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Spencer, Katie, Deere, Nicolas J., Aini, Muhammad, Avriandy, Ryan, Campbell-Smith, Gail, Cheyne, Susan M., Gaveau, David L. A., Humle, Tatyana, Hutabarat, Joseph A., Loken, Brent and others (2023) *Implications of large-scale infrastructure development for biodiversity in Indonesian Borneo.* Science of the Total Environment, 866 . ISSN 0048-9697.

1 **Implications of large-scale infrastructure development for biodiversity in Indonesian**

2 **Borneo**

3

4 **Abstract**

5 Indonesia is embarking on an ambitious relocation of its capital city to Kalimantan, Borneo,

6 bringing with it major urban and road infrastructure. Yet, despite being one of the world's

7 most biologically diverse regions, the potential implications of this development for wildlife

8 have yet to be fully assessed. We explored the potential impacts of the capital relocation, and

9 road expansion and upgrades to critical habitat for medium-large mammals (> 1 kg) using

10 camera trap data from 11 forested landscapes. We applied Bayesian multi-species occupancy

11 models to predict community and species-level responses to anthropogenic and

12 environmental factors. We extrapolated spatial patterns of occupancy and species diversity

13 across the forests of Kalimantan and identified "critical habitats" as the top 20th percentile of

14 occupancy and species richness values. We subsequently overlapped these critical habitat

15 layers with infrastructure impact zones to estimate the area that could potentially be affected

16 by direct or secondary impacts. At both the community and species-level, distance to primary

17 roads had the strongest negative influence on habitat-use. Occupancy was also influenced by

18 forest quality and multidimensional poverty conditions in adjacent villages, demonstrating

19 the sensitivity of biodiversity to socio-ecological pressures. Less than 1% of the critical

20 habitat for the threatened mammal community lay within the direct impact zone (30 km

21 radius) of the capital relocation. However, approximately 16% was located within 200 km

22 and could potentially be affected by uncontrolled secondary impacts such as urban sprawl

23 and associated regional development. The often-overlooked secondary implications of

24 upgrading existing roads could also intersect a large amount of critical habitat for lowland

25 species. Mitigating far-reaching secondary impacts of infrastructure development should be

26   fully incorporated into environmental impact assessments. This will provide Indonesia with

27   an opportunity to set an example of sustainable infrastructure development in the tropics.

28

29   **Keywords**

30   Kalimantan, Road expansion, Nusantara, Occupancy modelling, Camera traps, Mammal

31   ecology

32

33   **1. <u>Introduction</u>**

34   The tropics are experiencing a biodiversity crisis, with more threatened terrestrial

35   mammals residing in Southeast Asia than other comparable regions (Schipper et al., 2008).

36   With imminent large-scale infrastructure projects underway throughout Southeast Asia, it is

37   important to assess potential implications these developments might have for biodiversity

38   (Ng et al., 2020). Identifying these implications early in the development process allows for

39   adjustments and safeguards to be put in place so that infrastructure can be expanded in a

40   sustainable way (Garrard et al., 2018).

41   Declines in tropical biodiversity are driven by multiple interconnected ecological and

42   anthropogenic factors (Gallego-Zamorano et al., 2020). Habitat loss and degradation

43   influence animal communities through altered resource availability, reduced population

44   connectivity (Kaszta et al., 2020) and increased contact with people, often leading to conflict

45   and hunting (Azhar et al., 2013). Human-driven threats can be fuelled by demand for wild

46   meat (Ripple et al., 2016), traditional medicine (Davis et al., 2020), illegal or legal trade

47   (Symes et al., 2018), and negative human-wildlife interactions affecting people's livelihoods

48   (Rode-Margono et al., 2016). These ecological and anthropogenic factors are pervasive in the

49   tropics and can lead to defaunation even in intact or protected forests (Benitez-Lopez et al.,

50   2019). Since the mid-20th century, Asia has experienced strong economic growth (Bloom and

51 Finlay, 2009) and a tripling of its human population (Worldometer, 2022), which has

52 exacerbated demand for wildlife products and subsequent declines in mammal populations

53 (Linkie et al., 2018). For example, 79% of primate species in this region are threatened with

54 extinction (Schipper et al., 2008), and heavily traded and consumed species such as pangolin

55 (*Manis spp*.), tiger (*Panthera tigris spp*.) and banteng (*Bos javanicus*) have been relisted as

56 Endangered or Critically Endangered in recent years (Gardner et al., 2016; Challender et al.,

57 2019; Goodrich et al., 2022). These biodiversity declines will likely continue as countries

58 invest in large-scale infrastructure (Shira et al., 2011), unless well-planned mitigation

59 strategies are put in place.

