrate community, our results highlight how the application of more sustainable practices—reducing forest disturbance and managing unauthorized access to logging roads—resulted in more intact wildlife communities. Understanding how both disturbances combined affect the terrestrial vertebrate community is essential for evaluating and developing effective sustainability guidelines.

Abstract in Malay is available with online material.

KEYWORDS

Borneo, community occupancy, forest disturbance, Sabah, sustainable forest management

Seth T. Wong and Azlan Mohamed contributed equally to this study.

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1 | INTRODUCTION

Tropical rainforests are some of the most biodiverse regions with faunal diversity playing an essential role in maintaining ecosystem function and services (Andresen et al., 2018; Barlow et al., 2018). Terrestrial vertebrates in particular serve as indicators of ecosystem health while serving essential roles, for example as predators and/or seed dispersers (Ahumada et al., 2011; Bogoni et al., 2020). Much of the tropical forests, however, have been lost (Hansen et al., 2013). Southeast Asia in particular shows higher deforestation rates than other tropical regions (Miettinen et al., 2011; Stibig et al., 2014), having lost an estimated 610,000 square kilometers of forest between 2001 and 2019 (Feng et al., 2021). Consequently, the region has the highest proportion of threatened and endemic vertebrates compared to other tropical regions (Jenkins et al., 2013; Sodhi et al., 2004).

As of 2015, Southeast Asia was covered in 206.5 million hectares of forest, of which 38.3 million ha were considered intact and 38.5 million ha were protected areas (Estoque et al., 2019). The degradation of remaining forests through logging and clearing for industrial tree plantations leads to changes in forest structure and composition (Chaudhary et al., 2016; DeFries et al., 2005; Sodhi et al., 2010). Such disturbances alter habitat quality and are recognized as a major driver of biodiversity loss across Southeast Asia (Barlow et al., 2016; Curtis et al., 2018; Wilcove et al., 2013). The structure and composition of wildlife communities can vary significantly between different land uses and primary forest (Barlow et al., 2007; Edwards et al., 2014), though these effects may also vary across taxonomic groups (Barlow et al., 2007; Hill & Hamer, 2004). For tropical mammal communities, there is mixed evidence on the impacts of forest degradation on species richness (Boron et al., 2019; Brodie, Giordano, & Ambu, 2015; Wall et al., 2021), but modified landscapes harbor lower mammalian diversity and less even communities (dominated by few, more abundant species) compared to intact forests (Ahumada et al., 2011; Boron et al., 2019).

The magnitude of these changes varies with timber extraction techniques. Logging by clear-cutting is the most destructive, leaving an area deforested, altering abiotic conditions, and reducing biodiversity (Chaudhary et al., 2016; Pawson et al., 2006). With conventional selective logging, only the trees above a certain diameter are harvested, and remaining forests can harbor similar faunal communities to intact forest if trees are harvested at low densities (Edwards et al., 2014; Chaudhary et al., 2016). But disturbance from high intensity selective logging leaves the remaining forest degraded (Burivalova et al., 2014; Bicknell et al., 2014; Chaudhary et al., 2014; Jamhuri et al., 2018). Reduced impact logging (RIL) is considered to be a sustainable timber harvest system for conserving biodiversity and ecosystem services (Putz et al., 2001, 2008). Under RIL, forest degradation is reduced through preharvest inventories and planning, careful placement of logging roads and skid trails, directional felling of trees, and postharvest silviculture treatments (Edwards et al., 2012; Putz et al., 2001). Compared to other logging regimes, RIL has been shown to have the smallest impact on faunal

communities which are similar to communities in unlogged, primary forest (Bicknell et al., 2014; Bicknell & Peres, 2010; Burivalova et al., 2015; Edwards et al., 2012).

Though sustainable logging practices like RIL result in less forest degradation, any forest production activity is associated with road infrastructure, increasing accessibility for other human activities such as hunting (Brodie, Giordano, Zipkin, et al., 2015; Clements et al., 2014). Overexploitation of wildlife through hunting represents another major driver of biodiversity declines in Southeast Asia (Benítez-López et al., 2017; Gray et al., 2018; Tilker et al., 2019), causing local extinctions and reduced species diversity and abundance (Martínez-Ramos et al., 2016). The loss of large-bodied species such as herbivores can have cascading effects, shifting to a community dominated by smaller mammals such as rodents (Koerner et al., 2017; Scabin & Peres, 2021) and further altering the vegetation composition, affecting forest structure and function (Martínez-Ramos et al., 2016). For production forest management pursuing or adhering to sustainable forest certification schemes, hunting is restricted or prohibited (Robinson et al., 2009). Conversely, where there is no management of hunting, even structurally intact forests can be largely devoid of wildlife (Benítez-López et al., 2019; Tilker et al., 2019). Hunting activity, however, is challenging to measure directly or quantify. Traditional methods, such as social surveys, are fraught with biases, as people may not report their illegal activities honestly (e.g., Nuno & St John, 2015). The utilization of camera trap records of human presence similarly may not accurately reflect hunting intensity (Dobbins et al., 2020), as hunters cannot always be distinguished from other people. Rather than attempting to measure hunting directly, hunting potential can be quantified based on accessibility, which is a key determinant of actual hunting pressure (Clements et al., 2014; Laurance et al., 2006; Ziegler et al., 2016). A function of access points and terrain characteristics (Rees, 2004), accessibility can readily be determined from remotely sensed information.

Even though both habitat degradation and hunting are well known to impact communities of tropical wildlife, their effects are rarely assessed together (Eigenbrod et al., 2008; Deere et al., 2020, but see Brodie, Giordano, Zipkin, et al., 2015; Symes et al., 2018). Our objective was to jointly assess how diversity of the medium-to-large bodied terrestrial vertebrate community varied across the two main gradients of anthropogenic impact in tropical forests—forest degradation (due to logging activities) and potential hunting pressure (due to logging-related infrastructure)—in three production forest reserves with different past and current logging regimes. We expect community diversity to decline with increasing forest degradation and accessibility, but because access to all reserves is well-managed, we expect forest degradation to be a stronger driver. As species associations with forest degradation and accessibility vary across the community (Sollmann et al., 2017; Tilker et al., 2019), we expect that as these two measures increase, the community will become more dominated by disturbance-tolerant species. Understanding the compounding effects of habitat degradation and increased accessibility on wildlife communities is essential to evaluate management of

tropical production forests and aid the shift towards more sustainable forestry practices.

