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EXAMINING DIVERSITY OF TERRESTRIAL MAMMAL COMMUNITIES ACROSS FOREST RESERVES IN SABAH, BORNEO

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Abstract: Tropical forest reserves have conservation value for terrestrial mammals and are threatened by anthropogenic pressures, especially conversion to other land-use types. To assess mammalian biodiversity of forest reserves in Sabah, Borneo, we used camera trapping data to estimate species richness, beta diversity, phylogenetic and functional diversity in nine forest reserves with different management classifications and backgrounds. Multiregional multispecies occupancy models (MSOM) were used to differentiate species occupancy in the reserves, and the estimates were transformed into biodiversity metrics. We found a significant difference in mammal composition within each forest reserve, with various functional and phylogenetic clustering or dispersion levels indicated by the standard effect of mean pairwise distances (SES MPD). Redundancy analysis (RDA) was used for both the observed data and MSOM estimates, modeling numerous environmental covariates and the forest reserves as random effects, finding that the forest reserve random effects were mainly responsible for structuring the mammal communities. Deramakot Forest Reserve was found to have overall high species richness, phylogenetic and functional diversity compared to other reserves. This reserve has been particularly successful at sustainable forest management and long-term forest certification, highlighting long-term conservation gains of sustainability programs for terrestrial mammalian diversity. Conversely, several reserves showed lower diversity scores overall than IUCN presumed extant species lists, highlighting local defaunation while still retaining high profile (critically endangered, endangered, and vulnerable) species. This study highlights the fragility of terrestrial mammal assemblages in forest reserves across the state and the need for mitigation, refaunation, and an integrated approach to forest management and biodiversity conservation to allow for comprehensive sustainable management programs to ensure long-term conservation.

Keywords: Biodiversity, Camera Trap, Community Ecology, Forest Management, Functional Diversity, Phylogenetic Diversity

Introduction

Tropical forests are vital areas of high biospheric diversity continually threatened by degradation and loss of natural forests through logging activities and forest conversions to other land-use types, which imperil wildlife and their habitats (Gibson et al. 2011; Laurance et al. 2012; Burivalova et al. 2014; Brodie et al. 2015; Jati et al. 2018). Integrating production forests that repeatedly harvest timber into conservation priorities in tropical areas is challenging, especially in many parts of Borneo. The Bornean landscape has been and continues to be transformed mainly by repeated cycles of timber harvesting resulting in degraded forests or further converting forests to agricultural monocultures such as oil palm plantations (Elaeis guineensis) (Wearn et al. 2019).

The current and legacy anthropogenic pressure that has dramatically altered the state of the landscape in Sabah, Borneo, continues to have impacts widely throughout the forest reserves (Reynolds et al. 2011; Bryan et al. 2013). Bryan et al. (2013) showed that in 2009, the government had officially protected only 8% of intact forest, and established forest management plans resulted in 80% of Sabah undergoing extensive industrial deforestation, with 38% of forest cover remaining relatively intact, 39% degraded and 23% severely degraded (Bryan et al. 2013). Many large forest reserves in Sabah have been subject to conversion to agricultural plantations, or repeated rotational commercial logging (Sodhi et al. 2010; Reynolds et al. 2011), although reserves are currently phasing out these methods to implement Reduced-Impact logging programs (Sodhi et al. 2010; Reynolds et al. 2011). Even if forest reserves maintain production status and selective logging, protecting tropical forests from further conversion to agricultural land use or forest plantations can protect unique meta-community processes and maintain ecosystem functions and services (Wilcove et al. 2013; Edwards et al. 2014).

Conservation priorities for terrestrial mammals are most commonly measured by International Union for Conservation of Nature (IUCN) status or other state-level protected species status or through species richness estimates, although assessing species assemblages according to phylogenetic and functional traits diversity have become critical and well supported (Faith 1992; Redding and Mooers 2006; Isaac et al. 2007; Hidasi-Neto et al. 2015). Approximately 4.6% of the world's land surface contains taxonomic, phylogenetic, and functional diversity components separately relevant to conservation (Brum et al. 2017). Borneo has overlapping taxonomic, phylogenetic, and functional priorities; therefore, examining only one dimension would undermine conservation efforts (Brum et al. 2017). Recent studies have shown that land-use changes threaten the preservation of phylogenetic and functional ecosystem diversity (Graham et al. 2019). Efforts to understand global diversity have shown that Borneo is a global hotspot for losses in phylogenetic diversity through species extinctions due to land-use change (Chaudhary et al. 2018). Few studies have attempted to examine forest management or land-use impacts on functional or phylogenetic diversity since emerging analytical methods to quantify this appropriately for multiple taxa are newly developed and implemented for mammal communities (Frishkoff et al. 2017; Frank et al. 2017; Cadotte and Tucker 2018).

Multiple frameworks have been developed to explore why specific communities assemble across space, for example, along gradients of land use (Goijman et al. 2015; Wearn et al. 2019) or anthropogenic disturbances (Easter et al. 2019). Patterns in global biodiversity for functional groups and trait diversity indices have shown regional differences in communities' structure and responses to environmental gradients (Tenan et al. 2017; Wearn et al. 2017; Rovero et al. 2020). Previous research in a widely distributed Indonesian Borneo dataset has shown that anthropogenic impacts from logging and hunting have negatively affected mammalian community diversity (Brodie et al. 2015; Cheyne et al. 2016).

Surveys of mammal species richness are critical to establishing baseline estimates that identify priority-protected areas of high species richness value and represent essential functional and phylogenetic diversity (Faith 1992; Chapman et al. 2018; Cadotte and Tucker 2018). In this study, a multi-region multi-species occupancy modeling (MSOM) approach was used to estimate the species richness of mammal communities in several forest reserves in the state of Sabah and quantify the differences in diversity metrics. How well forest reserves in Sabah, a Malaysian state in Borneo, represent distinct species richness, phylogenetic, and functional diversity for terrestrial mammals is currently unknown. We also sought to understand further the influence of the landscape's environmental variability on the mammal community. Recently, there have been many advances to quantify various diversity metrics using MSOM estimates (Royle and Kery 2015) to derive species richness, beta diversity, functional and phylogenetic diversity (Iknayan et al. 2014; Jarzyna and Jetz 2016). Assemblages between regions can differ in phylogenetic and functional traits representation, resulting in clustering or dispersion. The study aimed to demonstrate the methodological approaches in visualizing and representing phylogenetic and functional diversity for terrestrial mammal communities to identify conservation priorities within production forests crucial for sustainable and conservation-related management.

