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

3  
4  
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23  
24 **Abstract:** Tropical forest reserves have conservation value for terrestrial mammals and are  
25 threatened by anthropogenic pressures, especially conversion to other land-use types. To assess  
26 mammalian biodiversity of forest reserves in Sabah, Borneo, we used camera trapping data to  
27 estimate species richness, beta diversity, phylogenetic and functional diversity in nine forest  
28 reserves with different management classifications and backgrounds. Multiregional multispecies  
29 occupancy models (MSOM) were used to differentiate species occupancy in the reserves, and the  
30 estimates were transformed into biodiversity metrics. We found a significant difference in  
31 mammal composition within each forest reserve, with various functional and phylogenetic  
32 clustering or dispersion levels indicated by the standard effect of mean pairwise distances (SES  
33 MPD). Redundancy analysis (RDA) was used for both the observed data and MSOM estimates,  
34 modeling numerous environmental covariates and the forest reserves as random effects, finding  
35 that the forest reserve random effects were mainly responsible for structuring the mammal  
36 communities. Deramakot Forest Reserve was found to have overall high species richness,  
37 phylogenetic and functional diversity compared to other reserves. This reserve has been  
38 particularly successful at sustainable forest management and long-term forest certification,  
39 highlighting long-term conservation gains of sustainability programs for terrestrial mammalian  
40 diversity. Conversely, several reserves showed lower diversity scores overall than IUCN  
41 presumed extant species lists, highlighting local defaunation while still retaining high profile  
42 (critically endangered, endangered, and vulnerable) species. This study highlights the fragility of

43 terrestrial mammal assemblages in forest reserves across the state and the need for mitigation,  
44 refaunation, and an integrated approach to forest management and biodiversity conservation to  
45 allow for comprehensive sustainable management programs to ensure long-term conservation.

46  
47 **Keywords:** Biodiversity, Camera Trap, Community Ecology, Forest Management, Functional  
48 Diversity, Phylogenetic Diversity

## 49 **Introduction**

50 Tropical forests are vital areas of high biospheric diversity continually threatened by  
51 degradation and loss of natural forests through logging activities and forest conversions to other  
52 land-use types, which imperil wildlife and their habitats (Gibson et al. 2011; Laurance et al.  
53 2012; Burivalova et al. 2014; Brodie et al. 2015; Jati et al. 2018). Integrating production forests  
54 that repeatedly harvest timber into conservation priorities in tropical areas is challenging,  
55 especially in many parts of Borneo. The Bornean landscape has been and continues to be  
56 transformed mainly by repeated cycles of timber harvesting resulting in degraded forests or  
57 further converting forests to agricultural monocultures such as oil palm plantations (*Elaeis*  
58 *guineensis*) (Wearn et al. 2019).

59 The current and legacy anthropogenic pressure that has dramatically altered the state of  
60 the landscape in Sabah, Borneo, continues to have impacts widely throughout the forest reserves  
61 (Reynolds et al. 2011; Bryan et al. 2013). Bryan et al. (2013) showed that in 2009, the  
62 government had officially protected only 8% of intact forest, and established forest management  
63 plans resulted in 80% of Sabah undergoing extensive industrial deforestation, with 38% of forest  
64 cover remaining relatively intact, 39% degraded and 23% severely degraded (Bryan et al. 2013).  
65 Many large forest reserves in Sabah have been subject to conversion to agricultural plantations,  
66 or repeated rotational commercial logging (Sodhi et al. 2010; Reynolds et al. 2011), although  
67 reserves are currently phasing out these methods to implement Reduced-Impact logging  
68 programs (Sodhi et al. 2010; Reynolds et al. 2011). Even if forest reserves maintain production

69 status and selective logging, protecting tropical forests from further conversion to agricultural  
70 land use or forest plantations can protect unique meta-community processes and maintain  
71 ecosystem functions and services (Wilcove et al. 2013; Edwards et al. 2014).

72 Conservation priorities for terrestrial mammals are most commonly measured by  
73 International Union for Conservation of Nature (IUCN) status or other state-level protected  
74 species status or through species richness estimates, although assessing species assemblages  
75 according to phylogenetic and functional traits diversity have become critical and well supported  
76 (Faith 1992; Redding and Mooers 2006; Isaac et al. 2007; Hidas-Neto et al. 2015).