60   Infrastructure development and urban land expansion are major drivers of habitat

61 disturbance and loss across the world (Laurance et al. 2015), but have received relatively

62 little attention when compared with other drivers of biodiversity decline such as agriculture

63 (Simkin et al., 2022). Asia is currently at the forefront of infrastructure development globally

64 with the "Belt and Road Initiative" – the largest infrastructure programme in human history -

65 passing through 72 countries and numerous fragile ecoregions and habitats (Ng et al., 2020).

66 The initiative is bolstered by ambitious national targets and development plans which are

67 already underway, including road and hydropower development in Myanmar (Kaszta et al.,

68 2020) and Malaysia (Alamgir et al., 2020), and a 10-year master plan for economic

69 development in Indonesia that aims to capitalise on natural resources and redistribute wealth

70 across the archipelago (Shira et al., 2011).

71   Indonesia's most ambitious infrastructure project is the relocation of its capital city

72 Jakarta, from Java to East Kalimantan (Indonesian Borneo). The new capital, "Nusantara",

73 will house Indonesia's national government and administration, which are currently hindered

74 by Jakarta's environmental and socio-economic issues arising from the rapidly growing

75 human population (Van de Vuurst and Escobar, 2020). There are more than 30 million people

76   residing in the Jakarta metropolitan area, with the inner city having an immensely high

77   population density of 14,464 people/km^2 (World Population Review, 2022). Jakarta

78   experiences problems with land subsidence, waste management, pollution and traffic

79   congestion, and is increasingly faced with flooding and rising sea levels linked to climate

80   change (Van de Vuurst and Escobar 2020). The US$32 billion capital relocation project,

81   originally planned for completion by 2024 but delayed during the pandemic, promotes

82   upgrades of airports, seaports, and new access roads to transform the region into a low carbon

83   superhub that facilitates economic development across the archipelago (Da Costa and Lamb,

84   2022). The relocation is expected to bring socioeconomic benefits and the government has

85   pledged a "smart, green and clean" capital city (Adri, 2019). However, there remains some

86   concerns that the environmental and societal challenges experienced in Jakarta will be

87   transferred to Borneo with potentially major repercussions for local wildlife and livelihoods

88   (Mutaqin et al., 2021; Van de Vuurst and Escobar, 2020).

89   The construction and expansion of urban centres and road networks across the world

90   are associated with numerous direct and secondary environmental impacts (Bennett, 2017;

91   Simkin et al., 2022). Construction and land clearance directly affect the surrounding

92   environment, whereas uncontrolled extractive industries (i.e., agriculture, mining and

93   logging), migration and urban sprawl also create secondary impacts that influence ecosystems

94   much further away from infrastructural localities and can be worse than the initial

95   development (Teo et al., 2020; Laurance et al., 2015). For example, the relocation of Brazil's

96   capital city to Brasília in the 1950's facilitated widespread road construction and human

97   intrusion in the Amazon rainforest, leading to deforestation in previously remote regions

98   (Laurance et al., 2015). In Kalimantan, the direct expansion of Nusantara could exceed a 30

99   km radius by 2045 with associated regional development and deforestation affecting up to a

100   200 km radius, intersecting forest, peat and mangroves (Teo et al., 2020). Therefore,

assessments of the effects this might have on biodiversity are needed before the eco-friendly

vision for this capital can be realised. Previous studies have explored potential consequences

for specific land-cover types (Teo et al., 2020), climate change (Van de Vuurst and Escobar

2020) and environmental degradation (Mutaqin et al., 2021; Farida 2021), but none have

explicitly investigated implications for biodiversity using empirical data.