Methods

Study Area

This research was conducted in secondary tropical lowland forests characterized by economically valuable trees from the Dipterocarpaceae family across the Malaysian state of Sabah in the north of Borneo (5.9788° N, 116.0753° E) (Fig 1). Sabah has a wet season (May-December) and a dry season (January to May), although rainfall is variable and unpredictable throughout the year. We explored patterns of species diversity in secondary tropical forests in nine regions of Sabah, namely: Paitan, Trusan Sugut, and Sugut (northeast), Sipitang (west coast), Tangkulap and Deramakot (central), Silabukan (east), Sapulut, Maliau Basin Conservation Area, and Madai-Baturong (south-central).

Figure 1. Map of the Malaysian state of Sabah on Borneo and the nine forest reserves, including camera trap stations (yellow dots).

Sabah Forestry Department maintains the forest reserve classifications. This study included forest reserves in the following categories: Class I, protection forest reserves (7% of total forest reserves), Class II, commercial forest reserves (76% of forest reserves), and Class VI, virgin jungle reserves meant for biodiversity research and conservation (2.7% of total forest reserves) (Table 1).

Table 1. Forest reserve names, classes for each forest reserve in this study, and a brief description of the reserves' history maintained by the Sabah Forestry Department.

Forest Reserve or Conservation Area	Size (km^2)	Class	Description
Deramakot Forest Reserve	551	II	Certified by Forest Stewardship Council in 1997 and currently in its fifth certification period. The forest had been logged at least once with subsequent silvicultural treatment and currently has a mix of production and conservation areas.
Madai Baturong Forest Reserve	58	VI	Virgin Jungle Reserve. First gazetted in 1932, with parts of the area degazetted in 1960, and then in 1977, both the reserve and the extension were partially degazetted, still retaining old-grown forest in the protected forest.
Maliau Basin Conservation Area	467	I	Designated a conservation area in 1981 in a matrix of production forest, formerly a timber concession of Yayasan Sabah, and
Sapulut Forest Reserve	2319	II	The management plan was established in 1997 for this production forest managed by Sapulut Forest Development Sdn Bhd (SFD) and certified by the Malaysian Timber Certification Scheme in 2018 and 2020.

Silabukan Protection Forest Reserve	113	I	First, it was gazetted in 1957, then partially degazetted four times (1963, 1966, 1981, and 1982), and regazetted in 1992.
Sipitang Forest Reserve	2505	II	Commercial logging by Sabah Forest Industries (SFI) was established in 1959. Part of the total area is classified as protected forest class I as of 1984.
Tangkulap Forest Reserve	273	I	A large portion of the forest area is heavily degraded due to excessive logging over the past 20 years, was certified by Forest Stewardship Council as "Well Managed" in June 2011
Sugut Conservation Area	87	I	Previously heavily logged for decades beginning in 1960, then stopping in 1996.
Paitan Forest Reserve	418	I	Predominantly commercial forests reclassified as Class I in 2020 and managed by Asian Forestry Company/Forest Solutions Malaysia Bhd and EcoPlantations Bhd.

Camera trap surveys and preparation of event data

Camera traps are a proven method for conducting mammal inventories (Tobler et al. 2008) and estimating species richness, occurrence, and abundance (O'Connell et al. 2011). Camera trapping across the state of Sabah was conducted to identify the elusive target species Bornean banteng (*Bos javanicus lowi* or *lowii*) for species conservation (Gardner et al. 2018). A total of 218 camera stations were deployed, with a mean number of 24 camera stations placed at each forest reserve (Table 2). Researchers placed cameras at intervals through forest reserves between June 2013 and Sept 2016. A pair of opposing cameras were placed at each station at approximately 50cm high and secured to trees approximately 5-8m apart. Cameras were enclosed in security cases that were padlocked and bolted to prevent theft. Vegetation was cleared at ground level to prevent camera obstruction. Stations were spaced at a mean of 998m apart (range: 87m -3642m). Cameras that were close together were paired on and off an animal trail to capture the range of diversity that may not be using the trails. The camera trap models used included Reconyx PC800 and PC650 Professional and HyperFire™ HC500 (Reconyx Inc., WI, USA). Cameras ran for a minimum of 33 days to a maximum of 422 days, with a mean of 136 days. Camera days represented the station with both cameras in tandem, not individual cameras. Cameras were checked approximately every 30 days when vegetation was cleared from the station, SD cards were retrieved and replaced, batteries were replaced, and silica gel desiccant was replaced. We defined camera trap events' independence by only using the first photographic capture of a given species at each station within 24 hours.

Table 2. Camera trap information for each forest reserve. The total number of camera stations, total camera station days, mean camera station days, minimum and maximum camera station days are reported for each forest reserve's camera trap setup. The start date and end date of camera trap deployment are also reported.

	Total stations	**Total station days**	**Mean station days**	**Min station days**	**Max station days**	**Start date**	**End date**
Deramakot	24	2849	119	66	188	03-2015	11-2015
Maliau Basin	26	5621	216	61	374	06-2013	05-2014
Madai Baturong	11	1581	144	58	422	10-2014	03-2015
Paitan	29	3257	112	107	116	04-2016	08-2016
Trusan Sugut	29	3197	110	90	151	02-2016	07-2016
Silabukan	18	3030	168	103	212	08-2014	03-2015
Sapulut	24	2793	116	33	147	11-2013	04-2014
Sipitang	27	3825	142	60	190	09-2013	03-2014
Tangkulap	30	2899	97	35	118	07-2015	11-2015

Environmental Covariates

This study hypothesized that several environmental covariates would influence the mammalian species richness. Covariates were derived from raster data derived from Google Earth Engine. Data layers included elevation, slope, and aspect generated from (90m, SRTM), mean temperature (900m, WorldClim1), forest canopy height (30m GLAD), woody biomass (500m, WHRC), canopy cover (30m, GLCF), forest loss, and forest gain generated from (30m, Hansen). Open street map shapefile data was also used to create a raster of the Euclidean distances to roads, waterways and streams, trails, and villages. Data were extracted at 20m buffers and averaged around each camera trap point. Covariate data were centered and scaled prior to analysis.