77 Approximately 4.6% of the world's land surface contains taxonomic, phylogenetic, and  
78 functional diversity components separately relevant to conservation (Brum et al. 2017). Borneo  
79 has overlapping taxonomic, phylogenetic, and functional priorities; therefore, examining only  
80 one dimension would undermine conservation efforts (Brum et al. 2017). Recent studies have  
81 shown that land-use changes threaten the preservation of phylogenetic and functional ecosystem  
82 diversity (Graham et al. 2019). Efforts to understand global diversity have shown that Borneo is  
83 a global hotspot for losses in phylogenetic diversity through species extinctions due to land-use  
84 change (Chaudhary et al. 2018). Few studies have attempted to examine forest management or  
85 land-use impacts on functional or phylogenetic diversity since emerging analytical methods to  
86 quantify this appropriately for multiple taxa are newly developed and implemented for mammal  
87 communities (Frishkoff et al. 2017; Frank et al. 2017; Cadotte and Tucker 2018).

88 Multiple frameworks have been developed to explore why specific communities  
89 assemble across space, for example, along gradients of land use (Goijman et al. 2015; Wearn et  
90 al. 2019) or anthropogenic disturbances (Easter et al. 2019). Patterns in global biodiversity for  
91 functional groups and trait diversity indices have shown regional differences in communities'

92 structure and responses to environmental gradients (Tenan et al. 2017; Wearn et al. 2017; Rovero  
93 et al. 2020). Previous research in a widely distributed Indonesian Borneo dataset has shown that  
94 anthropogenic impacts from logging and hunting have negatively affected mammalian  
95 community diversity (Brodie et al. 2015; Cheyne et al. 2016).

96 Surveys of mammal species richness are critical to establishing baseline estimates that  
97 identify priority-protected areas of high species richness value and represent essential functional  
98 and phylogenetic diversity (Faith 1992; Chapman et al. 2018; Cadotte and Tucker 2018). In this  
99 study, a multi-region multi-species occupancy modeling (MSOM) approach was used to estimate  
100 the species richness of mammal communities in several forest reserves in the state of Sabah and  
101 quantify the differences in diversity metrics. How well forest reserves in Sabah, a Malaysian  
102 state in Borneo, represent distinct species richness, phylogenetic, and functional diversity for  
103 terrestrial mammals is currently unknown. We also sought to understand further the influence of  
104 the landscape's environmental variability on the mammal community. Recently, there have been  
105 many advances to quantify various diversity metrics using MSOM estimates (Royle and Kery  
106 2015) to derive species richness, beta diversity, functional and phylogenetic diversity (Iknayan et  
107 al. 2014; Jarzyna and Jetz 2016). Assemblages between regions can differ in phylogenetic and  
108 functional traits representation, resulting in clustering or dispersion. The study aimed to  
109 demonstrate the methodological approaches in visualizing and representing phylogenetic and  
110 functional diversity for terrestrial mammal communities to identify conservation priorities within  
111 production forests crucial for sustainable and conservation-related management.

## 112 **Methods**

### 113 **Study Area**

114 This research was conducted in secondary tropical lowland forests characterized by  
115 economically valuable trees from the Dipterocarpaceae family across the Malaysian state of Sabah

116 in the north of Borneo (5.9788° N, 116.0753° E) (Fig 1). Sabah has a wet season (May-December)  
 117 and a dry season (January to May), although rainfall is variable and unpredictable throughout the  
 118 year. We explored patterns of species diversity in secondary tropical forests in nine regions of  
 119 Sabah, namely: Paitan, Trusan Sugut, and Sugut (northeast), Sipitang (west coast), Tangkulap and  
 120 Deramakot (central), Silabukan (east), Sapulut, Maliau Basin Conservation Area, and Madai-  
 121 Baturong (south-central).

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

124

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

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

131

Forest Reserve or Conservation Area	Size (km <sup>2</sup> )	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.