2 | METHODS

2.1 | Study area

We surveyed three adjacent forest reserves in central Sabah, Malaysian Borneo: Deramakot Forest Reserve, Tangkulap Forest Reserve, and Northern Kuamut Forest Reserve (Figure 1). All sites are predominantly mixed lowland dipterocarp forest with no apparent wet or dry seasons. Deramakot (551 km²) is a Forest Stewardship Council certified production forest reserve, implementing reduced impact logging methods since 1995. Only a small portion (~3%) of Deramakot is logged each year, with a 40-year harvest rotation allowing for forest regeneration (Ong et al., 2012). In contrast, Tangkulap (500 km²) and Northern Kuamut (650 km²) have been logged primarily through conventional selective logging practices. Tangkulap was selectively logged until 2001, when all operations ceased to allow for forest regeneration. The reserve has since

received Forest Stewardship Council certification in 2011 and was later declared a totally protected area in 2015. Northern Kuamut was heavily conventionally logged from 2004 to 2012, and was also declared a totally protected area in 2015. As a result of different logging histories and management practices, there is a gradient in forest degradation from Deramakot (lowest) to Tangkulap (intermediate) to Northern Kuamut (highest).

Forest reserves can be accessed primarily in three manners: along main (regularly maintained and graded) and secondary logging roads, by boat along the Kinabatangan River, or through neighboring oil palm plantations. All forest reserves have one main logging road with a network of secondary roads and skid trails and some level of access control through gates and checkpoints. Tangkulap is the most accessible with a publicly accessible main logging road, an intact network of secondary roads, and oil palm plantation estates along the borders to the north and west. Deramakot has intermediate accessibility with a gated main road and several well maintained secondary roads from ongoing logging activity, borders oil palm estates to the north, and the Kinabatangan River in the southeast. Kuamut is the least accessible with only one publically accessible main logging road, and, though it was most recently logged, secondary logging roads

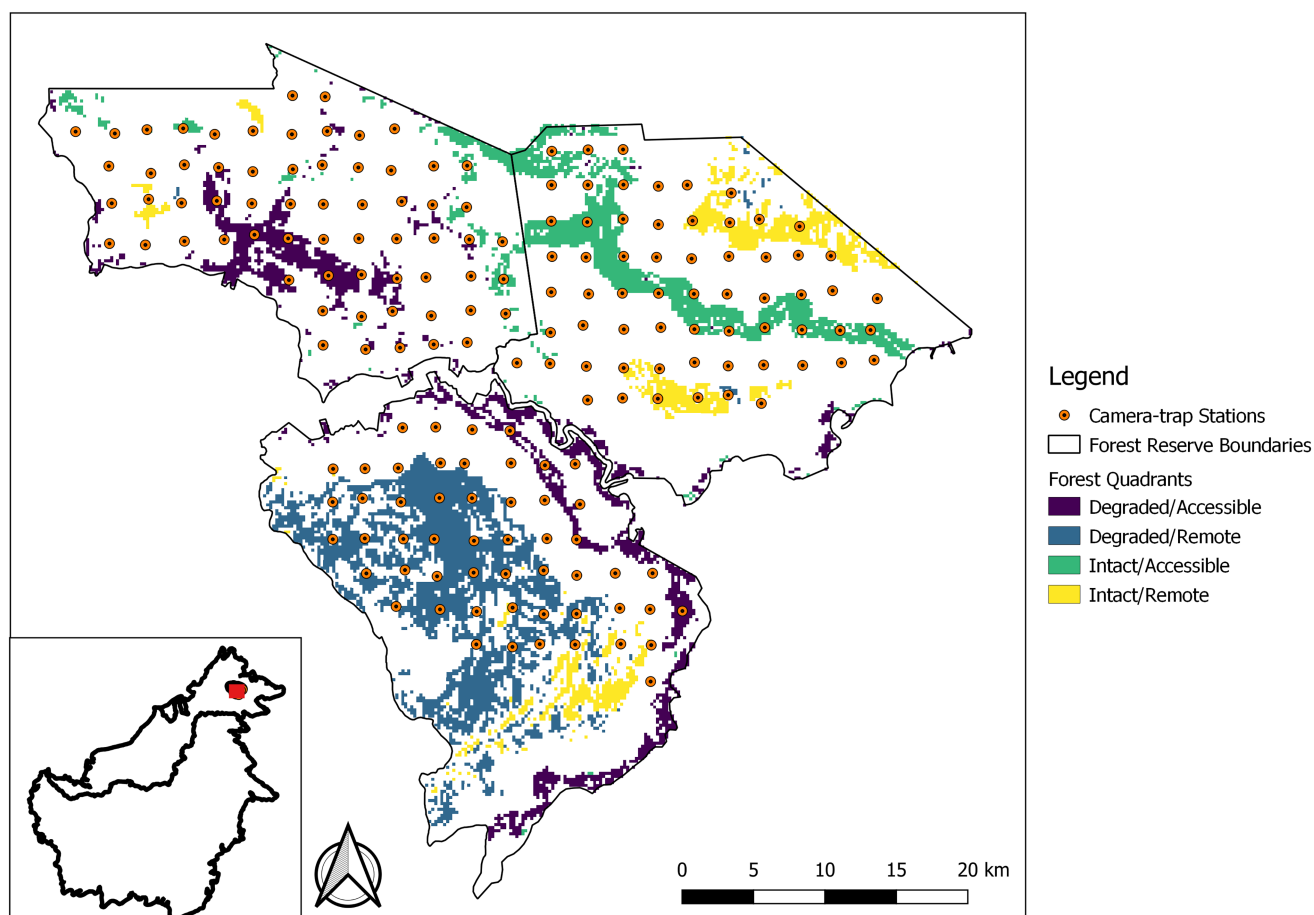


FIGURE 1 Study site map of camera-trap stations and forest “quadrants” across three forest reserves in central Sabah, Malaysian Borneo. Each 200 × 200-m pixel is classified into four quadrants based on two gradients of anthropogenic impact, forest disturbance (quantified by aboveground carbon density, ACD) and remoteness (quantified as hiking time in hours). “Remote” and “intact” forest has remoteness/ACD values >75th percentile of the respective covariate; “accessible” and “disturbed” forest has remoteness/ACD values <25th percentile.