Data Analysis

Multi-species Occupancy Models

Even systematic surveys vary according to study design and equipment, which are rarely capable of detecting all mammal species present at the site resulting in underestimating actual species abundances or falsely assuming a species is absent (MacKenzie et al. 2002). Species detectability with camera traps can differ due to equipment technology and biological factors like a species' body size, seasonal abundance, species rarity, interspecific effects of a competitor or predator (O'Connell et al. 2011), and environmental factors such as humidity and ambient temperature. Factors that affect a species' detectability can be accounted for using occupancy modeling, where samples of detection and non-detection data simulate a presence-absence framework, assuming some species are not genuinely absent and only imperfectly detected. The MSOM extends the single-species approach to multiple species to estimate species richness and community structure when accounting for imperfect detection (Dorazio et al. 2006). A species' imperfect detection causes problems as an undetected species may not be random but could be either locally distinct or redundant in fulfilling a unique position in the phylogeny or comprising a unique combination of functional traits (Jarzyna and Jetz 2016).

We used Bayesian hierarchical MSOM to estimate the community-level richness of terrestrial mammals, ranging from medium to large in body size, between different forest reserves. The models were parameterized using the forest reserve as a random block effect to make inferences on the entire collection of cameras at once to assess differences between forest reserves (Sutherland et al. 2016; Damschen et al. 2019; Stanton Jr. et al. 2020). Sutherland et al. (2016) developed a multi-region community model (MRCM) to estimate multi-species occupancy with covariates across geographically distinct regions using random block effects to improve statistical performance compared to single-region models (Sutherland et al. 2016). This model has been extended to include partitions of trophic strata (Tenan et al. 2017) and applied to forest mammal communities across protected areas monitored annually as part of Tropical Ecology Assessment and Monitoring TEAM network long-term camera trapping sites (Rovero et al. 2020). The modeled estimates that incorporate imperfect detection are essential to aid in wildlife management, identify the drivers of population changes, and mitigate conservation.

Observed data consisted of a site (*i*) x sample (*j*) matrix of presence/absence data for each species (*k*). Where y_{ijk} indicates a species (*k*,…, 40 species) was detected (y_{ijk}=1) or not detected (y_{ijk}=0), at site *i* (1,…,218 sites) during survey *j* (1,….,509 surveys). We describe the observation process (detection) (Eq 1).

$$y_{ijk}|z_{ik} \sim Bernoulli(z_{ik}\ x\ p_{ijk}) \tag{1}$$

Detectability is a product of the z-matrix (z_{ik}), or site x species matrix, for species *k* at site i, and the detection probability p_{ijk}, which is the probability of detecting species *k* at site *i* during survey *j*. Deriving the z-matrix is dependent on the ecological processes modeled by the probability of occupancy (ψ_{ik}) such as the true occurrence (Eq 2).

$$\mathrm{z_{ik}} \sim \mathrm{Bernoulli}(\psi_{\mathrm{ik}}). \tag{2}$$

The model of species heterogeneity for the ecological process (occupancy) (Eq 3 and 4):

$$\mathrm{logit}(\psi_{\mathrm{ik}}) = \beta[\text{forest reserve}(\mathrm{i}), \mathrm{k}]. \tag{3}$$

$$\mathrm{logit}(\mathrm{p_{ijk}}) = \alpha_{\mathrm{k}} \tag{4}$$

Hyperparameters were normally distributed $\beta_{rk} \sim Normal(\mu_{\beta_r}, \tau_{\beta_r})$, where μ_{β_r} and τ_{β_r} refer to the community-level mean and precision for each land use (*r*) , and $\alpha_k \sim Normal(\mu_a, \tau_\alpha)$ and μ_α and τ_α community-level mean and precision for detectability. Vague priors were used μ normally distributed, (μ=0, τ=0.6), σ uniformly distributed (0,10), and τ being power transformed (σ, -2).

Markov chains of 150,000 iterations were run, discarding 5000 as burn-in, with a thinning rate of 10. Model convergence was assessed by Gelman-Rubin R-hat values <1.1. We used the R package jagsUI (Kellner 2019) for modeling.

Diversity Indices

We used the mean posterior distribution of the site x species matrix, z_{ik} to reveal the presence-absence of the estimates of the MSOM for each species at each site. The binary z-matrix was then transformed into independent biodiversity metrics for community-level species richness: alpha diversity and Jaccard dissimilarity (beta diversity). The z-matrix also derived metrics representing phylogenetic diversity and functional diversity: standard effect sizes mean pairwise distances (SES MPD).

Beta diversity

Beta diversity components were derived using the Jaccard pairwise dissimilarity and reported the mean and 95% CI. Jaccard species richness is the general understanding of the beta diversity or degree of ecological uniqueness between community composition at stations within each forest reserve (Eq 5).

$$J_{r,s} = \frac{\sum z_{r,s}}{\sum z_r + \sum z_s - \sum z_{r,s}} \tag{5}$$

$$D_{r,s} = 1 - J_{r,s} \tag{6}$$

Where Z is the number of species represented between site r and site s, beta diversity examines overall beta diversity comprised of both turnover and nestedness across space and time, examining the variation in the mammal community's structure or level of biotic homogenization (Eq 6) (Anderson et al. 2011). Beta diversity can indicate areas of distinction and high value, or areas that are very degraded, species-poor, and still differ significantly from other areas or sites surveyed (Santos et al. 2021).

Phylogenetic and Functional Traits Structure

The phylogenetic tree was constructed by classifying all species' taxonomy using species information from the National Center for Biodiversity Information (NCBI). The taxonomies were linked to a Taxonomic Serial Number (TST) used to generate the hierarchical phylogenies that are ultrametric trees indicating times of divergence (in millions of years) represented by the branch lengths. Finally, the classification was converted to a phylogenetic distance matrix using the cophenetic pairwise distances between the pairs of tips from a phylogenetic tree using branch lengths. The phylogenies were generated using the taxize package in program R (Chamberlain and Szocs 2013).