132

133 **Camera trap surveys and preparation of event data**

134 Camera traps are a proven method for conducting mammal inventories (Tobler et al.  
135 2008) and estimating species richness, occurrence, and abundance (O'Connell et al. 2011).  
136 Camera trapping across the state of Sabah was conducted to identify the elusive target species  
137 Bornean banteng (*Bos javanicus lowi* or *lowii*) for species conservation (Gardner et al. 2018). A  
138 total of 218 camera stations were deployed, with a mean number of 24 camera stations placed at  
139 each forest reserve (Table 2). Researchers placed cameras at intervals through forest reserves  
140 between June 2013 and Sept 2016. A pair of opposing cameras were placed at each station at  
141 approximately 50cm high and secured to trees approximately 5-8m apart. Cameras were  
142 enclosed in security cases that were padlocked and bolted to prevent theft. Vegetation was  
143 cleared at ground level to prevent camera obstruction. Stations were spaced at a mean of 998m  
144 apart (range: 87m -3642m). Cameras that were close together were paired on and off an animal  
145 trail to capture the range of diversity that may not be using the trails. The camera trap models  
146 used included Reconyx PC800 and PC650 Professional and HyperFire™ HC500 (Reconyx Inc.,  
147 WI, USA). Cameras ran for a minimum of 33 days to a maximum of 422 days, with a mean of  
148 136 days. Camera days represented the station with both cameras in tandem, not individual

149 cameras. Cameras were checked approximately every 30 days when vegetation was cleared from  
 150 the station, SD cards were retrieved and replaced, batteries were replaced, and silica gel  
 151 desiccant was replaced. We defined camera trap events' independence by only using the first  
 152 photographic capture of a given species at each station within 24 hours.

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

	<b>Total stations</b>	<b>Total station days</b>	<b>Mean station days</b>	<b>Min station days</b>	<b>Max station days</b>	<b>Start date</b>	<b>End date</b>
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
Tangkalap	30	2899	97	35	118	07-2015	11-2015

157

### 158 **Environmental Covariates**

159 This study hypothesized that several environmental covariates would influence the  
 160 mammalian species richness. Covariates were derived from raster data derived from Google  
 161 Earth Engine. Data layers included elevation, slope, and aspect generated from (90m, SRTM),  
 162 mean temperature (900m, WorldClim1), forest canopy height (30m GLAD), woody biomass  
 163 (500m, WHRC), canopy cover (30m, GLCF), forest loss, and forest gain generated from (30m,  
 164 Hansen). Open street map shapefile data was also used to create a raster of the Euclidean  
 165 distances to roads, waterways and streams, trails, and villages. Data were extracted at 20m  
 166 buffers and averaged around each camera trap point. Covariate data were centered and scaled  
 167 prior to analysis.



168           **Data Analysis**

169           **Multi-species Occupancy Models**

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

184           We used Bayesian hierarchical MSOM to estimate the community-level richness of  
185 terrestrial mammals, ranging from medium to large in body size, between different forest  
186 reserves. The models were parameterized using the forest reserve as a random block effect to  
187 make inferences on the entire collection of cameras at once to assess differences between forest  
188 reserves (Sutherland et al. 2016; Damschen et al. 2019; Stanton Jr. et al. 2020). Sutherland et al.  
189 (2016) developed a multi-region community model (MRCM) to estimate multi-species  
190 occupancy with covariates across geographically distinct regions using random block effects to  
191 improve statistical performance compared to single-region models (Sutherland et al. 2016). This

192 model has been extended to include partitions of trophic strata (Tenan et al. 2017) and applied to  
 193 forest mammal communities across protected areas monitored annually as part of Tropical  
 194 Ecology Assessment and Monitoring TEAM network long-term camera trapping sites (Rovero et  
 195 al. 2020). The modeled estimates that incorporate imperfect detection are essential to aid in  
 196 wildlife management, identify the drivers of population changes, and mitigate conservation.

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

$$y_{ijk}|z_{ik} \sim \text{Bernoulli}(z_{ik} \times p_{ijk}) \quad (1)$$

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

$$z_{ik} \sim \text{Bernoulli}(\psi_{ik}). \quad (2)$$

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

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

$$\text{logit}(p_{ijk}) = \alpha_k \quad (4)$$

205 Hyperparameters were normally distributed  $\beta_{rk} \sim \text{Normal}(\mu_{\beta_r}, \tau_{\beta_r})$ , where  $\mu_{\beta_r}$  and  $\tau_{\beta_r}$   
 206 refer to the community-level mean and precision for each land use ( $r$ ), and  $\alpha_k \sim \text{Normal}(\mu_\alpha, \tau_\alpha)$   
 207 and  $\mu_\alpha$  and  $\tau_\alpha$  community-level mean and precision for detectability. Vague priors were used  $\mu$   
 208 normally distributed, ( $\mu=0, \tau=0.6$ ),  $\sigma$  uniformly distributed (0,10), and  $\tau$  being power  
 209 transformed ( $\sigma, -2$ ).