and skid trails were not maintained after timber harvesting; accessibility in Kuamut is further reduced by rugged terrain and the lack of major palm oil estates nearby. Though hunting is strictly prohibited in all forest reserves, we found some evidence of hunting activities. In our study region, hunting is primarily driven by subsistence needs and targets specific species, mainly bearded pig *Sus barbatus* or sambar *Rusa unicolor*, using firearms (Kurz et al., 2021). While snares are occasionally employed, their use is relatively infrequent compared to other regions in Southeast Asia (see Gray et al., 2018). During our surveys, evidence of hunting activities such as shotgun shells and camera-trap images generally occurred in close proximity to accessible logging roads and borders of oil palm estates. Additionally, there is a reported presence of illegal poachers accessing the study areas from the Kinabatangan River (Sabah Forestry Department, pers. comm.). In response to the potential threats posed by illegal activities, anti-encroachment measures such as regular vehicle patrols (along all roads and the Kinabatangan River) and inspections at logging camps are implemented along with access control through gates and checkpoints. Considering these measures, we characterize hunting pressure in our study areas as present but low.

2.2 | Data collection and preparation

We conducted camera-trap surveys in Deramakot from September to December 2014, Tangkulap from July to October 2015, and Northern Kuamut from March to July 2016. We set 63, 64, and 53 camera-trap stations in each forest reserve, respectively, with stations spaced at approximately 2.5-km intervals (Figure 1). At each station, we set two Reconyx PC850 cameras (Reconyx Inc., Holmen, Wisconsin, USA) at a height of 30–45 cm within 20 m of each other, often facing different trail features (e.g., ridges, wildlife trails, logging roads, and/or skid trails). We cleared vegetation to reduce false triggering of cameras and programmed cameras to take three consecutive images with no delay between triggers. Cameras were retrieved after a minimum of 60 days of operation.

We identified animals in images to species, with mousedeer (greater mousedeer *Tragulus napu* and lesser mousedeer *T. kanchil*) identified only to genus due to similarities in morphology and ecology. For each station, we combined all records taken by both cameras and records of the same species >60 min apart were considered independent records. We used the package “camtrapR” version 2.1.1 (Niedballa et al., 2016) in program R version 4.0.3 (R Core Team, 2020) to organize and build a record database and camera effort matrix, and then to convert the raw data to binary species detection histories, with 5-day sampling occasions (to avoid excess zeros especially for rarely detected species), for analysis with community occupancy models (see Analysis; Dorazio & Royle, 2005; Royle & Dorazio, 2006). To define our final community, we excluded all species with <5 detections from the analysis. Additionally, we excluded small mammal (rodents and tree shrews) and small bird (passerines) species, as they are poorly sampled by our camera-trap setup. Furthermore, we exclude wide ranging species (i.e., bearded

pig, Sunda clouded leopard *Neofelis diardi*, and Bornean elephant *Elephas maximus borneensis*) to approximate the assumption of sampling location independence.

2.3 | Habitat covariates

To characterize forest degradation across the survey sites, we initially considered two covariates: normalized difference moisture index (NDMI) and aboveground carbon density (ACD). The NDMI is a vegetation index based on moisture content from forest canopies, and it has been shown to be a good indicator of forest degradation from logging activity (Hayes et al., 2008; Schultz et al., 2016). As NDMI may not be very sensitive in high moisture environments, we also considered ACD. While factors other than forest degradation affect ACD, forest carbon storage is a good measure of forest complexity and degradation from logging activities (Pacheco et al., 2021; Wekesa et al., 2016; Yohannes & Soromessa, 2015), and a strong relationship between the two has been demonstrated in our study region (Asner et al., 2018). Both ACD and NDMI are inversely related to forest degradation, that is, lower values indicate more disturbed forest. We obtained annual mean NDMI values from Landsat eight imagery (30-m resolution) for each forest reserve according to their respective survey years, and we extracted ACD values from the ground-truthed ACD dataset for Sabah, Malaysian Borneo by Asner et al. (2018) (Figure S1). The ACD dataset was assembled in 2016 and therefore matched our data collection period closely.

To quantify forest accessibility, we calculated remoteness as hours walking time to each point in the landscape from a set of start points using a hiking function/least-cost paths analysis (Rees, 2004). With shapefiles of roads, rivers, and reserve boundaries provided by the Sabah Forestry Department, we used the “Extract Vertices” geoprocessing tool in QGIS (version 3.28.12; QGIS Development Team, 2023) to generate start points (Figure S2) for the hiking function along main logging roads and secondary roads (nongated and accessible by vehicles; nonmaintained logging roads were inaccessible and therefore excluded), the Kinabatangan river (accessible by boat), and oil palm plantation boundaries (accessible by foot or motorbike and in close proximity to large roads or worker camps). Remoteness is inversely related to accessibility, so that lower values indicate more accessible forest (Figure S3). Beyond these predictors of main interest, we also included the elevation at each camera station (extracted from a digital elevation model, SRTM 30-m resolution) due to its potential to influence species richness and distributions (Amatulli et al., 2018).