Additionally, we report and discuss the top species on the evolutionary distinctive globally endangered (EDGE) list of species priorities (Isaac et al. 2007; Safi et al. 2013). The EDGE metric ranks species into an evolutionary distinctiveness (ED) metric that uses the phylogeny branch lengths in combination with IUCN status, where species with longer branch lengths are ranked higher because they have no close relatives on the phylogenetic tree.

Functional diversity describes how the representation of species traits within a community differentially affects the ecosystem's ability to function (Petchey and Gaston 2006). Trait-based distance matrices are calculated as the distance between species according to various traits, such as diet, daily activity, and body mass (g). In this study, 14 variables were used to construct our trait matrix. Functional diversity was derived from trait information from the EltonTraits 1.0 database (Wilman et al. 2014). The Elton Traits variables for diet included a percentage of each mammal's diet and were divided into the appropriate categories: Insectivores (invertebrates), Carnivores ("vend" (mammals, birds), "vect" (reptiles, snakes, amphibians, salamanders), fish, "vunk" (vertebrates general), scavenger (carcasses, carrion)), Frugivores: (fruit (fruit, drupe)), Herbivores (seed (seed, maize, nuts, grains), or plants). Activity patterns included binary categories for diurnal, crepuscular, and nocturnal, with many species being included in multiple categories based on the literature. The final variable included is biomass (g), or the rough average weight of the mammal at full size. All continuous covariates were centered and scaled before constructing the distance matrix.

To assess the potential assembly mechanisms driving mammal communities in each forest reserve, we looked at the standard effect sizes of the mean pairwise distances. Phylogenetic and functional distance matrices were analyzed using standardized effect size of mean pairwise distance (SES MPD) (Weiher and Keddy 1995; Webb et al. 2008). The traits or phylogenies from a randomly generated community configuration from simulations were used as a null model. These random communities were obtained from 1,000 randomly generated communities drawn to maintain sample species richness, not abundance weighted, from the species pool of Bornean taxa. To calculate the standard effect sizes (SES), the expected differences were calculated by: (observed – expected) / standard deviation.   Positive values for SES MPD ($P < 0.05$) indicate dispersion, whereas negative values for SES MPD ($P < 0.05$) indicate clustering, and are also statistically significant when compared to randomly generated communities. If the values are close to 0, then the SES values indicate that deterministic mechanisms do not structure the communities. The functional and phylogenetic procedures were performed in R packages vegan, Picante, and FD (Laliberté et al. 2014; Oksanen et al. 2019; Kembel et al. 2020) in program R version 3.6.1.

Diversity metrics were derived from the mean and 95% CI of all the posterior sample's estimates and visualized using plots. Estimates of diversity were derived using the z-matrix (site x species occupancy matrix), and then site-specific subsets were extracted to deduce forest reserve level value. For example, species were summed across stations and grouped within the forest reserve when calculating the alpha diversity for each of the 58,000 posterior sample's z-matrices. We also tested the multivariate differences among forest reserves using the permutational MANOVA using the vegan package.

Redundancy Analysis

Redundancy analysis was conducted to examine multi-species and environment relationships 1) observed raw data and 2) mean posterior estimates from the z-matrix from the multi-regional MSOM with FMU block effects. Redundancy Analysis (RDA) uses multiple regression on multivariate biodiversity data response to covariates, and uses a principal coordinates analysis (PCoA) on the fitted values. These analyses can determine which environmental covariates are significant for the mammal community, and can include random effects for block the different FMU's.

$$y = \beta_{1-n} + \beta[\text{forest reserve}]. \tag{7}$$

The model assumes linear dependence of the response and predictor variables. A global test of the RDA was run for 1000 permutations to determine model significance (α=0.05). Then, stepwise selection was used to identify the explanatory variables with the highest R^2 for subsequent model refitting. The vegan package in program R was used to generate RDA results.

Results

A total of 8181 survey days were recorded across 218 sites in nine forest reserves (Table 3). There were 29,052 camera trap days with an average of 3,228 and a median of 3,030 camera trap days. There was a median capture of 20 mammals per forest reserve and 1082 detections per forest reserve.

Table 3. Total mammal detections, i.e., independent camera trap records and number of mammals detected at each forest reserve. IUCN status for critically endangered (CR), endangered (EN) and vulnerable (VU) species are also tabulated. Number of species in orders Artiodactyla, Carnivora, Primates, and Rodentia at each forest reserve are reported.

Site	**Detections**	**Mammals**	**CR**	**EN**	**VU**	**Artiodactyla**	**Carnivora**	**Primates**	**Rodentia**
Deramakot	1704	24	1	2	8	5	9	4	3
Madai Baturong	699	21	-	-	9	3	8	4	3
Maliau Basin	4061	22	-	2	7	4	12	3	3
Paitan	1042	20	1	-	7	5	8	3	2
Sapulut	688	13	1	-	5	5	3	2	1
Silabukan	1559	22	1	1	8	4	7	6	2
Sipitang	1807	20	1	2	6	4	7	3	2
Tangkulap	1082	19	1	1	5	5	3	3	3
Trusan Sugut	783	18	1	2	7	5	7	4	1

The camera trap surveys were mainly completed according to species accumulation curves, which showed a leveling curve for nearly all natural reserves, except Madai Baturong (Fig 2). Surveys in Madai Baturong require more camera days or station locations, having not reached an asymptote characteristic of complete surveys.

Fig 2. The species accumulation curve for the camera trap data and 95% CI (grey).

A total of 40 species of terrestrial vertebrates were recorded (Table 4). None of the forest reserves detected the maximum of 40 species during the entire study, and the mammalian community composition varied dramatically between the forest reserves (Fig. 3). The species' diets varied and often overlapped since we had used the percentage of each of the diet categories and the species often had a mixed diet: 20 were partially insectivores, 14 partially carnivores, 25 partially frugivores, and 23 were partially herbivores. For this analysis, all species detected during camera trapping surveys (n =40) were included. The complete list includes species detected in some forest areas but not others, essentially estimating species-specific detectability from all study sites.

