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SECONDARY FORESTS WITHIN AN INDUSTRIAL TIMBER PLANTATION CONTRIBUTE TO A DIVERSE MAMMAL COMMUNITY
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Abstract:	Industrial tree plantations of fast-growing species have become increasingly important in Southeast Asia to meet global demand for wood and wood fibre products. There is a growing need to understand more about their value for wildlife and how they can be managed for biodiversity. We evaluated the effects of landscape attributes on mammal communities in a plantation and secondary forest mosaic in northern Sabah, Malaysia. Using remote cameras, we compared mammalian species assemblages of secondary and industrial forest stands and identified habitat covariates associated with mammal species detections and species richness in the landscape mosaic. We used 89 remote camera stations deployed for a minimum of 23 days across two major land-use types: previously logged natural forests and planted forests composed mostly of Acacia mangium and Eucalyptus pellita. We used sample-based rarefaction to evaluate variation in species richness in these two major land use categories and generalized linear models to assess the effects of natural and anthropogenic predictors on variation in mammal detections and species richness. We also assessed mammal species responses to different environmental gradients using ordination. We detected at least 23 large and medium-sized mammal species over 2035 trap nights. Fourteen of those species were classified as threatened or near-threatened by the International Union for the Conservation of Nature. Rarefaction did not reveal differences in mammal species richness or diversity between plantation and secondary forests, and ordination analysis did not indicate significant associations between mammal species and environmental gradients. In contrast, generalized linear models indicated lower mammal richness and detection as proportions of planted forest and proximity to human settlements increased. Mammal detections, including those of threatened mammals, increased with greater proportions of secondary forest. The retention of secondary forest within plantation areas appears to be important to maintain mammalian species richness and contributes to the conservation value of industrial timber plantations. These findings may assist in the management of mammals of conservation concern and implementation of adaptive management plans to enhance biodiversity conservation in commercial forest plantations.
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SECONDARY FOREST WITHIN A TIMBER PLANTATION CONCESSION IN BORNEO CONTRIBUTES TO A DIVERSE MAMMAL ASSEMBLAGE

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ABSTRACT

Commercial tree plantations of fast-growing species have become increasingly important in Southeast Asia to meet global demand for wood and wood fibre products. There is a growing need to understand more about their value for wildlife and how they can be managed for biodiversity. We evaluated the effects of landscape attributes on mammal communities in a timber concession consisting of 83% secondary forest and 17% tree plantations in northern Sabah, Malaysia. Using camera traps, we compared mammalian species assemblages of secondary forest and commercial tree plantation stands and identified habitat predictors associated with total mammal species detections and species richness in the landscape mosaic. We used 87 camera stations deployed for 23 days across two major land-use types: 62 sites in secondary forest (previously logged natural forest) and 25 sites in tree plantations. We evaluated variation in species richness in these two major land-use categories and assessed the effects of natural and anthropogenic predictors on variation in total mammal detections and species richness. We detected at least 23 large and medium-sized mammal species over 2035 trap nights. Fourteen of those species were classified as threatened or near-threatened by the International Union for the Conservation of Nature. Rarefaction did not reveal differences in mammal species richness or diversity between camera sites placed in tree plantations and secondary forests, likely because most camera sites in tree plantations were close to secondary forest and comprised <30% of all sites. However, generalized linear models indicated lower mammal diversity as proportions of tree plantation and proximity to human settlements increased. Total mammal records, including those of threatened mammals, increased with greater proportions of secondary forest. Retention of larger tracts of secondary forest around plantation areas appears to be important to maintain mammalian species richness and contributes to the conservation value of commercial timber plantations. These findings may assist in the management of mammals of conservation concern and implementation of adaptive management plans to enhance biodiversity conservation in commercial plantations.

Keywords– Habitat use, mammal conservation, commercial forest, camera trap, Borneo, forest mosaic

1. INTRODUCTION

The tropical rainforests of Southeast Asia contain some of the highest levels of species richness and endemism in the world (Sodhi et al., 2004; Laurance, 2007; Brodie et al., 2015), and the region is considered a biodiversity hotspot (Myers et al., 2000). However, the loss of tropical forests from anthropogenic activities occurs at an exceptionally high rate here (Miettinen et al., 2011). Driven by population growth, economic development, and global demand for natural resources such as timber, rubber, and palm oil (Laurance, 2007; Sodhi et al., 2010; Wilcove et al., 2013), Southeast Asia had the highest annual deforestation rates (0.8%) among humid tropical regions of the world between 1990 and 1997 (Achard et al., 2002; Mayaux et al., 2005; Sodhi et al., 2010), and deforestation has accelerated since 2000 (Miettinen et al., 2011). If these trends continue, the region is predicted to lose 75% of its native habitats and 42% of its biodiversity by the year 2100 (McShea et al., 2009; Sodhi et al., 2004). Thus, there is an urgent need for more sustainable management of forest resources, which are considered vital for the maintenance of essential social, economic, and ecological services, and for halting the loss of biodiversity (Sodhi et al., 2010; Edwards et al., 2014; Struebig et al., 2015).

Commercial plantations play an important role in developing countries by providing economic and social benefits (Carle and Holmgren, 2008). Although consisting mostly of large areas of monoculture with uniform age structure and relatively low biodiversity (Brockerhoff et al., 2008), they may also contribute to forest conservation by reducing further exploitation of natural forests. The capacity for altered habitats such as plantations to support vertebrate species has received increasing attention (Norris et al., 2008; Brodie et al., 2015). In Malaysia, a country with extremely high rates of forest loss (Sodhi et al., 2010; Hansen et al., 2013), extensive commercial timber plantations have been established with fast-growing exotic trees such as *Acacia* spp. and *Eucalyptus* spp. (Gaveau et al., 2016). Recent studies have shown that these plantations may offer suitable habitat for threatened mammal species (McShea et al., 2009; Bernard et al., 2014; Ng et al., 2021), but more work is needed to understand which attributes of these forests influence the presence of different species and how they can be managed effectively to enhance biodiversity at local and regional scales (Meijaard et al., 2010; Mang and Brodie, 2015).