Raster data for each covariate were resampled to 200×200 m resolution before values were extracted for each camera-trap station. Habitat covariates were then scaled (mean of zero and standard deviation of 1) and tested for correlations by calculating Spearman Rank Correlation coefficients (Figure S4); covariates were considered substantially correlated if the absolute value of the coefficient was >0.7 (Dormann et al., 2013). Our final selection of habitat covariates to represent the conditions around each camera-trap station included ACD, remoteness, and elevation.

2.4 | Data analysis

We modeled the response of community and species-specific occurrence to the three habitat covariates using a Bayesian community occupancy model framework (e.g., Dorazio & Royle, 2005; Royle & Dorazio, 2006) without data augmentation (i.e., considering only detected species). Occupancy models estimate species occupancy probability and its relationship with predictor variables while accounting for imperfect species detection (MacKenzie et al., 2006). By jointly analyzing data from multiple species, community occupancy models increase the precision of parameter estimates for rare species by “borrowing” information from data-rich species, assuming that species-level parameters come from a common parametric distribution (Royle & Dorazio, 2008).

As arboreal species have a lower chance to be detected by a terrestrial camera-trap, we modeled detection probability as having a species-specific random intercept with group-specific hyperparameters (arboreal or nonarboreal). Additionally, we accounted for varying survey effort due to malfunctioning camera-traps by including the number of days each camera at a station was functional within a 5-day occasion as a fixed effect, and the effect of camera placement by including whether at least one camera at a station was set on-road as a species-specific random effect on detection. Finally, to account for potential differences in detection among forest reserves (e.g., due to sampling at different times and seasonality affecting animal activity levels; different field teams affecting camera setup; differences in animal abundance among reserves), we included a categorical reserve covariate with species-specific effects on detection probability. Finally, to improve model fit, we added a species-specific station-level random effect to the detection model. We modeled occupancy probability as having a species-specific random intercept and included species-specific linear effects of the three habitat covariates (ACD, remoteness, and elevation) on occupancy. Results from the equivalent model using NDMI instead of ACD were very similar and are provided in Figure S5. We also explored a model with an interaction between ACD and remoteness, but found very little evidence for such an interaction and therefore retained the original model without interaction.

We implemented the model (see Appendix S1) in a Bayesian framework using JAGS version 4.3.0 (Plummer, 2003) through the R-package “jagsUI” version 1.5.1 (Kellner, 2018). We used conventional vague Normal priors (mean=0, precision=0.05) on community means, and vague Gamma priors (shape=rate=0.1) on community precision parameters. We overlaid prior and posterior distributions of all community parameters and found no evidence that community-level posterior estimates were strongly influenced by the choice of priors. We ran three parallel Markov chains with 300,000 iterations each, of which we discarded the first 50,000 as burn-in and further thinned the remaining iterations by 20. We assessed chain convergence using the R-hat statistic (all chains showed R-hat values <1.1 indicating convergence, Gelman et al., 2004). We assessed model fit by calculating a Bayesian *p*-value (Gelman et al., 1996). We report model estimates as posterior mean, standard deviation, and the 95%

and 75% Bayesian credible intervals. We consider a coefficient to have strong support if the 95% BCI did not overlap zero and moderate support if the posterior 75% BCI did not overlap zero.

To compare wildlife communities across different levels of forest degradation and accessibility, we first established two categories each for ACD and remoteness based on the upper and lower quartiles (75th and 25th percentiles) of the distribution of covariate values across sampled locations (Table S1). That is, ACD values < lower quartile were categorized as “degraded forest” and remoteness values < lower quartile were categorized as accessible forest; in contrast, ACD/remoteness values > upper quartile were categorized as “intact forest” and “remote forest”, respectively. By combining categories across gradients, we obtained four forest types (in order of their anthropogenic impact): “degraded and accessible”, “degraded and remote”, “intact and accessible”, “intact and remote”. Using covariate rasters of the entire study areas, we identified all pixels that fell into each forest type (see Figure 1, see Table S2 for summary of camera-trap stations in each of the four forest types). We excluded pixels whose covariate values were below/above the minimum and maximum covariate values across the sampling stations, to avoid extrapolation to unsampled habitat conditions. For each forest type, we then randomly selected 1000 pixels, extracted all covariate information (including elevation) for these pixels, and used the parameter estimates from the community model to predict the occupancy probability for all species to these pixels. We used these predictions to characterize and contrast community diversity and composition in the four forest types. Specifically, we calculated mean probability of occupancy for each species in each forest type. We compared and correlated mean species occupancy probability per forest type against mean occupancy probability in “intact and remote” forest to investigate changes in community composition due to anthropogenic influences, that is, whether common or rare species changed among forest types.

We further used mean probability of occupancy to generate a species defaunation index and biodiversity profiles. The defaunation index is a measure of community dissimilarity compared to a reference community (Giacomini & Galetti, 2013), here, “intact and remote” forest. Dissimilarity values range between −1 and 1, where negative values indicate a more complete community compared to the reference assemblage, 0 indicates no differences in assemblages, and positive values indicate less complete community compared to the reference assemblage (where “less complete” can mean loss and/or depletion of species). The index is typically calculated based on species abundance in each assemblage, but has also been calculated based on occupancy (e.g., Tilker et al., 2019; Wong et al., 2022).

Similarly, we used mean predicted occupancy to generate species diversity profiles which are a representation of community diversity (Abrams et al., 2021). Diversity profiles are a plotted series of Hill numbers, including multiple common diversity indices, along a gradient *q* (Sensitivity parameter) that quantifies the impact of rare species on diversity (Leinster & Cobbold, 2012). At *q*=0, all species contribute to diversity equally (i.e., richness); as *q* increases, rare species contribute less to diversity. The shape of the diversity profile

informs us about the evenness of a community where a more steeply declining profile indicates a community that is less even.