Table 4. Summary of animals photographed within Sabah's forest reserves, Borneo as part of Bornean banteng-related camera trap surveys. #FR, number of forest reserves, #E number of independent photographs. IUCN, Red List of globally threatened species status, CR=critically endangered, EN=endangered, VU=vulnerable, NT=near threatened LC= least concern. Percentage of diet (Insectivore, Carnivore, Frugivore, Herbivore) are listed.

Order	**Family**	**Species**	**English Name**	**IUCN**	**# FR**	**#E**	**Insectivore**	**Carnivore**	**Frugivore**	**Herbivore**
Artiodactyla	Bovidae	*Bos javanicus*	Bornean Banteng	EN	7	329	0	0	0	100
	Cervidae	*Muntiacus atherodes*	Bornean Yellow Muntjac	NT	6	215	0	0	20	80
		Muntiacus muntjak	Southern Red Muntjac	LC	9	884	0	0	30	70
		Rusa unicolor	Sambar	VU	9	2534	0	0	10	90
	Suidae	*Sus barbatus*	Bearded Pig	VU	9	3746	10	10	0	70
	Tragulidae	*Tragulus napu*	Greater Oriental Mouse Deer	LC	9	698	0	0	20	80
Carnivora	Canidae	*Canis familiaris*	Dog	LC	4	22	0	100	0	0
	Felidae	*Catopuma badia*	Borneo Bay Cat	EN	2	2	0	100	0	0
		Neofelis diardi	Sunda Clouded Leopard	VU	6	15	0	100	0	0
		Pardofelis marmorata	Marbled Cat	NT	1	2	0	100	0	0
		Prionailurus bengalensis	Leopard Cat	LC	4	16	0	100	0	0
	Herpestidae	*Herpestes brachyurus*	Short-tailed Mongoose	NT	4	15	30	60	10	0
		Herpestes semitorquatus	Collared Mongoose	NT	1	1	30	60	10	0
	Mephitidae	*Mydaus javanensis*	Sunda Stink Badger	LC	5	12	80	0	0	20
	Mustelidae	*Lutrogale perspicillata*	Smooth-coated Otter	VU	1	1	30	70	0	0
		Martes flavigula	Yellow-throated Marten	LC	7	10	10	60	10	0
		Mustela nudipes	Malay Weasel	LC	1	1	0	100	0	0
	Ursidae	*Helarctos malayanus*	Sun Bear	VU	9	101	50	20	20	10
	Viverridae	*Arctictis binturong*	Binturong	VU	3	6	0	50	30	20
		Hemigalus derbyanus	Banded Palm Civet	NT	6	26	100	0	0	0
		Paguma larvata	Masked Palm Civet	LC	1	1	20	60	20	0

		Paradoxurus hermaphroditus	Common Palm Civet	LC	4	15	20	0	20	20
		Viverra tangalunga	Malay Civet	LC	6	42	10	60	10	10
Eulipotyphla	Erinaceidae	*Echinosorex gymnura*	Moonrat	LC	2	5	50	50	0	0
Pholidota	Manidae	*Manis javanica*	Sunda Pangolin	CR	1	1	100	0	0	0
Primates	Cercopithecidae	*Macaca fascicularis*	Long-tailed Macaque	VU	8	168	50	0	40	10
		Macaca nemestrina	Pig-tailed Macaque	VU	9	1537	10	0	70	20
		Nasalis larvatus	Proboscis Monkey	EN	1	13	0	0	20	80
		Presbytis hosei	Hose's Langur	VU	1	1	0	0	40	60
		Presbytis rubicunda	Red Langur	VU	4	6	0	0	40	60
		Trachypithecus cristatus	Silvered Langur	VU	3	23	0	0	30	70
	Hominidae	*Pongo pygmaeus*	Bornean Orangutan	CR	4	81	10	0	80	0
	Hylobatidae	*Hylobates muelleri*	Bornean Gibbon	EN	1	1	10	0	70	20
Proboscidea	Elephantidae	*Elephas maximus borneensis*	Bornean Elephant	EN	6	154	0	0	0	100
Rodentia	Hystricidae	*Hystrix brachyura*	Malayan Porcupine	LC	8	197	0	0	20	80
		Hystrix crassispinis	Thick-spined Porcupine	LC	6	39	0	0	20	80
		Trichys fasciculata	Long-tailed Porcupine	LC	5	15	0	0	30	70
	Sciuridae	*Dremomys everetti*	Mt. Ground Squirrel	LC	1	1	20	0	30	50
		Ratufa affinis	Pale Giant Squirrel	NT	1	1	10	0	30	50
Scandentia	Tupaiidae	*Tupaia glis*	Common Treeshrew	LC	1	3	90	0	0	10

Figure 3. Phylogenetic tree, species list, and species presences in each of the nine forest reserves.

IUCN range maps show the extant presence of 20 carnivores (compared to 16 found in this study) and 10 primates (compared to 8 found in this study). Seven mammals were thought to be within species range and extant according to IUCN, although not captured during these surveys (Table 5). Three endangered species were not detected during surveys, although thought to be extant, within range for our surveys, and simultaneously arboreal and challenging to detect with the camera trapping methodologies.

Table 5. Summary of mammals not detected within the nine forest reserves during the camera trap surveys. Comp is the year compiled by IUCN. IUCN Red List of globally threatened species status. EN=endangered, VU=vulnerable, NT=near threatened, LC=least concern. Whether the mammal is considered arboreal (Y=Yes, N=No, P=Partially).

Order	**Family**	**Name**	**English Name**	**IUCN**	**Arboreal**
Carnivora	Prionodontidae	*Prionodon linsang*	Banded Linsang	LC	P
	Viverridae	*Cynogale bennettii*	Otter Civet	EN	Y
		Diplogale hosei	Hose's civet	VU	N
		Arctogalidia trivirgata	Small-toothed Palm Civet	LC	Y
Dermoptera	Cynocephalidae	*Galeopterus variegatus*	Sunda Flying Lemur	LC	Y
Primates	Lorisidae	*Nycticebus menagensis*	Philippine Slow Loris	VU	Y
	Tarsiidae	*Cephalopachus bancanus*	Horsfield's Tarsier	VU	Y

Multi-species occupancy results

K-fold cross-validation resulted in model evaluation metrics (Deviance=28678 AUC=0.92 Brier's log=3288), indicating the model fit well. Species richness estimates from MSOM were calculated for each camera station, averaged across each forest reserve, and then compared to the observed dataset (Figure 4).