Mammals are widely considered to be a high priority for conservation because of their vulnerability to habitat loss and overexploitation (Hoffmann et al., 2011; Wilcove et

96   al., 2013), and because many species play keystone roles in ecosystems, including

97   seed dispersal (Fragoso et al., 2003), predation (Terborgh, 2001), and maintenance of

98   plant community composition through grazing (Young et al., 2013). Mammals also

99   are an important resource for local human communities (Brown and Williams 2003).

100 Current extinction rates for mammals are well above background rates (Barnosky et

101 al., 2011), and many larger mammals serve as umbrella species for conservation

102 through their ecological requirements and co-occurrence with other species of

103 conservation concern (Caro, 2003; Noss, 1990; Ratnayeke and van Manen, 2012;

104 Brodie et al., 2015). Large and medium-sized mammals are especially at risk in

105 Southeast Asia where the threats of habitat loss and poaching are compounded by

106 their large area requirements, movements patterns, and low population densities

107 (Hoffmann et al., 2011).

108 The island of Borneo is home to 247 terrestrial mammals, of which 63 (25.5%) are

109 considered endemic (Phillipps and Phillipps, 2018). Many of these species are

110 threatened by deforestation and habitat fragmentation, with Borneo's forest cover

111 declining by 30% between 1973 and 2010, largely due to the replacement of rainforest

112 with commercial oil palm and timber plantations (Gaveau et al., 2017). Although

113 much of the early expansion of oil palm and timber plantations in Borneo occurred on

114 previously deforested and degraded land, more recently (2005–2015), commercial

115 tree plantations were the primary cause of direct deforestation (Gaveau et al., 2017).

116 By 2015, only about 28% of Borneo remained as intact, unlogged forest. Commercial

117 timber lands currently comprise less than a fourth of industrial plantations but are

118 likely to expand in the future to meet growing demands for pulpwood. Effective and

119 sustainable management of commercial timber plantations can play an important role

120 in the conservation of Borneo's mammals, but further research is needed on which

121 species use these timber plantations and how.

122 In this study, we used camera traps to evaluate associations of landscape and habitat

123 attributes with large and medium-sized mammals in a plantation and secondary forest

124 mosaic in Kota Marudu and Pitas districts, Sabah, Malaysia. Our primary goal was to

125 evaluate the role of secondary forest within timber plantations to sustain mammal

126 assemblages. We hypothesized that mammal diversity would be greater in secondary

127 forest than in plantations. Specifically, our aims were to assess mammal species

128 richness, composition, and associated habitat and landscape attributes in the study

4

129 area. We constructed sample-based rarefaction and extrapolation curves to estimate

130 species richness of large and medium-sized mammals in plantation and secondary

131 forest stands, given unbalanced sampling effort between the two land-use types.

132 Secondly, we identified landscape and habitat predictors associated with total

133 mammal detections and species richness.

134

2. METHODS

2.1 Study area

137 The study area was located in a commercial plantation (~60,000 ha) adjoining a Class

138 I natural forest reserve (Mandamai Forest Reserve; ~5,330 ha) that was strictly

139 protected and two Class II reserves (Paitan Forest Reserve and Lingkabau Forest

140 Reserve) that were allocated for timber harvest and other forest products (Figure 1).

141 The study area is a 60-year concession to the Asian Forestry Company Sabah (AFCS)

142 for a long-term commercial tree plantation (AFCS, 2010). The AFCS concession area

143 was once covered with lowland mixed *Dipterocarpus* forests. However, in the early

144 1970s, valuable timber species were severely depleted because of heavy logging.

145 Currently, previously logged forests in most of the AFCS concession area are

146 dominated by pioneer species such as *Macaranga* spp. Extensive areas of scattered,

147 naturally regenerated *Acacia mangium* and *Paraserianthes falcataria* (locally known

148 as Batai) also occur. For the purpose of our study, we defined these areas as secondary

149 forest.

150 The AFCS concession area contains 28 management units called coupes, each of which

151 consists of an area of approximately 1,000 ha. We only conducted sampling in active

152 coupes (Coupes 1–5, 7–8, and 10–15; Figure 1), areas within the concession where

153 plantation operations (logging, tree planting or silviculture treatment and road

154 construction or maintenance) occurred. Tree plantations consisted of fast-growing trees,

155 such as *Acacia mangium, Eucalyptus pellita,* and *Albizia falcataria*.

156 The wide range of geology, soils, and forest types within the AFCS area (AFCS, 2010)

157 created a mosaic of habitats. Corridors of native forest consisted of sensitive areas, such

158 as riparian reserves, and steep areas were retained to ensure a representative range of

159 forest types in areas of plantation development and to compensate for fragmentation of

160 native forests (AFCS, 2010). Other than secondary forest, private small-holdings of oil

161 palm, rubber, coconut, and shifting agriculture occurred along major roads, particularly

162 near community settlements. These types of land uses were excised from the AFCS

163 concession and excluded from the study.

164 AFCS started planting operations in 2010 and to date they have operated in

165 approximately 24,000 ha. Around 83% of that area is in secondary forest, which

166 includes land allocated for tree plantations that are yet to be cleared and riparian

167 reserves, steep areas, and water catchments retained for conservation. (Figure 1). The

168 remainder consists of tree plantations of *Eucalyptus pellita* (67%), *Acacia mangium*

169 (28%), and *Albizia falcataria* (5%) monocultures Baseline camera surveys conducted

170 by AFCS during 2013–2017 revealed a diversity of large to medium-sized mammals in

171 the concession area, including several species of conservation concern (Appendix A.1).

172

2.2 Mammal surveys

173

174 We used passive infrared camera traps to obtain presence data on large and medium-

175 sized mammals. We examined random and systematic random sampling designs for

176 establishing camera sites. Given the size of the study area, systematic sampling

177 permitted greater sampling coverage of the two forest types of interest (i.e., mature tree

178 plantations and secondary forest) and associated range of spatial predictors. Most

179 studies deploying camera traps for mammal surveys use spacing of 1 to 2 km to

180 maintain spatial independence among sample units (e.g., Kai et al., 2017; Sollmann et

181 al., 2017; Ng et al., 2021; Tee et al., 2021). We used a minimum spacing of 1 km to

182 maintain consistency with studies conducted in similar landscapes in Sabah, Borneo

183 (e.g., Tee et al., 2021; Ng et al., 2021). We used the Manifold geographic information

184 system (GIS) software package to demarcate coordinates for 87 pre-determined

185 locations (Manifold Software Limited, Hong Kong). We deployed cameras at these

186 sites from March through December 2018, covering an area of approximately 253 km^2.