3 | RESULTS

We collected 9823 independent records of 37 species (28 mammals and nine birds) over the course of 12,385 trap nights. Our final analyzed community consisted of 32 species (Table S3). Community- and species-specific occurrence responses to ACD and remoteness were generally positive but varied in strength (Figure 2); ACD was a more important predictor of occupancy than remoteness. At the community level, there was strong evidence for a positive association of occupancy probability with ACD. Furthermore, our model results showed strong evidence for an association with ACD for nine species (eight positive and one negative) and moderate evidence for positive associations for six species. Occupancy probability was positively associated with remoteness for the community and four species, though these effects had mostly moderate support with only one species having a strong positive association. See Supplementary information (Figures S6 and S7, Table S4) for additional results on nonfocal occupancy predictors, detection effects, and pixel-level species richness.

Owing to the generally positive associations with ACD, most species had higher mean predicted occupancy in the two intact forest types (Table S5). Compared to intact-remote forest, four species had a significantly different mean predicted occupancy (estimate outside of 95% BCI of that in intact-remote forest) in intact-accessible forest, two higher and two lower. In contrast, in degraded-remote and degraded-accessible forest, six and five species decreased significantly in occupancy, respectively, with only one species increasing. Correlation between mean species occupancy in intact remote forest and other forest types decreased with increasing disturbance (Figure 3), suggesting that species common in intact remote forest tended to get rarer, and rare species tended to get more common in more disturbed forest.

Both the occupancy-based defaunation index and diversity profiles suggested a slight decline in diversity from intact to disturbed forest. The occupancy-based defaunation index for degraded-accessible forest was significantly different from 0 (0.11 ± 0.04 , 95% BCI 0.03–0.19) and almost two times greater than for degraded-remote forest (0.06 ± 0.02), suggesting that combined high levels of forest degradation and accessibility were associated with a less complete community (Figure 4). The defaunation index value for intact-accessible forest was negligible (0.002 ± 0.021) suggesting that high accessibility alone did not cause community change. Occupancy-based diversity profiles declined most quickly in

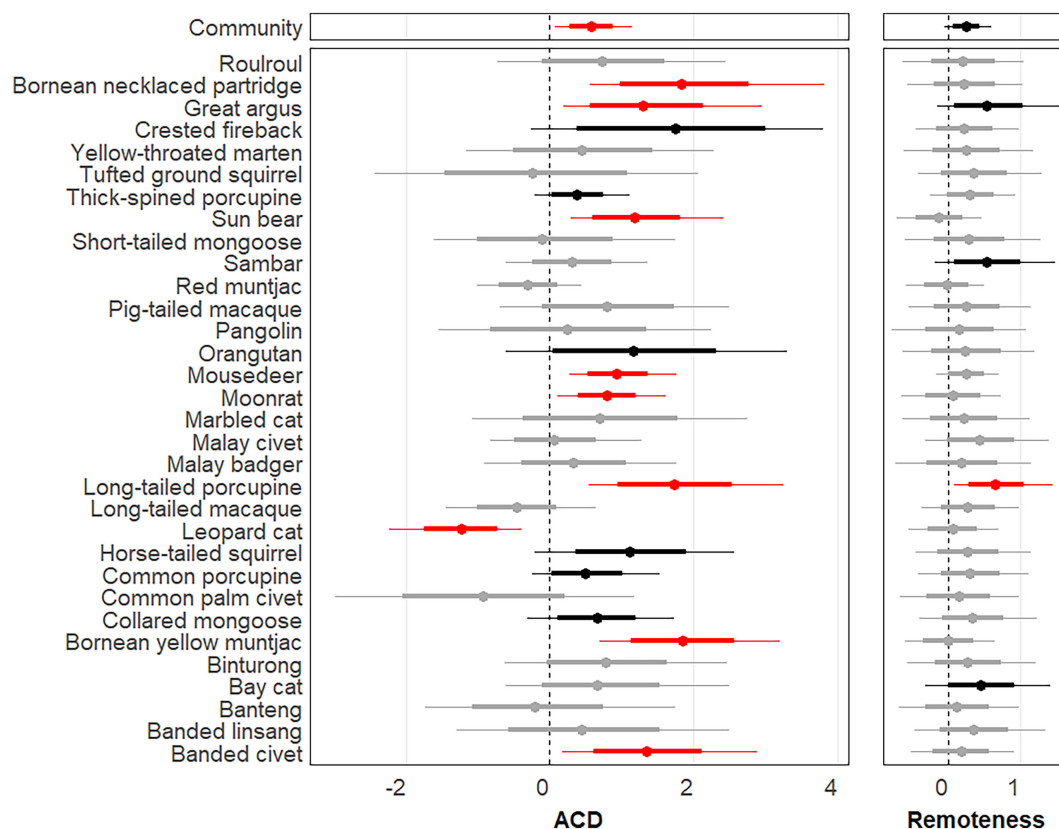


FIGURE 2 Model coefficients (mean and Bayesian Credible Intervals, BCI) for the effects of aboveground carbon density (ACD) and remoteness on the occupancy probabilities of 32 vertebrate species using community occupancy model fit to camera-trap data from three commercial forest reserves in Sabah, Malaysian Borneo. Thin error bars represent the 95% BCI and the thick error bar represents the 75% BCI. Red dots/bars indicate strong associations between a covariate and occupancy (95% BCI not overlapping zero), black dots/bars represent moderate associations (75% BCI not overlapping zero), and gray represents weak association.