The capital relocation should also be considered alongside broader consequences of

road expansion – so-called economic corridors – that will connect Nusantara to other growing

urban areas across Borneo whilst also facilitating extraction and transportation of the island's

natural resources such as coal, timber, and palm oil (Shira et al., 2011). In Borneo, roads are

reported to be upgraded or expanded by > 3,300 km and 1,920 km, respectively, with

potentially negative consequences for protected areas and landscape connectivity (Alamgir et

al., 2019). The negative consequences of roads on wildlife are well-documented. These

include direct impacts such as wildlife-vehicle collisions (Silva et al., 2020), edge-effects

(Pfeifer et al., 2017), habitat fragmentation (Kaszta et al., 2020), and forest clearance (Barber

et al., 2014). However, similarly to other infrastructure types, roads are also accompanied by

secondary disturbances such as mining, agriculture, and associated deforestation and hunting

that radiate further than the linear clearing itself due to increased accessibility into previously

remote areas (Asner et al., 2013; Gaveau et al., 2021).

Here, we provide the first large-scale appraisal of the potential biodiversity impacts of

infrastructure development in Kalimantan using empirical data. We compiled camera trap

data from 11 sites across Kalimantan to predict the spatial patterns of mammal occurrence

and diversity and quantify the effects of infrastructure development to critical habitats of

threatened species. Using multi-species occupancy models, we; 1) determine how mammal

populations respond to current environmental and anthropogenic factors across the region; 2)

estimate the proportion of critical habitat of threatened mammals that could potentially be

126 implicated by uncontrolled direct and secondary impacts of infrastructure development; and

127 3) provide recommendations to minimise these impacts. Our study provides an important

128 baseline from which mammal populations can be monitored in relation to continued

129 infrastructural expansion, and an evidence-base to support actions to reduce habitat loss. The

130 analytical framework could be readily applied to similar large-scale infrastructural

131 assessments worldwide.

132

2 Methods and materials

Study region

135 Kalimantan encompasses 73% of Borneo (533,400 km^2), approximately half of which is

136 comprised of forest habitat, including lowland and hill dipterocarp forests, peatland and

137 freshwater swamps in coastal and low-lying areas, and mountainous forests in the interior.

138 Over 30% of Kalimantan's forests have been converted to other land-uses since the 1970s

139 with less than 43% intact forest cover and 26% logged forest remaining (Gaveau et al., 2014).

140 To date deforestation has largely occurred in unprotected areas and in land gazetted for

141 conversion to industrial plantations (Voigt et al., 2022). However, protected forests can also

142 be subject to illegal logging, hunting, and small-scale conversion to plantations (Fawzi et al.,

143 2018). Most development is concentrated on the coastal lowlands of the region's five

144 provinces (Central, East, North, South, West), where plantation agriculture dominates. Urban

145 areas and primary road networks are also predominantly located in these lowland regions,

146 with East Kalimantan particularly influenced by infrastructure development and human

147 population growth (Fuller et al., 2010).

148

Camera trap sampling of medium-large mammals

150 We collated camera trap data from 11 sites across West ($n = 4$), Central ($n = 3$) and East

151 Kalimantan ($n = 4$) (Fig. 1) spanning a gradient of habitat (primarily lowland and hill

152 dipterocarp forests, and peat swamp) and management types (Table 1). Surveys were

153 implemented in forests allocated specifically for conservation ($n = 7$), watershed protection (n

154 $= 3$) and logging ($n = 2$) (S1 and Table S1). Sites were sampled between 2012 and 2019,

155 comprising an average of 44 camera stations per site (range: 19 – 79) separated by a mean

156 inter-trap distance of 0.78 km. Cameras were positioned approximately 0.5 m from the

157 ground and positioned on or near animal trails or key environmental resources (i.e., salt licks,

158 water sources) to maximise detections. Length of camera deployment was variable between

159 years, stations, and sites, therefore, to standardise sampling effort and meet assumptions of

160 demographic closure for occupancy analysis we limited sampling periods to 90 consecutive

161 nights per camera station per site. Camera data were pooled to make inferences at the

162 landscape level whilst accounting for site-level heterogeneity.

163 We define the mammal community as medium-large bodied (> 1 kg), terrestrial

164 species (Table S2). Taxonomically ambiguous species (e.g., lesser mouse deer *Tragulus*

165 *kanchil*, and greater mouse deer *T. napu*; Bornean red muntjac *Muntiacus muntjac*, and

166 Bornean yellow muntjac *M. atherodes*) were pooled into genus-level categories due to

167 inconsistency in species identification among datasets. We excluded primarily arboreal

168 species (e.g., red leaf monkey, *Presbytis rubicunda*) since these were unlikely to be reliably

169 detected by cameras placed at ground-level. The Bornean orangutan *Pongo pygmaeus* was

170 included since terrestrial activity is common for this species (Ancrenaz et al., 2014).