187 The systematic sampling was designed to sample broad environmental conditions using

188 spatial predictor variables, with proportions of secondary forest and tree plantation

189 within 500 m of camera sites ranging from 4.8 to 99.4% and 0 to 91.7%, respectively.

190 Sixty two sites were in secondary forest and 25 in tree plantations, with 1, 5, and 16

191 sites placed in *Albizia falcataria*, *Acacia mangium*, and *Eucalyptus pellita*,

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192 respectively. We used a total of 31 cameras; 17 Bushnell Trophy Cam units (Bushnell

193 Outdoor Products, Overland Park, KS, USA); 12 Moultrie M990i Gen2 Digital Game

194 Cameras (Pradco Outdoor Brands, Birmingham, AL, USA) and 2 Reconyx HC500

195 units (RECONYX, Inc., Holmen, WI, USA). We mounted cameras at a height of 30–

196 40 cm (e.g., Granados et al., 2016) above ground level and used a clinometer used to

197 level the position of the camera sensor to the focal point of detection. We programmed

198 cameras to operate 24 h a day in motion-detect mode, 10-megapixel resolution, three

199 photos per trigger in rapid succession, followed by 10 seconds of video with no delay.

200 One exception to these settings were the 2 Reconyx HC500 cameras, which did not

201 possess a video function. Species accumulation curves constructed from 2013–2015

202 survey data collected in the same area indicated that most mammal species were

203 detected within 16–20 days of camera operation (Appendix B.1). Thus, we deployed

204 cameras for at least 23 days at all sites. Camera sites were revisited every 7 days to

205 replace memory cards, refresh lure, and to check battery status. Typically, we operated

206 10–15 cameras in the field at any one time.

207 Because most cameras were not deployed along trails, we used a scent lure to enhance

208 detectability of species that typically occur at low densities, such as felids and other

209 carnivores (Meek et al., 2014). We used a small amount (~100 g) of dried salted fish

210 and fermented shrimp paste, locally known as *belacan*, to enhance the probability of

211 detecting animals that were in the vicinity of the camera site (Ng et al., 2021; Tee et al.,

212 2021). We hung the lure approximately 50 cm above ground level and 2.5 m in front of

213 the camera.

214 **2.3 Predictors of total mammal detections and species richness**

215 We calculated values for 11 environmental predictor variables associated with each

216 camera station. We obtained data for 10 predictors from a GIS database managed by

217 AFCS and measured 1 predictor, horizontal cover, on site. Predictor variables included

218 1) slope, 2) elevation (m), 3) distance (m) to the nearest human settlement, 4) distance

219 (m) to nearest road, 5) distance (m) to nearest river, 6) area (ha) of secondary forest, 7)

220 area (ha) of planted forest (i.e., *Acacia mangium, Eucalyptus pellita, Albizia falcataria*),

221 8) distance (m) to nearest boundary of a forest reserve, 9) horizontal cover (m), 10) area

222 (ha) of cleared forest (ha), and 11) distance to the nearest active coupe.

223 We measured area of secondary, plantation, and cleared forest within a 500-m radius
224 (area of buffer = 78.5 ha) of each camera site to reflect use of habitat by a range of
225 medium to large-sized mammals detected by the camera. This radius also helped ensure
226 that habitat measurements among camera sites, which were spaced ~1 km apart, were
227 independent. Raster layers for these predictor variables were generated with a spatial
228 resolution of 30 m.

229 We measured sighting distance as a surrogate of horizontal cover (understory
230 vegetation density) at each camera site, following Ordiz et al. (2009) and Sahlén et al.
231 (2011), who used the method to measure cover at brown bear (*Ursus arctos*) day beds.
232 We used a white plastic cylinder (70 cm height, 10 cm diameter), placed it in front of
233 the camera, and measure the minimum distance from which the cylinder was at least
234 95% invisible. We averaged 4 such measurements, starting with a random azimuth and
235 subsequent measurements at 90 degrees. Lower vegetation density corresponded to
236 larger sighting distances at this height (Ordiz et al., 2011).

237 **2.4 Analysis**

238 **2.4.1** *Species identification and detection rates*

239 We identified mammals from photographs and video to species level based on Phillipps
240 and Phillipps (2018), IUCN (2020) websites, personal experience, and confirmation
241 from species experts. We excluded photos of animals that could not be confidently
242 identified because of poor image quality, or where only parts of the animals were visible.
243 Volant and non-volant mammals, that were too small to be identified to species were
244 also excluded (i.e., most species of bats, tree shrews, rats, and squirrels). The greater
245 mouse-deer (*Tragulus napu*) and lesser mouse-deer (*Tragulus kanchil*) were treated as
246 belonging to one taxon (*Tragulus* spp.) as were the red muntjac (*Muntiacus muntjak*)
247 and Bornean yellow muntjac (*Muntiacus aetherodes*).

248 We calculated camera detection rates (*D*) of all species following Bernard et al. (2014),
249 with *D* defined as the number of independent photographs of a species (*C*) per 100
250 camera nights using the formula: $D = C \times 100 / \sum N$, where $\sum N$ was the total number of
251 camera nights accumulated over the study. We used a minimum threshold of 24 hours
252 for species occurrences at each site. Thus, we treated detections of the same species
253 across separate 24-hour periods as independent events. We tabulated detection rates for
254 each species according to where cameras sites were placed within the study sites (i.e.,

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255 planted forest versus secondary forest) and classified threatened mammals following
256 the 2021 IUCN Red List of Threatened Species.