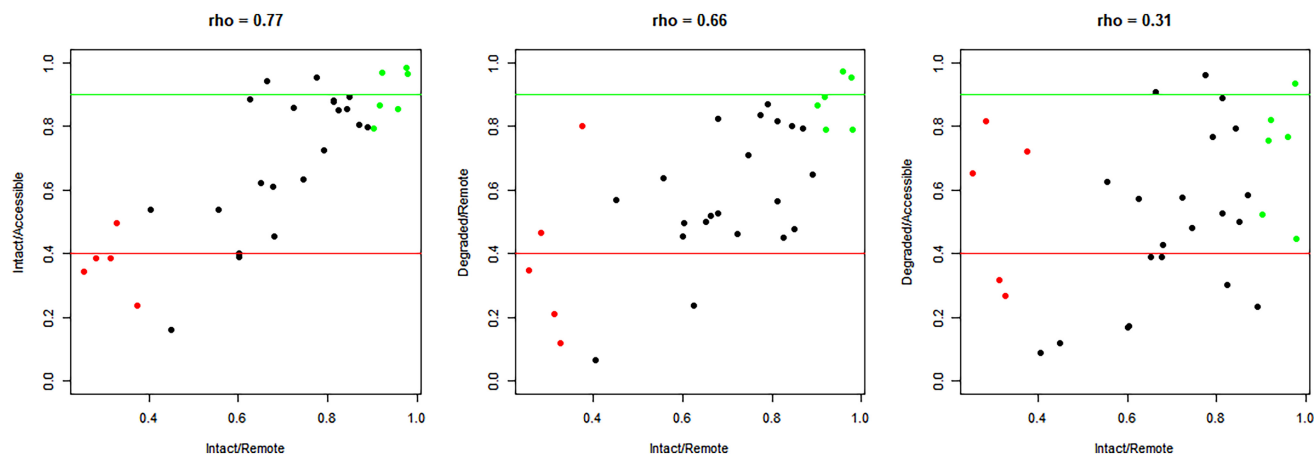


FIGURE 3 Correlation in mean occupancy for 32 species between each forest type (y-axis) and intact remote forest (x-axis). Species with mean occupancy >0.90 in intact remote forest are considered “common” in this forest type and highlighted in green. Species with mean occupancy <0.40 in intact remote forest are considered “rare” and highlighted in red. Horizontal lines represent respective occupancy cutoffs for “rare” and “common” species. The intact forests show high correlation between “rare” and “common” species, whereas in degraded forests, species mean occupancy has lower correlation due to a shift from “rare” to “common” and vice versa.

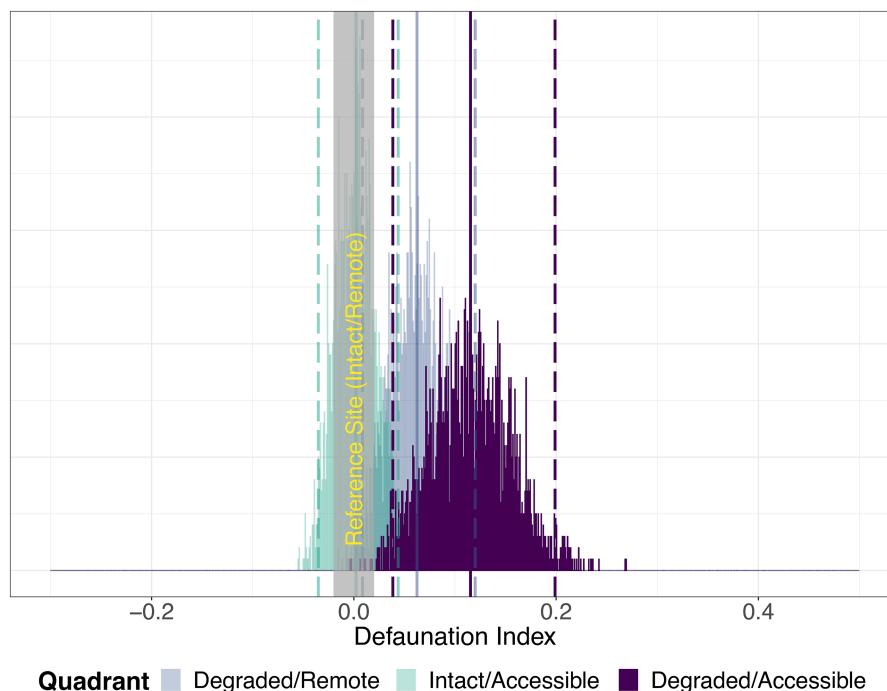


FIGURE 4 Occupancy-based species defaunation index for a 32-species community in three forest reserves in Malaysian Borneo. Forest is classified into four quadrants, based on two gradients of anthropogenic impact, forest disturbance (quantified by aboveground carbon density, ACD) and remoteness (quantified as hiking time from nearest access point). “Remote” and “intact” forest has remoteness/ACD values >75 th percentile of the respective covariate; “accessible” and “disturbed” forest has remoteness/ACD values <25 th percentile. The Intact-Remote forest quadrant is used as a reference site (zero defaunation). Solid lines represents mean values; dotted lines represent the 95% Bayesian credible intervals.

degraded-accessible forest with degraded-remote forest having the second fastest decline, indicating less even communities in degraded forest types (Figure 5, Table S6). The profile for both intact forest types were similar. Bayesian credible intervals for all four profiles

overlapped, suggesting that diversity patterns were similar across all forest types. Additionally, curves across all forest types were relatively flat, suggesting similar and low sensitivity of diversity to occurrence of rare species.