Figure 4. Total species richness per forest reserve a) observed species richness b) model estimated mean species richness with 95% CI.

After accounting for imperfect detection, the models predicted much higher species richness estimates across trophic levels than the original data (Figure 5).

Figure 5. Total species richness (alpha diversity) of each trophic level per protected area. a) observed species richness b) estimated mean species richness.

These species richness estimates indicated that Deramakot, Tangkulap, and Silabukan had much higher species richness overall at each camera station when compared to other forest reserves (Figure 6). Conversely, Sapulut, Paitan, and Trusan Sugut had lower species richness levels at each camera station and were lower overall across trophic levels.

Figure 6. Mean species richness per camera station. a) observed species richness b) estimated mean species richness with 95% CI.

Beta diversity

Observed and estimated beta diversity estimates (95% CI) were also compared (Figure 7). The comparisons revealed that estimates for the dissimilarity between sites among reserves were very different and revealed distinct forest reserves in terms of species composition. Trusan Sugut, Paitan, Silabukan, and Deramakot Forest Reserves observed the largest dissimilarity scores metrics. These results indicate that the beta diversity of Madai Baturong and Silabukan was generally lower than in other sites. These lower beta diversity metrics indicate less difference between the species pool between the camera sites.

Figure 7. Jaccard dissimilarity for each forest reserve a) observed b) estimated with 95% CI.

Functional and phylogenetic structure

The results indicated that the mammal assemblage's functional diversity (SES MPD) varies between forest reserves (Figure 8). Madai Baturong and Deramakot had the most phylogenetically "even" or diverse assemblage indicating the most diverse species' traits (biomass, diet, and activity patterns). Other sites showed negative values indicating a more clustered representation of traits.

Figure 8. Standard effect sizes of trait diversity (standard effect mean pairwise distances) a) observed b) estimated (95% CI).

In examining the SES MPD of the phylogenetic distance, results showed Sipitang retained the highest metrics and that several forest reserves had positive values (Deramakot, Maliau Basin, and Tangkulap), indicating that there was phylogenetic evenness (Figure 9). The species within the community are more distantly related than expected by chance. Other sites showed negative values (Madai Baturong, Sapulut, and Trusan Sugut), indicating that phylogenetic clustering was occurring and that the surveyed community is more closely related than expected.

Figure 9. Standard effect sizes of phylogenetic evenness (mean pairwise distances) a) observed b) estimated (95% CI).

These results indicate that phylogenetic diversity did indicate functional diversity in some cases. Other sites showed negative values (Sapulut), indicating a clustered evolutionary phylogenetic distance and a clustered representation of traits. Other sites hovered around a mean of zero, indicating neither substantial diversity nor clustering. The MANOVA method compares the variance in beta diversity and found a significant difference in these metrics between all forest reserves for both observed and estimated datasets ($p<0.001$, $R^2=0.16$). These results indicate that each forest reserve comprises a relatively unique assemblage compared to the others, and none are redundant.

In addition to the phylogenetic diversity scores generated by SES MPD, we also wanted to highlight mammals in the area that were particularly important according to the evolutionary distinctiveness (ED) metric, a separate score for phylogenetic diversity that weighs species with very distinct phylogenetic branching with their endangered status, although the current scores were incomplete for our entire species list (Isaac et al. 2007). The highest ED scores were found for Bornean elephant (*Elephas maximus borneensis*) (ED = 39.66), Sunda pangolin (*Manis javanica*) (ED = 20.68), sun bear (*Helarctos malayanus*) (ED = 16.65), Bornean orangutan (*Pongo pygmaeus*) (ED = 13.67), and Binturong (*Arctictis binturong*) (ED=11.7114). These species showed increased vulnerability as their phylogenetic distinctiveness intensified their current conservation status.

Redundancy Analysis

The observed and estimated site x species matrices were Hellinger transformed, and an initial model was run with all available covariates. Using a combination of forward and backward selection, then several covariates were selected based on significance (Table 6)

Table 6. Final variables used after performing a stepwise selection of all variables.

Model	Final Covariates
Model 1 Raw camera trap data	Mean Temperature, Hansen Canopy Cover, Distance to Water , Hansen Forest Loss , Woody Biomass, Forest Canopy Height , [Block effect for FMU]

Model 2 MSOM mean posterior	Mean Temperature, Woody Biomass , Distance to Water , Distance to Villages , Canopy Height, Hansen Forest Loss , Hansen Forest Gain , Distance to Trails [Block effect for FMU]

Results of the redundancy reveal the variation in the data is mainly explained by the conditional block effects of the FMU, showing that the block effects account for 18% of the variation in the observed camera trap data, and 38% of the variation in the modeled dataset (Table 7). The environmental variables account for 4% of the variation in the data after accounting for the block effects, revealing no significant trends in this multivariate framework that the environmental variation on the landscape is predicting the differences of the mammal community.

Table. Redundancy analysis reveals the proportions of conditional, constrained, and unconstrained variation in the observed data.

Observed Camera Trap Data			**MSOM Mean Posterior Estimates**		
	Inertia	Proportion		Inertia	Proportion
Total	0.47	1.00	Total	0.25	1.00
Conditional	0.08	0.18	Conditional	0.09	0.38
Constrained	0.02	0.04	Constrained	0.01	0.04
Unconstrained	0.36	0.77	Unconstrained	0.13	0.56

Discussion

This study provides valuable information regarding the diversity found regionally in Sabah between forest reserves and the conservation value of phylogenetic and functional trait-based assemblage differences in the broader scheme of conservation perspectives. Phylogenetic and functional trait distances allowed for a more in-depth analysis concurrent to the raw alpha and beta diversity metrics (Swenson 2011), which can be discussed in sustainable forest management and landscape conservation. We confirmed that several forest reserves were phylogenetically and functionally clustered or dispersed, more so than would be expected by random chance. This study focused on a multi-regional covariate "block" on the forest reserves, which was the main predictive factor for the species richness within each reserve, as shown by the RDA. In this study, we determined that most of the variation in these data can be explained by the conditional block effects of the forest reserves and not by the environmental variation of the landscape represented by multiple covariates.