257 **2.4.2** *Rarefaction and extrapolation for estimating species richness and diversity*
258 Biodiversity samples are usually incomplete and undetected species are a common
259 problem (Chao et al., 2014). Estimates of species richness from finite samples are
260 therefore dependent on the number of camera trap nights and number of camera stations
261 (i.e., sample size). Sample sizes of camera sites in plantations versus secondary forests
262 were unequal in this study. We used rarefaction and extrapolation (R/E) curves to
263 account for unequal sample sizes for plantation vs. secondary forest and provide an
264 estimate of sample completeness, also referred to as sample coverage (Gotelli and
265 Colwell, 2011). Rarefaction down-samples a larger sample to the size of the smallest
266 sample. Smaller samples can be extrapolated to a larger sample size, guided by an
267 estimate of asymptotic richness.

268 We constructed sample-based R/E curves (Chao et al., 2014) to compare sampling
269 completeness or effort and estimate the 'true' or effective number of species (i.e.,
270 estimated species richness; Colwell et al., 2012) for sites in plantations and secondary
271 forest. Sites were classified as being in plantation or secondary forest based on their
272 physical location and the camera's field of view. We created R/E curves by randomly
273 re-sampling from available camera sites 5000 times and plotting the mean number of
274 species found at each sample size. We generated these curves and associated 95%
275 confidence intervals using the 'iNEXT' package (Hsieh et al., 2016) in R environment
276 3.6.1 (R Core Team 2019). Sample completeness is measured by the fraction of the
277 total number of individuals that belong to species detected in the sample (sample
278 coverage; Hsieh et al. 2016). We tabulated presence (1) or absence (0) for each species
279 at each camera site for plantation or secondary forest, standardized by limiting
280 observations to the first 23 nights, which was the minimum period of camera operation.
281 We computed three sets of sample-based rarefaction and extrapolation curves (Gotelli
282 and Colwell, 2011): 1) species accumulation curves with extrapolation to estimate the
283 'true' number of species (sample-size-based approach, standardized based on sample
284 effort; Colwell et al., 2012); 2) sample completeness curves to estimate the sample
285 coverage rate of planted versus secondary forest, which had unequal sample sizes; and
286 3) coverage-based rarefaction and extrapolation curves to estimate species diversity, in
287 which samples were standardized based on sample completeness (Chao and Jost, 2012).

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2.4.3 *Variation in total mammal detections and species richness with environmental predictor variables*

Given our camera sampling design, we first considered multi-species occupancy models to evaluate relationships with environmental predictor variables. However, Tingley et al. (2019) evaluated multi-species occupancy models and concluded they perform poorly when the average occupancy of species in the community assemblage is low, which is reflective of our study area. Therefore, we used generalized linear models (GLM) to investigate the relationship between species richness, total mammal detections (total count of mammal detections per camera site), and total threatened mammal detections as respective response variables with the 11 environmental variables. Generalized linear models fitted with a Poisson distribution are especially suited for count data such as species richness, and permit predictions as counts (Jones et al., 2002).

We standardized all environmental variables to a mean of 0 and a standard deviation of 1 to allow assessment of the relative strength of parameter estimates (Ramette, 2007). We assessed multicollinearity among predictor variables with package 'faraway' (Faraway, 2016), using the variance inflation factor (VIF) with acceptable values below a threshold of 10 (Dormann et al., 2013), although some authors suggest using more stringent criteria (e.g., Zuur et al. 2010). We examined correlations among predictors with package 'Hmisc' (Harrell 2014). Distributions of all but one predictor were not normal (Shapiro-Wilk test), thus we used non parametric Spearman rank tests to examine the strength of correlations. We used a regression-based *t*-test (Cameron and Trivedi, 1990) with package 'AER' to test the assumption that the variances and means of response variables were equal (Kleiber and Zeileis, 2008). If overdispersion was evident, we used GLMs fitted with a negative binomial distribution (Coxe et al., 2009) with package 'MASS' (Venables and Ripley, 2002).

We used plots to assess trends in the data (Appendix B.2 to 4) and information from the literature to develop a set of 20 *a priori* models to examine potential relationships of species richness and mammal detections with the environmental variables. With a total of 87 sites, we limited the number of predictors in any single model to four or fewer. We hypothesized that proximity to source habitats, such as forest reserves and greater areas of secondary forest within the 500-m buffer, would be important positive predictors of mammal species richness and detection (e.g., McShea et al., 2009, Yaap

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et al., 2018; Ng et al., 2021). We included these two variables in 13 models, along with combinations of one or two additional variables. Seven models consisted of combinations of variables that were potential negative predictors of mammal species richness or detection: distance to roads, human settlements, or the nearest active coupe, and greater areas of cleared forest or planted forest. Active coupes were areas where plantation activities such as clear felling, planting, weeding, and pruning occurred concurrent with camera operations. We included one model with an interaction between distance to the nearest active coupe and the area of planted forest to test whether the response of species richness, detections, or threatened species detections differed as a function of camera proximity to plantation activity.

Because we used three different camera models, we evaluated if we needed to account for camera differences by fitting a random effect using generalized linear mixed models (GLMM; Bolker et al., 2009). We conducted these analyses using the 'glmer' function in R package 'lme4' (Bates et al., 2015) and fitted models with and without camera model as a random effect. We compared conditional R^2 values (i.e., the variance explained by both random and fixed effects) with marginal R^2 values (variance explained only by fixed effects) to evaluate whether inclusion of a random effect improved model fit (Nakagawa and Schielzeth, 2013). Differences in marginal and conditional R^2 values for models with and without the random effect for camera model were small (<0.04, all $P > 0.05$; Appendix A.2). We further conducted likelihood ratio tests (Luke, 2017) to compare those models, which did not support inclusion of a random effect for camera type ($P > 0.05$). Thus, we proceeded without fitting a random effect for camera model.

We used Akaike's Information Criterion corrected for small sample sizes (AIC$_c$; Akaike, 1974) to rank and select the most plausible models (Burnham and Anderson, 2002). If there was uncertainty in selecting a single top model (i.e., models differed by <2 AIC$_c$ units), we used model-averaging with shrinkage to estimate the effects of coefficients using R package 'MuMln' (Barton, 2019) and reported the 85% confidence intervals of model-averaged coefficients (Arnold, 2010). We used package 'effects' (Fox, 2003) in R to plot the relationship between the environmental predictor and response variables based on the highest-ranking regression models for species richness and total mammal detections.