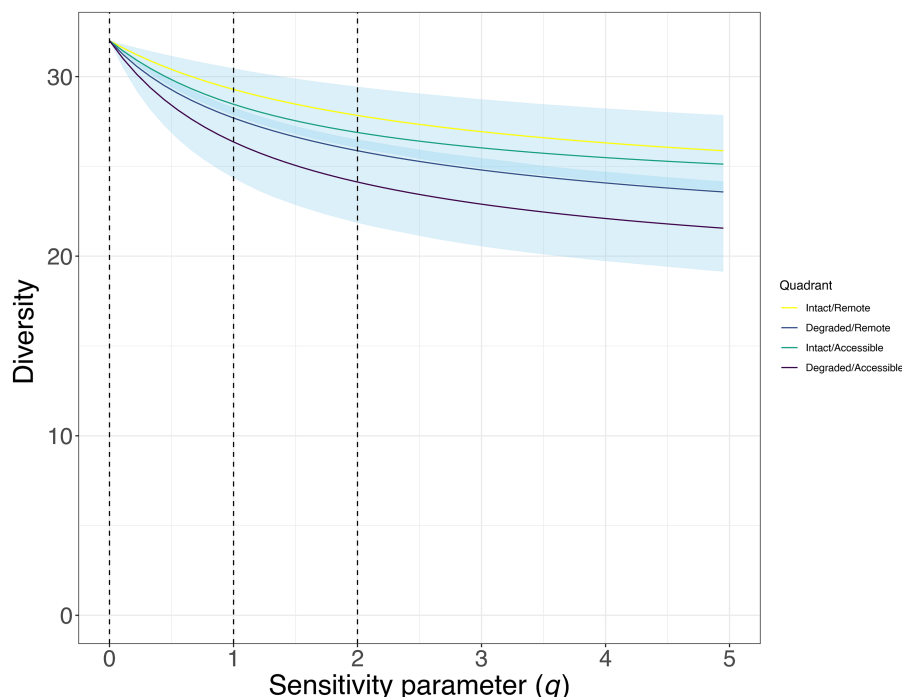


FIGURE 5 Occupancy-based species diversity profiles calculated for a 32-species community in three forest reserves in Malaysian Borneo. Forest is classified into four quadrants, based on two gradients of anthropogenic impact, forest disturbance (quantified by aboveground carbon density, ACD) and remoteness (quantified as hiking time per m). “Remote” and “intact” forest has remoteness/ACD values >75th percentile of the respective covariate; “accessible” and “disturbed” forest has remoteness/ACD values <25th percentile. Includes three diversity indices (vertical dotted lines): species richness ($q=0$), Shannon Index ($q=1$), and Simpson Index ($q=2$). Bayesian credible intervals (light blue shading) are displayed for only the highest (Intact/Remote) and lowest (Degraded/Accessible) profiles.

4 | DISCUSSION

Our study across three production forests in Sabah, Malaysian Borneo, confirmed our prediction that species occupancy and community diversity generally declined along the two major gradients of anthropogenic impact in tropical forests: structural forest degradation and accessibility. As expected, forest degradation was a much stronger driver of the occurrence of the terrestrial vertebrate community and individual species in our study landscape than forest accessibility, likely owing to the relatively high level of antipoaching measures taken by forest managers. Nonetheless, accessibility had compounding effects on a wildlife community already affected negatively by forest degradation. This was reflected in both measures of species diversity, with degraded accessible forest showing the least even community (though differences were not significant), significant defaunation, and a stronger shift in community composition compared to degraded remote forest.

Richness was estimated to be equal in all forest types, which, though ecologically reasonable owing to the mobility of the study species, can also be an artifact of considering a species as present in a forest type as long as average occupancy is >0 (i.e., even at very low occupancy). This is consistent with previous studies where species richness did not differ significantly between primary-unlogged forests and secondary-selectively logged forests (Barlow et al., 2007; Wall et al., 2021). Nonetheless, species within the community can be affected negatively by

forest disturbances from logging activity (for example, by occupying smaller areas in logged forest), such as larger carnivores (Brodie, Giordano, & Ambu, 2015) and arboreal species (Haysom et al., 2021). In our analysis, the majority of species were positively associated with less-disturbed forest. These included the largest carnivore in our analysis, the Sun bear *Helarctos malayanus*, most galliform birds, and some arboreal species (e.g., Bornean orangutan *Pongo pygmaeus*, semiarboreal banded civet *Hemigalus derbyanus*), but also species from other taxonomic groups and functional roles (e.g., moonrat *Echinosorex gymnura* and Bornean yellow muntjac *Muntiacus atherodes*). These results were consistent with studies that found these species to be forest-dependent and associated with less disturbed forests (Brozovic et al., 2018; Heydon, 1994; Nijman, 1998; Ross et al., 2016; Savini et al., 2021; Scotson et al., 2017; Timmins et al., 2016; Winarni et al., 2009). The leopard cat *Prionailurus bengalensis* was the only species with a significant negative association. Leopard cats are known to do well in human-modified landscapes, benefiting from disturbances such as logging activities which increase canopy gaps and understorey growth, boosting prey availability (Mohamed et al., 2013).

Such species-specific responses to forest degradation subsequently influence shifts in community composition. Mammal communities in disturbed and highly fragmented forests have been shown to exhibit higher dominance (less even community comprised of more abundant species) and fewer forest-unique species relative to intact forest (Ahumada et al., 2011; Barlow et al., 2007; Boron

et al., 2019), a pattern we also observed in this study. In our focal community, forest-dependent species such as the Bornean yellow muntjac, sun bear, and banded civet had the highest mean predicted occupancy probabilities within intact remote forest, and these significantly decreased in the two degraded forest types. Conversely, disturbance-tolerant species such as leopard cat and common palm civet, which were rather rare in the intact-remote forest, had the highest occupancy gains in the degraded forests. These shifts led to degraded-accessible forest having a slightly less even community.

The weak/nonsignificant decreases in mean occupancy probability in degraded forest for most species may be in part attributed to the limited range of forest degradation considered in this study. At the time of our surveys, only a small portion of Deramakot was undergoing active reduced-impact logging; any areas that had previously undergone any form of logging had at least 5 years of forest regeneration. As a result, even the most degraded pixels in our sample would not be considered degraded if more intensely logged (<40 megagrams of carbon per hectare, see Asner et al., 2018) or clear-cut forest was included.