Patterns of phylogenetic diversity indicate whether the species in one area are more closely related than expected by chance. Previous phylogenetic diversity studies have been instrumental in understanding how communities in modified areas can retain species diversity of "phylogenetic relatedness" (Frank et al. 2017). For example, if two areas have equal numbers of species, an area with lower phylogenetic diversity could have recent speciation events, where the species are naturally more related to one another or can indicate faster local extinction rates.

Research at macroecological scales suggests that the mechanism for diversification in the tropics has resulted in the baseline historical composition of species having similar ecological niches and functional traits, with slow trait evolution resulting in closely related species with shared functional similarities and redundancy without simultaneously experiencing high local species extinction (Safi et al. 2011). Functional diversity has been shown to decrease when confronted with significant anthropogenic changes such as habitat loss, patch isolation, and fragmentation, which also can lead to the loss of essential ecological functions and ecosystem services (Magioli et al. 2021). Research has shown that certain traits are more prone to multiple pathways to local extinction, such as body mass and activity pattern (Davidson et al. 2009), and that losing large sized-herbivores and apex predators then results in cascading changes to the ecosystem, impacting downstream trophic levels and processes (Magioli et al. 2021). Similar to this study, functional trait diversity studies have sought to estimate taxa differences in traits, such as habitat preferences or diet (Pacifici et al. 2014), habitat "generalist" or "specialist" species (Frishkoff and Karp 2019), habitat or climatic niches (Frishkoff et al. 2016) to classify species into functional roles they may fulfill within the ecosystem. Functional traits clustering was standard or neutral across all reserves, except Deramakot and Madai Baturong, the only two sites with an even or "diverse" distribution of functional traits across biomass, diet, and activity patterns (i.e., diurnal, nocturnal, crepuscular).

One sustainably managed commercial forest reserve, Deramakot, showed both phylogenetic evenness and functional trait evenness, indicating a diverse range of captures across phylogenetic and functional trait space (diet, body mass, activity pattern). This particular forest reserve was logged between 1955 and 1989, then subsequently changed to sustainable forest management practices, and since 1997 has been assessed and certified by the Malaysian Forest Stewardship council as a well-managed forest (Mannan et al. 2002) and considered a model forest management system (Sabah Forestry Department 2020a). While the results from this study indicate the success of this sustainable forest management program for conserving a rich array of phylogenetic and functional mammal diversity, factors like sustainable management programs and resultant environmental quality are likely both contribute to the retention and community structure in these areas.

Another example, we find an exceptionally high estimated functional diversity and species richness in Madai Baturong. This forest reserve is a class VI virgin forest, with some of the remaining old-growth forests, and the only forest reserve in this classification in our study. This forest reserve had high diversity results even though it had the lowest number of cameras (n=10) deployed, the lowest number of camera trap days 1581, and the smallest area (58 km^2)

across the study. The cameras from this forest reserve showed the highest mean number of species per station. Despite the limited camera effort, the results showed a far superior functional diversity than other forest reserves, indicating an assemblage of species performing diverse roles to maintain the ecosystem. The beta diversity metric was the lowest, indicating a somewhat encompassing species similarity to other forest reserves. The species accumulation curve indicated increased survey stations or camera trap days could reach a survey completion asymptote with even more species.

As Sabah faces increasing pressure to expand road networks and economic developments (Sloan et al. 2019), understanding conservation priorities from an integrated set of diversity metrics becomes essential. As forest reserves are becoming more vulnerable to habitat and land-use changes, understanding what kind of diversity persists can be critical to the ecological valuation of the landscape and systematic conservation efforts to prioritize essential sites for conservation and restoration activities (Cimon-Morin et al. 2013). Furthermore, the potential for forest reserves to undergo defaunation in the face of the increased trajectory of development, climate change, overexploitation, invasive species, and numerous other drivers of defaunation is also a significant and growing threat, where various biodiversity metrics can address regional conservation priorities.

For example, Paitan and Trusan Sugut also showed a relatively lower mean number of species captured at each station (18 and 20, respectively) and incurred clustered functional traits and phylogenetic distribution. Trusan Sugut forests are found in coastal lowland areas with <200m (Sabah Forestry Department 2020b). Notably, Trusan Sugut Forest Reserve has been awarded Forest Stewardship Council (FSC) Well Managed Forest certification for five years, where multiple restoration activities are ongoing throughout the area (Sabah Forestry

Department 2020b). These two forest reserves retain the presence of endangered mammals, like Bornean banteng, Bornean orangutan, proboscis monkey, sun bear, red langur (*Presbytis rubicunda*), and Sunda clouded leopard. These two reserves were notably higher in beta diversity than the other study areas, indicating a distinct assemblage compared to the other reserves. This indicates a specific terrestrial mammal community composition in this area and the unique qualities of this coastal region of Sabah. For example, some species, like Bornean elephant, are unable to traverse the steep slopes of the surrounding landscape to access the Paitan region. However, the clustered functional and phylogenetic traits also indicate there are species losses to be remediated in this area and a need for continued concerted attention to the conservation and refaunation of terrestrial mammals.

Another example is that the Sapulut forest reserve showed the lowest species richness for any forest reserve, with 13 species captured and clustered phylogenetic and functional diversity. These metrics indicate local extinction and remaining species share similar features, such as diet, activity pattern, and body size. Five forest ungulate species dominate the reserve, alongside three carnivores and two primate species. When these results are compared to IUCN species ranges, despite being coarse-scale and often inaccurate at fine scales, IUCN reports that seven ungulates, 18 carnivores, 10 primates are still presumed extant in this area. Additionally, nearly half (6 out of 10) detected species were IUCN listed as critically endangered or vulnerable. Sapulut retains the presence of large endangered mammals, like the Bornean banteng, Bornean elephant, and sun bear. In this case, the low number of carnivore and primate species can indicate functional ecosystem losses in the area, as they fulfill multiple trophic roles such as predation, seed predation, and seed dispersal. This case reveals a view of the possibility of dramatic rates of species losses and defaunation occurring in forest reserves, where mitigating land-use change and intensifying sustainable forest management are feasible actions that can be taken immediately (Dirzo et al. 2014). Efforts are underway for further sustainable management of Sapulut forest reserves to ensure the conservation of forest resources (Sapulut Forest Development Sdn Bhd 2020). However, alongside these restorative forestry initiatives, Sapulut-Kalabakan has a forest logging road surrounded by Class II forest reserves to four-lane highways where impending threats to the regional mammalian biodiversity would benefit from mitigation, increased protection, and conservation planning to maintain the vulnerable species composition in this area or promote refaunation (Sloan et al. 2019). The pantropical defaunation crisis requires multiple pathways of collaboration where identifying spatial patterns can help stakeholders identify priority areas with indicators of defaunation to prioritize the allocation of finite conservation resources towards mitigation and restoration to enable ecosystem recovery (Tilker et al. 2020).