353 We used ArcMap 10.3.1 Spatial Analyst tools (Esri, Redlands, California, USA) to

354 create predictive maps of mammal species richness and detections in the study area.

355 We calculated predictions separately for each of the models with $\Delta AIC_c < 2$. Geospatial

356 layers for distance to the nearest active coupe and horizontal cover were unavailable,

357 so we applied values of horizontal cover and distance to active coupes based on the

358 average of all sites. We multiplied each predictive layer of models with $\Delta AIC_c < 2$ by

359 its respective AIC_c weight, and then summed these layers to create model-averaged

360 predictions of species richness or detection (Cade, 2015).

361

362 **3. RESULTS**

363 **3.1 Mammal diversity across plantation and secondary forests**

364 The cameras we deployed across the 87 sites recorded more than 23 species of large to

365 medium-sized mammals (Table 1). Sixty percent of the mammal species we detected

366 were classified as threatened by the IUCN (IUCN, 2020), including one Critically

367 Endangered mammal, the Sunda pangolin (*Manis javanica*). The majority of camera

368 sites (71%) were located in secondary forest; all 23 species or species groups were

369 documented in this habitat, and all but 6 species were documented in planted forest.

370 Detection rates in secondary forest were twice as high as those in planted forest. The

371 most frequently detected mammals across the study area were pig-tailed macaques

372 (*Macaca nemestrina*; $n = 142$ detections), bearded pigs (*Sus barbatus*; $n = 58$), civets

373 ($n = 69$ total), mouse-deer ($n = 56$), and muntjacs ($n = 45$). Detection rates were lowest

374 (0.10–0.15 per 100 sampling occasions) for collared mongoose (*Herpestes*

375 *semitorquatus*), marbled cat (*Pardofelis marmorata*), western tarsier (*Cephalopachus*

376 *bancanus*), bearcat (*Arctictis binturong*), Sunda clouded leopard (*Neofelis diardi*), and

377 Sunda pangolin.

378 **Table 1:** Mammal species detected with camera traps at 87 sites within tree plantation ($n = 25$ sites) and secondary forests ($n = 62$ sites) within

379 the study site in an Asian Forestry Company (Sabah) commercial tree plantation. Habitats refer to the physical location of the camera traps

380 (i.e., in tree plantations or secondary forest) and camera field of view, but proportion of plantation and secondary forests varied (see text).

381 IUCN status: CR = Critically Endangered; EN = Endangered; VU: Vulnerable; NT = Near Threatened; LC = Least Concern.

		Detections		Detection rate/ 100 sampling occasions			
Scientific name	Common name	Tree plantation	Secondary forest	Tree plantation	Secondary forest	No. camera sites	IUCN (2020)
Manis javanica	Sunda pangolin	2	1	0.35	0.07	3	CR
Macaca nemestrina	Pig-tailed macaque	18	124	3.16	8.46	55	VU
Sus barbatus	Bearded pig	1	57	0.18	3.89	20	VU
Neofelis diardi	Sunda clouded leopard	0	3	0.00	0.20	3	VU
Arctictis binturong	Bearcat	0	3	0.00	0.20	3	VU
Helarctos malayanus	Sun bear	1	7	0.18	0.48	6	VU
Rusa unicolor	Sambar deer	1	5	0.18	0.34	6	VU
Macaca fascicularis	Long-tailed macaque	1	8	0.18	0.55	6	VU
Rheithrosciurus macrotis	Tufted ground squirrel	0	5	0.00	0.34	5	VU
Cephalopachus bancanus	Western tarsier	0	3	0.00	0.20	3	VU
Pardofelis marmorata	Marbled cat	0	3	0.00	0.20	3	NT
Muntiacus spp.	Muntjacs	7	38	1.23	2.59	27	NT
Hemigalus derbyanus	Banded palm civet	2	31	0.35	2.11	22	NT
Herpestes semitorquatus	Collared mongoose	0	2	0.00	0.14	2	NT
Prionailurus javanensis	Leopard cat	5	2	0.88	0.14	6	LC
Tragulus spp.	Mouse-deer	16	40	2.81	2.73	23	LC

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Mydaus javanensis	Malay badger	10	8	1.76	0.55	12	LC
Trichys fasciculata	Long-tailed porcupine	1	43	0.18	2.93	20	LC
Thecurus crassispinis	Thick-spined porcupine	2	45	0.35	3.07	16	LC
Martes flavigula	Yellow-throated marten	4	5	0.70	0.34	8	LC
Viverra tangalunga	Malay civet	5	35	0.88	2.39	22	LC
Paguma larvata	Masked palm civet	10	12	1.76	0.82	12	LC
Paradoxurus philippinensis	Common palm civet	4	3	0.70	0.20	6	LC
Total	**23 spp.**	**90**	**483**	**15.82**	**32.95**	**289**	

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Asymptotic estimates of species richness for planted ($n = 25$ sites) and secondary forest ($n = 62$ sites) were similar, even when species richness in secondary forest (~20) was rarefied to the level of sampling effort in tree plantations (Figure 2a). Sample completeness for the smaller sample (plantation) approached 90% (Figure 2b), but at any sample size less than 26, curves indicated that sample completeness within secondary forest was higher than in tree plantation. Species richness estimates for cameras placed in planted versus secondary forest were almost identical when rarefied to the minimum sample coverage of 90% (Figure 2c).

3.2 Variation in mammal species richness with environmental predictor variables

Tests for multicollinearity among predictor variables generated VIF values ranging from 1.22 to 4.29. Spearman correlation tests between variables indicated a strong negative correlation between area of secondary and tree plantation within the 500-m buffer (Appendix B.5), thus we did not combine these two variables in any single model. Models of GLMs fitted with a Poisson distribution were overdispersed for species richness, mammal detections, and threatened mammal detections. Therefore, we used the negative binomial distribution to assess relationships between response variables and environmental predictors.