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

### 213 **Diversity Indices**

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

### 220 **Beta diversity**

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

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

$$D_{r,s} = 1 - J_{r,s} \quad (6)$$

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

## 231 **Phylogenetic and Functional Traits Structure**

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

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

245 Functional diversity describes how the representation of species traits within a  
246 community differentially affects the ecosystem's ability to function (Petchey and Gaston 2006).  
247 Trait-based distance matrices are calculated as the distance between species according to various  
248 traits, such as diet, daily activity, and body mass (g). In this study, 14 variables were used to  
249 construct our trait matrix. Functional diversity was derived from trait information from the  
250 EltonTraits 1.0 database (Wilman et al. 2014). The Elton Traits variables for diet included a  
251 percentage of each mammal's diet and were divided into the appropriate categories: Insectivores  
252 (invertebrates), Carnivores ("vend" (mammals, birds), "vect" (reptiles, snakes, amphibians,  
253 salamanders), fish, "vunk" (vertebrates general), scavenger (carcasses, carrion)), Frugivores:  
254 (fruit (fruit, drupe)), Herbivores (seed (seed, maize, nuts, grains), or plants). Activity patterns

255 included binary categories for diurnal, crepuscular, and nocturnal, with many species being  
256 included in multiple categories based on the literature. The final variable included is biomass (g),  
257 or the rough average weight of the mammal at full size. All continuous covariates were centered  
258 and scaled before constructing the distance matrix.

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

274         Diversity metrics were derived from the mean and 95% CI of all the posterior sample's  
275 estimates and visualized using plots. Estimates of diversity were derived using the z-matrix (site  
276 x species occupancy matrix), and then site-specific subsets were extracted to deduce forest  
277 reserve level value. For example, species were summed across stations and grouped within the

278 forest reserve when calculating the alpha diversity for each of the 58,000 posterior sample's z-  
279 matrices. We also tested the multivariate differences among forest reserves using the  
280 permutational MANOVA using the vegan package.

### 281 **Redundancy Analysis**

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

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

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

### 293 **Results**

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

298 Table 3. Total mammal detections, i.e., independent camera trap records and number of  
299 mammals detected at each forest reserve. IUCN status for critically endangered (CR),  
300 endangered (EN) and vulnerable (VU) species are also tabulated. Number of species in  
301 orders Artiodactyla, Carnivora, Primates, and Rodentia at each forest reserve are  
302 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

303

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

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

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

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



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

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

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

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

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

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### 345 Multi-species occupancy results

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

350

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

353

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

356

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

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

365

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

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### **Beta diversity**

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

377

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

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### **Functional and phylogenetic structure**

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

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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.

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

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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

403 of zero, indicating neither substantial diversity nor clustering. The MANOVA method compares  
 404 the variance in beta diversity and found a significant difference in these metrics between all  
 405 forest reserves for both observed and estimated datasets ( $p < 0.001$ ,  $R^2 = 0.16$ ). These results  
 406 indicate that each forest reserve comprises a relatively unique assemblage compared to the  
 407 others, and none are redundant.

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

### 418 Redundancy Analysis

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

422 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]
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424 Results of the redundancy reveal the variation in the data is mainly explained by the conditional  
 425 block effects of the FMU, showing that the block effects account for 18% of the variation in the  
 426 observed camera trap data, and 38% of the variation in the modeled dataset (Table 7). The  
 427 environmental variables account for 4% of the variation in the data after accounting for the block  
 428 effects, revealing no significant trends in this multivariate framework that the environmental  
 429 variation on the landscape is predicting the differences of the mammal community.

430

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

	<b>Observed Camera Trap Data</b>		<b>MSOM Mean Posterior Estimates</b>		
	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

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### Discussion

436 This study provides valuable information regarding the diversity found regionally in  
 437 Sabah between forest reserves and the conservation value of phylogenetic and functional trait-  
 438 based assemblage differences in the broader scheme of conservation perspectives. Phylogenetic  
 439 and functional trait distances allowed for a more in-depth analysis concurrent to the raw alpha  
 440 and beta diversity metrics (Swenson 2011), which can be discussed in sustainable forest  
 441 management and landscape conservation. We confirmed that several forest reserves were

442 phylogenetically and functionally clustered or dispersed, more so than would be expected by  
443 random chance. This study focused on a multi-regional covariate "block" on the forest reserves,  
444 which was the main predictive factor for the species richness within each reserve, as shown by  
445 the RDA. In this study, we determined that most of the variation in these data can be explained  
446 by the conditional block effects of the forest reserves and not by the environmental variation of  
447 the landscape represented by multiple covariates.