Strengths and Limitations.

These camera trap surveys are among the most extensive camera trap datasets combined for a multi-regional biodiversity analysis for forest reserves in Sabah. This study is the first attempt to perform a large-scale analysis to understand forest management impacts on terrestrial mammalian species richness, phylogenetic and functional diversity, all three relevant for conservation. There was an advantage in using MSOM for statistical modeling as it included imperfect detection into model estimates able to output the desired biodiversity metrics. We also determined that the random effects of the forest reserves themselves were largely responsible for the variation in the mammal composition, not the environmental variability of numerous raster covariates. These results indicate that progress in sustainable forest management and forest protection has positive results for mammalian biodiversity.

Current studies on phylogenetic and functional diversity often include weighted abundance estimates that better predict ecosystem processes (Cadotte et al. 2010). In this study, we are doing multi-species occupancy-related research on diversity metrics, which provide presence-absence estimates for imperfect detection. The output of an MSOM is a binary z-matrix (site x species). However, N-mixture models have accommodated multiple species (Gomez et al. 2018), which may be explored for further research on terrestrial mammals and diversity metrics. There is a caveat to using N-mixture models to estimate abundance using camera trapping data. Abundances derived from camera trap data can be misleading, as the same animal can cross in front of the camera several separate hours in one day and then be counted as separate animals. Animals traveling in groups are easier to estimate abundance than solitary animals.

Other limitations include a lack of data collection methods for many primate or mesocarnivore species, likely due to the arboreal habit of these species. Including methodologies for arboreal species through drone surveys (Kays et al. 2019), arboreal camera traps (Moore et al. 2021), or other methods may prove advantageous for detecting species that were missed in our surveys.

Extensions of this initial work may seek to understand more about species representations within these mammal communities, including understanding which species, in particular, are contributing to these functional and phylogenetic diversity scores in these areas to enhance species-specific conservation efforts. For example, this study did not extensively dissect the results to determine whether species contributing to phylogenetic diversity are particularly rare or scarce species or if certain species possessing unique functional traits are threatened or endangered. Previous studies investigated global mammalian distributions in taxonomic, phylogenetic, and functional traits for an integrative approach to species prioritizations (Isaac et al. 2007; Hidasi-Neto et al. 2015; Brum et al. 2017), where future research may attempt to prioritize specific species.

Conclusions

Our results indicate that terrestrial mammal assemblages across forest reserves in Sabah show differential levels of species richness, phylogenetic and functional diversity, redefining conservation priorities to include comprehensive biodiversity metrics. Community-level ecological modeling has become an essential tool for understanding the diversity of terrestrial vertebrates. The estimates from multi-regional multi-species occupancy models performed very well and included imperfect detection, highlighting the model estimates' efficacy to a deeper level analysis of biodiversity potential. We determined by RDA that the variation in mammal communities is primarily determined by the forest reserve random effects and not significantly by the environmental covariate information. We modeled the observed data and MSOM estimates that included the effects of imperfect detection, then performed RDA to determine the effects of environmental covariates on the mammal community. Understanding these community-level multi-species occupancy workflows is at the forefront of ecological and conservation research (Royle and Kery 2015), where these results can provide more scientific knowledge for planning and management efforts.

We found that mammal communities in Deramakot showed high functional, phylogenetic, and species diversity and were the most surprisingly diverse region in our study. Deramakot also has the longest-running forest certification program in Sabah, indicating success for sustainable forestry management strategies. The area had species richness and functional diversity measures comparable to Madai Baturong, the only class VI virgin forest classified in our study. The remaining forest reserves showed a broad range of phylogenetic and functional traits diversity, showing opportunities for conservation and restoration interventions to include a broad range of diverse species, considering discussion beyond a species richness measure or the most endangered and vulnerable. This study echoes the overall message put forth by previous research seeking to quantify diversity using a range of diversity metrics is essential as the metrics respond differently according to landscape pressures, such as landscape management (Ehlers Smith et al. 2020).

Previously logged forests in Sabah still retain unique assemblages that can be discussed through perspectives in beta, phylogenetic and functional diversity, which is essential in conserving terrestrial mammalian biodiversity. We have added knowledge of nine forest reserves and their importance as critical areas for mammal conservation. Many forest reserves and protected areas in the region lack basic information about mammalian diversity. Further conservation planning is necessary to maintain the integrity of forest reserves to achieve sustainable management. Therefore, supportive scientific research, inclusive of local research and management personnel, is advisable to increase comprehensive biodiversity knowledge at the policy and planning processes interface. The network of protected areas and forest reserves across the "Heart of Borneo", and those in areas adjacent to this core region, crucially important, where the structural connectivity shows vulnerability to increased road development and fragmentation (Sloan et al. 2019), or oil palm expansion (Savilaakso et al. 2014). Land-use changes are associated with severe declines in biodiversity, such as losses in species richness associated with forest conversion or agricultural expansion (Gibson et al. 2011; Laurance et al. 2014) and loss of functional diversity associated with anthropogenic changes (Gorczynski et al. 2021; Magioli et al. 2021). Forest reserves play an essential role in preventing local extinction, highlighting the need to protect and preserve these areas with more intensified sustainable management actions.

Declarations

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Ethics Approval waive

Consent to participate and publication: All authors consented to participate and publish this article.

Data Availability: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request for research purposes and is entirely up to the researchers to decide whether the request is granted.

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