Four competing models captured 73% of the total AIC_c weight for species richness (Appendix A.3). The area of tree plantation within the 500-m buffer of a site was the strongest predictor variable, indicating lower species richness with increasing area of tree plantation (Figure 3). Mean predicted species richness across all sites was 3.29 (sd = 0.96). As an indication of effect size, increasing the area of tree plantation by 25 or 50% would predict a decline in species richness to 2.46 and 1.84, respectively. Confidence intervals excluded zero for parameter estimates of two additional predictor variables: species richness was greater with increasing distance from human settlements and at sites with less horizontal cover (Table 4). Patterns of species richness in the study area reflect the combined effects of plantation and settlements, with greater species richness where plantations and human settlements were absent (Figure 4).

Three negative binomial models of total mammal detections had ΔAIC_c values <2, with decreasing area of tree plantation and increasing distance from human settlements predicting greater mammal detections (see effects plots, Appendix B.6). Increasing the area of tree plantation by 25 or 50% of the buffer area would decrease detections from a mean of 6.58 to 4.43 and 3.01, respectively. In threatened mammals, decreasing the area of secondary forest by 25 or 50% of the buffer area would result in declines from a mean of 3.19 detections to 2.11 and 1.43, respectively.

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416

4. DISCUSSION

417 Our analyses using camera trap data revealed that at least 23 large and medium-sized mammals

419 used the mosaic of plantation and secondary forests stands. Rarefaction/extrapolation (R/E)

420 analyses suggested no differences in species richness among plantation and secondary forest

421 sites, and effective diversity indices were similar as well. R/E is designed for datasets with

422 unequal samples and incomplete inventories in different habitat types; nevertheless, the wide

423 confidence intervals around extrapolated species richness in the smaller dataset reflect

424 considerable uncertainty about estimated species richness in plantations. These results likely

425 owe to the limited number of camera sites ($n = 25$) in tree plantations compared with secondary

426 forest ($n = 62$). Moreover, for R/E analysis, sites were classified according to the physical

427 location and field of view of the camera. Plantation sites typically had a mix of secondary forest

428 nearby and thus a mixture of habitat types existed within the vicinity of sample sites. In contrast

429 to R/E analysis, GLMs explored variation in forest composition (i.e., within a 500-m buffer) of

430 87 sample sites and included additional landscape variables that were not captured in the R/E

431 analysis. The proportion of tree plantation within the 500-m buffer was the strongest predictor

432 of species richness and mammal detections, both of which declined as the proportion of tree

433 plantation increased. The area of secondary forest was also a strong positive predictor of

434 mammal detections, including detections of threatened mammals. Distance from human

435 settlements played a secondary role, with greater species richness, total mammal detections,

436 and threatened mammal detections predicted farther away from settlements. Combined, these

437 results suggest that commercial tree plantations limit use by native mammals but that retention

438 of larger areas of secondary forest around plantations likely contributes toward the

439 conservation of large and medium-sized mammals in managed landscapes, including predators

440 (e.g., wild felids) and seed dispersers (e.g., bearded pig, primates, sun bear).

441

442 We note that mammal diversity in primary forests is greater than those in the mosaic of

443 plantation and secondary forests we studied. Indeed, findings from other camera trap studies

444 of mammals in northern Borneo suggest that natural forests with limited human impacts (e.g.,

445 from logging) possess greater species richness (27–33 species) and contain more threatened

446 mammals compared with plantations (e.g., Samejima et al. 2012, Bernard et al. 2013, Sollman

447 et al. 2017). Where oil palm and commercial plantations have replaced secondary forest,

448 remnants of natural forest seem important, if not crucial, for many species (e.g., McShea et al.,

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2009; Bernard et al., 2014; Ng et al., 2021). Plantation monocultures of exotic trees are likely to remove resources and disrupt co-evolved relationships among species that secondary forests will still retain. Also, secondary forests possess more canopy openings, allowing for greater light penetration and thus herbaceous cover and browse, that can support a complex assemblage of herbivores and higher trophic level species. Indeed, the presence of apex mammalian carnivores such as tiger (*Panthera tigris*), leopard (*Panthera pardus*), and dhole (*Cuon alpinus*) in degraded secondary forests in Peninsular Malaysia, confirms the conservation value of these modified forest habitats (Rayan and Mohamed 2009, Rayan and Linkie 2016). Long-established *Acacia* plantations may eventually support mammal communities that have habituated to altered conditions; for example, detections of bearded pig, muntjacs, western tarsiers, and civets were greater in *Acacia* plantations than in natural forests in a nearly 40-year-old commercial plantation mosaic in northern Sabah (Ng et al. 2021). Notably, less than 20% of the Ng et al. (2021) study area consisted of natural (secondary) forest, whereas McShea et al.'s (2009) study area and ours consisted of 53 and 83% secondary forest respectively, with the oldest *Acacia* stands planted just eight years preceding both studies. Considering medium to large mammals alone, McShea et al. (2009) recorded 24 species in a 644-km^2 study area compared with the 23 species in our 240-km^2 study area. Ng et al. (2021) reported 21 species in their 250-km^2 study area, which is slightly less, but they grouped all civet species.

In Southeast Asia, tree plantations other than oil palm are not always associated with reductions in species diversity. For example, Mang and Brodie (2015) noted that older (>10 yrs) *Acacia* plantations supported native biodiversity more effectively than young *Acacia* or other plantation types, and they attributed this in part to the complex understory that develops over time in older plantations. Tree plantations may have variable effects on vegetation diversity depending on the original land cover of the area (Bremer and Farley 2010). A global metanalysis of native mammal diversity in tree plantations reports reductions in both richness and abundance, but, regardless of plantation type, where heterogenous understories with native forest vegetation occurred, mammal diversity increased, occasionally displaying greater diversity than in natural forests. (Ramirez and Simonetti 2011). In our study area, although 19 (67%) of the 25 camera sites in plantations were in *Eucalyptus pellita*, the oldest plantations stands were less than 6 years old. The effects of tree plantations on species diversity therefore may depend on a multiplicity of factors, including plantation age, vegetation profile, and the nature of land cover preceding plantation establishment.