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

454         Research at macroecological scales suggests that the mechanism for diversification in the  
455 tropics has resulted in the baseline historical composition of species having similar ecological  
456 niches and functional traits, with slow trait evolution resulting in closely related species with  
457 shared functional similarities and redundancy without simultaneously experiencing high local  
458 species extinction (Safi et al. 2011). Functional diversity has been shown to decrease when  
459 confronted with significant anthropogenic changes such as habitat loss, patch isolation, and  
460 fragmentation, which also can lead to the loss of essential ecological functions and ecosystem  
461 services (Magioli et al. 2021). Research has shown that certain traits are more prone to multiple  
462 pathways to local extinction, such as body mass and activity pattern (Davidson et al. 2009), and  
463 that losing large sized-herbivores and apex predators then results in cascading changes to the  
464 ecosystem, impacting downstream trophic levels and processes (Magioli et al. 2021). Similar to

465 this study, functional trait diversity studies have sought to estimate taxa differences in traits, such  
466 as habitat preferences or diet (Pacifci et al. 2014), habitat "generalist" or "specialist" species  
467 (Frishkoff and Karp 2019), habitat or climatic niches (Frishkoff et al. 2016) to classify species  
468 into functional roles they may fulfill within the ecosystem. Functional traits clustering was  
469 standard or neutral across all reserves, except Deramakot and Madai Baturong, the only two sites  
470 with an even or "diverse" distribution of functional traits across biomass, diet, and activity  
471 patterns (i.e., diurnal, nocturnal, crepuscular).

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

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



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

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

505         For example, Paitan and Trusan Sugut also showed a relatively lower mean number of  
506 species captured at each station (18 and 20, respectively) and incurred clustered functional traits  
507 and phylogenetic distribution. Trusan Sugut forests are found in coastal lowland areas with  
508 <200m (Sabah Forestry Department 2020b). Notably, Trusan Sugut Forest Reserve has been  
509 awarded Forest Stewardship Council (FSC) Well Managed Forest certification for five years,  
510 where multiple restoration activities are ongoing throughout the area (Sabah Forestry

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

521 Another example is that the Sapulut forest reserve showed the lowest species richness for  
522 any forest reserve, with 13 species captured and clustered phylogenetic and functional diversity.  
523 These metrics indicate local extinction and remaining species share similar features, such as diet,  
524 activity pattern, and body size. Five forest ungulate species dominate the reserve, alongside three  
525 carnivores and two primate species. When these results are compared to IUCN species ranges,  
526 despite being coarse-scale and often inaccurate at fine scales, IUCN reports that seven ungulates,  
527 18 carnivores, 10 primates are still presumed extant in this area. Additionally, nearly half (6 out  
528 of 10) detected species were IUCN listed as critically endangered or vulnerable. Sapulut retains  
529 the presence of large endangered mammals, like the Bornean banteng, Bornean elephant, and sun  
530 bear. In this case, the low number of carnivore and primate species can indicate functional  
531 ecosystem losses in the area, as they fulfill multiple trophic roles such as predation, seed  
532 predation, and seed dispersal. This case reveals a view of the possibility of dramatic rates of  
533 species losses and defaunation occurring in forest reserves, where mitigating land-use change

534 and intensifying sustainable forest management are feasible actions that can be taken  
535 immediately (Dirzo et al. 2014). Efforts are underway for further sustainable management of  
536 Sapulut forest reserves to ensure the conservation of forest resources (Sapulut Forest  
537 Development Sdn Bhd 2020). However, alongside these restorative forestry initiatives, Sapulut-  
538 Kalabakan has a forest logging road surrounded by Class II forest reserves to four-lane highways  
539 where impending threats to the regional mammalian biodiversity would benefit from mitigation,  
540 increased protection, and conservation planning to maintain the vulnerable species composition  
541 in this area or promote refaunation (Sloan et al. 2019). The pantropical defaunation crisis  
542 requires multiple pathways of collaboration where identifying spatial patterns can help  
543 stakeholders identify priority areas with indicators of defaunation to prioritize the allocation of  
544 finite conservation resources towards mitigation and restoration to enable ecosystem recovery  
545 (Tilker et al. 2020).