Accessibility, which we interpret as a proxy for hunting pressure, was a much weaker predictor of species occupancy and community diversity in our study. Only one species responded strongly to accessibility, and high accessibility alone (i.e., intact accessible forest) did not lead to defaunation or appreciable declines in species mean occupancy or community evenness. During our study, we obtained very few photographic records of hunters—though photographic records have been shown to underestimate hunting occurrence (Dobbins et al., 2020). The conditions in our study sites, therefore, do not reflect the hunting pressure that exists in other parts of Southeast Asia (Gray et al., 2018). In regions where there is higher hunting pressure, it has been shown to be a stronger driver of species distribution than forest structural integrity (e.g., Tilker et al., 2019). Our accessibility measure incorporates both small scale terrain information, which is important for how hunters use landscapes (Deith & Brodie, 2020), as well as roads, which serve as starting points for hunting incursions. Roads are often interpreted as a proxy for hunting pressure (Clements et al., 2014; Laurance et al., 2006; Ziegler et al., 2016) but they also have other ecological effects (Bennett, 2017). They create habitat edges, which impacts vertebrate abundance and changes plant species composition (Martínez-Ramos et al., 2016; Pfeifer et al., 2017); they are often used by carnivores and may thus be high risk landscape features for potential prey (Brodie, Giordano, & Ambu, 2015; Kautz et al., 2021). If they are regularly accessed by vehicles, they can be avoided by wildlife due to fear (Gaynor et al., 2019; Laundre et al., 2010). Similarly, oil palm plantations, which also constituted starting points in our accessibility calculations, can have effects other than access (Daniel et al., 2022; Padfield et al., 2019). We cannot disentangle whether the consistently negative (though weak) effects of accessibility are due to a low-level hunting pressure or other ecological effects correlated with accessibility. However, given that species-specific responses to accessibility were much weaker than to forest degradation, the overall management of access to our study sites likely plays an important role of mitigating accessibility effects.

As noted above, in spite of the weak species-specific and community-wide effects of accessibility alone, high accessibility compounded effects of forest degradation on species average occupancy, defaunation, community evenness, and composition. This is likely due to species responses to elevation, which contributes to predicted species occupancy probabilities and the (weak) correlation of this variable with accessibility. In other words, areas that are both degraded by logging and highly accessible seem to be located to some degree in areas less “suitable” for several species according to their elevation. This pattern could arise in two (not mutually exclusive) ways. On one hand, regardless of anthropogenic impact, species can show preferences for certain elevations and terrain features (e.g., Kameníšťák et al., 2020; Sundqvist et al., 2013); in that case, part of the compounding effect of accessibility on average species occupancy, defaunation, and community evenness/composition may in fact be due to natural abiotic landscape features. On the other hand, species may retreat to higher elevations and more rugged terrain because these tend to be less impacted by humans (e.g., Nguyen et al., 2022); in that case, the abovementioned compounding effects of accessibility would be representative of anthropogenic effects, more broadly.

While accessibility primarily reflects human access, it encompasses activities beyond hunting, such as vehicle traffic (from logging trucks and road maintenance) and the presence of tourists in our study sites, which can also impact species fitness and behavior (Brown et al., 2012; Grubb et al., 2013; Ngoprasert et al., 2017; Whittington et al., 2019). It is crucial to recognize that our current approach to assessing accessibility serves as a conservative and limited proxy for hunting pressure, with limitations in its ability to fully capture the complexity of hunting dynamics. Although remoteness in our study incorporates small-scale terrain features, additional factors contributing to hunting pressure include land cover type, distance to settlements, human population density, and distribution and characteristics of targeted species. Despite the integration of such information in previous studies (Benítez-López et al., 2019; Deith & Brodie, 2020), they, too, serve as proxies for potential hunting rather than actual hunting. While methods have been developed to capture hunting activity over space and time (e.g., Dobbins et al., 2020), limitations persist, particularly concerning the diverse methods of hunting. Given the low hunting pressure in our study site and the data available, our utilization of accessibility represents the most suitable option available.

Despite the negative impacts of forest degradation and—to a lesser degree—accessibility reported here and in other studies, well-managed production forests are important for the conservation of tropical biodiversity (Berry et al., 2010; Gunarso et al., 2007). Though we did not explicitly compare communities among forest reserves, each with their respective logging histories, our results provide further support for the benefits of sustainable forest management practices for wildlife communities (e.g., Brodie, Giordano, & Ambu, 2015; Meijaard et al., 2005; Sollmann et al., 2017). Only a small fraction of forest pixels (<1% of pixels) within the boundaries of Deramakot forest reserve were considered disturbed forest

which is most likely a result of reduced impact logging methods, which serve to mitigate forest disturbances (Enters et al., 2002; Putz et al., 2001). Additionally, sustainable forestry certification schemes often include measures to manage hunting and encroachment, such as placing gates and checkpoints, and employing forest guards and patrols to protect wildlife. A well-managed production forest that combines low-impact harvesting with such protective measures can mitigate the impacts of both forest degradation and hunting. Management of tropical production forests is increasingly shifting towards more sustainable practices, which includes further improving harvest practices and road infrastructure (Dufлот et al., 2022; Ellis et al., 2019; Keller & Berry, 2007), better criteria for identifying high conservation value areas (Asner et al., 2018; Styring et al., 2022), and understanding economic benefits and trade-offs (Boltz et al., 2003; Chaudhary et al., 2016). Further evaluating and understanding the relationships between different aspects of disturbance resulting from forest management and species communities is essential to inform effective sustainability guidelines.

5 | CONCLUSION

We showed that species community occupancy and diversity generally declined along the two major gradients of anthropogenic impact in tropical forests: structural forest degradation and accessibility. Forest degradation was a much stronger driver of the occurrence of the terrestrial vertebrate community and individual species, and subsequently influenced shifts in community composition. Accessibility, which is interpreted as a proxy for hunting pressure, had a weaker compounding effect, potentially mitigated by the management of access to our study sites. Despite the negative impacts of forest disturbances, well-managed production forests are crucial the conservation of terrestrial wildlife communities.

AUTHOR CONTRIBUTIONS

Seth T. Wong was involved in methodology, formal analysis, investigation, data curation, writing—original draft, writing—review and editing, project administration, and funding acquisition. Azlan Mohamed was involved in conceptualization, methodology, investigation, data curation, project administration, and funding acquisition. John Mathai and Jürgen Niedballa were involved in investigation and resources. Johnny Kissing, Peter Lagan, and Alexander Y. L. Hastie were involved in resources. Andreas Wilting was involved in conceptualization, methodology, resources, supervision, and funding acquisition. Rahel Sollmann was involved in conceptualization, methodology, formal analysis, writing—review and editing, and supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing interests that could influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

Input data and model implementation code are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.q83bk3jqn>.

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