Sixty percent of the large and medium-sized mammals we detected were classified as Near Threatened ($n = 4$), Vulnerable ($n = 9$), or Critically Endangered ($n = 1$; IUCN, 2020). The Critically Endangered Sunda pangolin was detected in secondary and tree plantations in this study as well as in *Acacia* plantations in the Bengkoka Peninsula (Ng et al. 2021). We detected one species, *Herpestes semitorquatus*, that was not recorded during previous (2013–2017) surveys within the study site. The clouded leopard, the top predator in Borneo, was only detected at natural forest sites, along with binturong, marbled cat, collared mongoose, tufted ground squirrel, and western tarsier. In previous surveys and our study, the leopard cat was relatively common compared with other felids and occurred in multiple habitat types. Maiwald et al. (2021) suggested that carnivores such as the leopard cat occur as frequently in logged forest and sites with active logging operations as unlogged forests. Species in our study that frequently occurred in both secondary and tree plantations were among those that are most widespread in Sabah's forests (e.g., pig-tailed macaques, mouse-deer, Malay badgers, and the masked palm civet).

The positive relationship of mammal species richness with decreasing horizontal cover suggests that local sites with lower densities of understory vegetation may provide habitat conditions that allow use by multiple species or simply reflect a path of least resistance for animal movement. Horizontal cover was not associated with total and threatened mammal detections, however, suggesting that detection was likely not affected by variation in understory vegetation. Although roads and plantation activities were not important predictors in our models, proximity to human settlements was associated with lower species richness and mammal detections. Furthermore, secondary forests closer to settlements and plantations contained greater densities of *Acacia mangium* and pioneer species compared to secondary forest located farther away, which more closely resembled Class 1 reserves. The presence of *Acacia mangium* near human settlements preceded the establishment of the plantation, and together with poaching, may have contributed to reduced species richness and occupancy by wild mammals. Similar trends were also reported in an *Acacia* plantation in Sarawak (e.g., McShea et al., 2009). For our analysis, we mapped 52 villages or settlements within the study area and additional campsites for plantation workers. Avoidance of anthropogenic sites by large and medium-sized mammals has been reported in other studies. In Tabin Wildlife Reserve in Sabah, Tee et al. (2021) suggested that sun bears near the periphery of the reserve altered activity patterns in response to anthropogenic activities associated with adjacent oil palm plantations. Besides mammal avoidance, our findings of lower mammalian species richness

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and detections near settlements may also be a function of demographic impacts of poaching on mammal populations. For example, Guharajan et al. (2022) noted that sun bear distribution was influenced by human settlement density and related this to poaching pressure. Poaching was evident from our camera trap photos and from direct encounters while installing or checking cameras. The main road to enter the study site was guarded and gated to control access and hunting within the study area was prohibited. Thus, poaching was likely associated with local villagers that lived within and near the study area that could access the forest on foot without the need for road access. Poaching poses one of the greatest threats to vertebrate species in Southeast Asia. Of particular concern are home-made snares, which are ubiquitous in Bornean forests, and easily constructed from cheap materials that are widely available (Gray et al., 2018). Home-made snares represent the most popular hunting method of local villagers within and surrounding the study area, and because they kill or maim numerous species indiscriminately, snares are extremely harmful to vertebrate populations (Gray et al., 2017; Gray et al., 2018). In Southeast Asia, a growing middle class, increasing wealth, and traditional beliefs in the health benefits of wildlife products are important drivers of poaching, resulting in high rates of biodiversity loss in protected and unprotected areas (TRAFFIC 2008, Harrison et al., 2016).

There are several caveats regarding interpretation of our findings. First, we used scented lures to improve detection probabilities. Attraction to the scent may vary among species, which could have introduced detection bias. However, a wide range of mammals (carnivores, omnivores, and herbivores) showed interest in the lures and this potential bias must be weighed against failing to detect a species within a sampling unit because it was not within the relatively small detection range of the camera. For example, an animal may forage behind the camera, but not in front of it (e.g., du Preez et al., 2014). Whereas the use of scent lures likely enhanced detection probabilities, we may not have documented several rare species, even if they occur in the broader area (i.e., bay cat [*Catopuma badia*] was recorded once in the study area during previous monitoring efforts by the first author). Secondly, in our study design we designated sample sites as plantation or secondary forest based on placement and field of view of the camera, which was skewed toward secondary forests because of their greater prevalence within the study area. We likely accounted for some these sample size differences by using rarefaction analyses to estimate species richness and diversity. Additionally, this was less of a concern for our GLM analyses because we used proportions of plantation and secondary forests with 500 m of camera sites as metrics, along with other spatial predictor variables. Because of spatial heterogeneity in the study, these metrics allowed us to sample a broad range of forest conditions.

551 Also, we did not sample areas in the immediate vicinity of villages because of high risk of

552 camera theft, areas under native land claims or land disputes (Figure 1: C6, C9, C10, C11, C12,

553 C14), and several areas where terrain and lack of roads limited access (Figure 1: C13, C14).

554 These areas were primarily secondary forest and thus limited the impact of these sampling

555 decisions on overall results. Finally, we note that our study area was relatively small. Thus, we

556 did not explicitly measure the influence of overall proportions and spatial arrangement of

557 plantation and secondary forests on mammalian diversity and species assemblages, which

558 would require assessment and comparisons across larger and varying landscapes. Similarly, the

559 strongest predictor in GLM analyses, namely plantation forest area, was measured only at the

560 500-m scale. Examination of area variables at multiple scales would help ascertain the most

561 informative scale for detecting an effect. Additional research across larger study areas will be

562 needed to further quantify these spatial relationships and scales and optimize conservation

563 values under different forest management scenarios.

564

565 The demand for timber from natural forests has been in steady decline since its peak in 1989

566 and the global demand for roundwood is now adequately met by commercial tree plantations

567 (Warman, 2014). In Borneo, pulpwood plantations (i.e., *Acacia* and *Eucalyptus* spp.) are

568 important contributors to the region's economy (Gaveau et al., 2016). Mammalian diversity

569 objectives may be effectively incorporated into the implementation of adaptive management

570 plans for commercial plantations in Southeast Asia by maintaining landscape mosaics. Data

571 from our study show that landscape mosaics of commercial plantations and secondary or

572 natural forest can support a diverse assemblage of mammals, including many species that are

573 classified as threatened. Patterns of predicted species richness in the study area (Figure 4)

574 suggest where and how managers can configure the placement of future timber stands, worker

575 camps, and conservation areas to maximize mammal diversity and reduce human impacts.