#### 546 **Strengths and Limitations.**

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

557 Current studies on phylogenetic and functional diversity often include weighted  
558 abundance estimates that better predict ecosystem processes (Cadotte et al. 2010). In this study,  
559 we are doing multi-species occupancy-related research on diversity metrics, which provide  
560 presence-absence estimates for imperfect detection. The output of an MSOM is a binary z-matrix  
561 (site x species). However, N-mixture models have accommodated multiple species (Gomez et al.  
562 2018), which may be explored for further research on terrestrial mammals and diversity metrics.  
563 There is a caveat to using N-mixture models to estimate abundance using camera trapping data.  
564 Abundances derived from camera trap data can be misleading, as the same animal can cross in  
565 front of the camera several separate hours in one day and then be counted as separate animals.  
566 Animals traveling in groups are easier to estimate abundance than solitary animals.

567 Other limitations include a lack of data collection methods for many primate or  
568 mesocarnivore species, likely due to the arboreal habit of these species. Including methodologies  
569 for arboreal species through drone surveys (Kays et al. 2019), arboreal camera traps (Moore et al.  
570 2021), or other methods may prove advantageous for detecting species that were missed in our  
571 surveys.

572 Extensions of this initial work may seek to understand more about species representations  
573 within these mammal communities, including understanding which species, in particular, are  
574 contributing to these functional and phylogenetic diversity scores in these areas to enhance  
575 species-specific conservation efforts. For example, this study did not extensively dissect the  
576 results to determine whether species contributing to phylogenetic diversity are particularly rare  
577 or scarce species or if certain species possessing unique functional traits are threatened or  
578 endangered. Previous studies investigated global mammalian distributions in taxonomic,  
579 phylogenetic, and functional traits for an integrative approach to species prioritizations (Isaac et

580 al. 2007; Hidasi-Neto et al. 2015; Brum et al. 2017), where future research may attempt to  
581 prioritize specific species.

## 582 **Conclusions**

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

597 We found that mammal communities in Deramakot showed high functional,  
598 phylogenetic, and species diversity and were the most surprisingly diverse region in our study.  
599 Deramakot also has the longest-running forest certification program in Sabah, indicating success  
600 for sustainable forestry management strategies. The area had species richness and functional  
601 diversity measures comparable to Madai Baturong, the only class VI virgin forest classified in  
602 our study. The remaining forest reserves showed a broad range of phylogenetic and functional  
603 traits diversity, showing opportunities for conservation and restoration interventions to include a

604 broad range of diverse species, considering discussion beyond a species richness measure or the  
605 most endangered and vulnerable. This study echoes the overall message put forth by previous  
606 research seeking to quantify diversity using a range of diversity metrics is essential as the metrics  
607 respond differently according to landscape pressures, such as landscape management (Ehlers  
608 Smith et al. 2020).

609         Previously logged forests in Sabah still retain unique assemblages that can be discussed  
610 through perspectives in beta, phylogenetic and functional diversity, which is essential in  
611 conserving terrestrial mammalian biodiversity. We have added knowledge of nine forest reserves  
612 and their importance as critical areas for mammal conservation. Many forest reserves and  
613 protected areas in the region lack basic information about mammalian diversity. Further  
614 conservation planning is necessary to maintain the integrity of forest reserves to achieve  
615 sustainable management. Therefore, supportive scientific research, inclusive of local research  
616 and management personnel, is advisable to increase comprehensive biodiversity knowledge at  
617 the policy and planning processes interface. The network of protected areas and forest reserves  
618 across the "Heart of Borneo", and those in areas adjacent to this core region, crucially important,  
619 where the structural connectivity shows vulnerability to increased road development and  
620 fragmentation (Sloan et al. 2019), or oil palm expansion (Savilaakso et al. 2014). Land-use  
621 changes are associated with severe declines in biodiversity, such as losses in species richness  
622 associated with forest conversion or agricultural expansion (Gibson et al. 2011; Laurance et al.  
623 2014) and loss of functional diversity associated with anthropogenic changes (Gorczyński et al.  
624 2021; Magioli et al. 2021). Forest reserves play an essential role in preventing local extinction,  
625 highlighting the need to protect and preserve these areas with more intensified sustainable  
626 management actions.

627

628 **Declarations**

629 **Funding** The funds for PCG and BG by Houston Zoo, Malaysian Palm Oil Council, Woodland  
630 Park Zoo, Mohammed bin Zayed Species Conservation Fund, Sime Darby Foundation, and EB  
631 by Florida Institute for Built Environment Resilience and Center for Landscape Conservation  
632 Planning.

633

634 **Conflicts of Interest/Competing Interests** None

635 **Ethics Approval** waive

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641

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