576 Sustainable management of these types of landscapes may be crucial for biodiversity

577 conservation in Southeast Asia while meeting the worldwide demand for wood and wood

578 products.

579

5. CONCLUSIONS

581 Retention of secondary forest within plantation areas has high conservation value. Secondary

582 forest (i.e., riparian reserves, steep areas, and water catchments) within plantation areas play a

583 significant role in supporting populations of large and medium-sized mammals in Borneo and

584 Sumatra (e.g., McShea et al. 2009, Yaap et al., 2016, Ng et al. 2021). Furthermore, secondary

20

forests can potentially serve as movement corridors and secure habitat to provide connectivity across broader landscapes associated with commercial tree plantations (Mohd-Azlan, 2006; McShea et al., 2009; Yaap et al., 2016). Protecting these areas may be accomplished through enhanced enforcement and monitoring of harvesting operations, which will be critical to minimize damage, disturbance, and human encroachment. Where possible, degraded secondary forest within the plantation areas may be identified and their value to mammal species enhanced through rehabilitation or replanting of native tree species, such as Fig (*Ficus* spp.). Encouraging the regeneration of native trees within tree plantations themselves will enhance mammal diversity. Of course, in natural tropical forests that are relatively undisturbed, mammalian richness and diversity are greater and include more threatened and specialist species than what we observed in the mosaic of plantation and secondary forests. However, within managed forest landscapes, even small areas of secondary forest can be important, although more research is needed to determine area and interspersion configurations for retention of secondary forests that best support mammal conservation. Finally, monitoring of wildlife populations in plantation areas will be important to inform adaptive conservation strategies, enhance sustainable forest practices, and for early detection of threats such as poaching.

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868

Figure Captions

870 Figure 1: Land use of the study area in a commercial tree plantation area of Asian Forestry

871 Company Sabah (AFCS) located in Kota Marudu and Pitas districts, Sabah, Malaysia (2018

872 data). White shaded areas indicate native-claimed lands under dispute and were excluded

873 from the study area. Camera traps were not placed within coupes C6, C9, and portions of

874 C10–14 because of land disputes and a high risk of camera theft.

875

876 Figure 2: Mammal species richness metrics derived from camera trap data collected within a

877 commercial tree plantation in Kota Marudu and Pitas districts, Sabah, Malaysia, 2018. The *y*

878 axes represents both rarefied and extrapolated values. Solid lines represent rarefaction

879 (estimates of richness or sample coverage in the larger sample at a comparable sampling

880 effort); solid symbols represent reference samples and dashed lines represent extrapolation up

881 to the maximum sample size of 62, the largest reference sample size. Shaded areas indicate

882 95% confidence intervals based on 5,000 bootstrap replications. Observed species richness

883 and reference samples are represented by solid icons. a) Sample-size-based rarefaction and

884 extrapolation estimates of species richness in secondary forest and tree plantation (sample

885 size and observed species richness for each reference sample in parentheses); b) sample

886 coverage for rarefied samples and extrapolated samples as a function of sample size (sample

887 size and observed sample coverage for each reference sample in parentheses); c) coverage-

888 based rarefaction and extrapolation curves (observed sample coverage and species richness

889 for each reference sample in parentheses).

890

891 Figure 3: Standardized parameter estimates of model-averaged regression models showing the

892 relative influence of habitat predictor variables on mammal species richness, all mammal

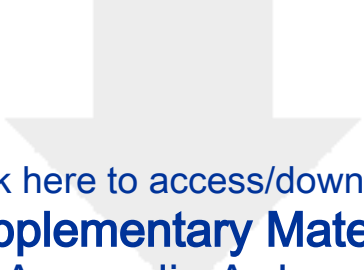893 detections, and threatened mammal detections at an Asian Forestry Company (Sabah)

31

894 commercial tree plantation area, Sabah, Malaysia, 2018. Black circles show the parameter

895 estimate and gray horizontal lines represent the 85% confidence interval (Arnold, 2010). Forest

896 cover (i.e., secondary forest, tree plantation) was based on an area (ha) measurement within a

897 500-m buffer of each camera site. Distance (m) variables were measured to the nearest point,

898 linear, or polygon feature. Horizontal cover was measured by sighting distance (m); positive

899 coefficients for horizontal cover indicate greater sighting distance and thus less horizontal

900 cover.

901

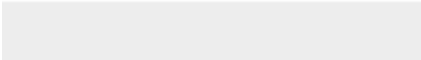902 Figure 4: Predicted mammal species richness based on model-averaged ($\Delta AIC_c \leq 2$) parameter

903 estimates of regression models for an Asian Forestry Company (Sabah) commercial tree

904 plantation in Kota Marudu and Pitas Districts, Sabah, Malaysia, 2018. Predictions are provided

905 for the study area only.

906

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Supplementary Material
Appendix A.docx

Declaration of interests

☐The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☒The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Wilvia Olivia William reports financial support was provided by Forest Solutions Malaysia Sdn. Bhd. Wilvia Olivia William reports a relationship with Forest Solutions Malaysia Sdn. Bhd. that includes: employment and funding grants.

Legend

- ⊙ Camera Station
- △ Settlements
- ----- Road
- —— River/Stream
- ☐ AFCS Coupe Boundary
- ☐ Forest Reserve Boundary
- ☐ River Buffer
- ☐ Cleared Forest
- ☐ Secondary Forest

Planted Forest
- ☐ Acacia spp.
- ☐ Albizia spp.
- ☐ *Eucalyptus pellita*

Scale 1:100000
Datum: Timbalai 1948 (Brunei, East Malaysia)
Projection: Borneo RSO (GP)
Unit: Meter

0   8 km

a)

b)

c)

Mammal species richness

Total mammal detections

Threatened mammal detections

Legend

AFCS concession boundary

Forest Reserve

▲ Settlement

- - - Road

● Camera station

Predicted species richness

7.4

3.3

0.7

N

0   2.5   5   7.5   10
Kilometers