171 Mammals < 1 kg in size (e.g., murid rodents and squirrels) were discarded due to highly

172 variable detection and species identification between study sites.

173 Prior to analysis, we developed a detection matrix for each of the remaining species,

174 whereby 90-day sampling periods were divided into 5-day temporal replicates. Collapsing the

7

175   survey period helps to reduce over-dispersion and increase temporal independence of

176   detections (Penjor et al., 2019). Species with fewer than five detections in the detection

177   matrix (banteng *Bos banteng*, flat-headed cat *Prionailurus planiceps*, bay cat *Catopuma*

178   *badia*, Hose's palm civet *Diplogale hosei* and otter civet *Cynogale bennettii*) were removed

179   from analysis because differences in detectability and occurrence cannot be reliably

180   differentiated when observation data are sparse (Brodie et al., 2015b). Camera stations active

181   for fewer than 10 days were also excluded, resulting in 485 stations each with four to 19

182   sampling occasions.

183

184   Covariates

185   We explored 10 anthropogenic and environmental covariates derived from remotely-sensed

186   data based on their reported influence on mammalian habitat-use at either the community or

187   species levels (e.g. Deere et al., 2020; Tilker et al., 2019b) (Table S3). Human disturbance

188   and hunting patterns are difficult to quantify directly due to the complex nature of human

189   behaviour but can be inferred over large spatial scales using established proxy variables from

190   remote sensing (Tilker et al., 2019a). Therefore, we explored five such proxies to reflect

191   anthropogenic disturbance ranging from traditional metrics (distance to primary roads and

192   density of logging roads) to more bespoke measures: landscape accessibility, human

193   population pressure, and a village-level multidimensional poverty index. We also explored

194   five environmental covariates to capture local environmental conditions around camera traps,

195   including percentage of forest cover (an indicator of habitat availability), aboveground

196   biomass (an indicator of habitat quality), elevation, and characteristics of regional fire

197   regimes (frequency and radiative power). All covariates were time-calibrated to the nearest

198   year of data collection for each site reducing biases associated with different sampling years

199   (Semper-Pascual et al., 2020), except for biomass which was only available for 2018. Further

200   information regarding the source and processing of each covariate can be found in S2 and

201   Table S3. Prior to analysis all continuous covariates were centred around their mean values

202   and scaled to one-unit standard deviation to place the covariates on a comparable scale.

203

204   **Modelling framework**

205   We implemented Royle-Nichols multi-species occupancy models to estimate community and

206   species-specific occurrence probabilities, while correcting for imperfect detection (Royle and

207   Nichols, 2003). This model outperforms other analytical frameworks when variation in local

208   abundance, non-random movement of animals or a biased sampling design induces high

209   levels of heterogeneity in camera trap detection rates (Tobler et al., 2015). To account for

210   overdispersion in the data, we modelled the local abundance a of species i at trapping station

211   j, a_{ij}, as a realisation of a negative binomial process, governed by success parameter, λ_{ij},

212   representing the total number of individuals of each species using the habitat surrounding a

213   camera station (Tobler et al., 2015), and a species-specific dispersion parameter, r_i, to

214   explicitly model spatial variation in abundance:

215   $$a_{ij} \sim NegBin(\lambda_{ij}, r_i)$$

216   Simulated assessments have found the negative binomial model specification to

217   provide numerically unstable parameter estimates (Royle and Nichols, 2003). However, we

218   found no evidence of this when applied to our data. As true abundance is imperfectly

219   observed, summarised detection histories of species i at station j (y_{ij}) were described as

220   realisations of a binomial process:

221   $$y_{ij} \sim Binomial(k_j, 1-(1-p_{ij})^{a_{ij}})$$

9

222   where k_j represents the number of temporal replicates at each station and p_{ij} denotes the

223   probability of detecting species i at camera station j, which was specified to be functionally

224   dependent on mean local abundance (a_{ij}). We estimate occupancy post-hoc, derived as a

225   deterministic function of abundance (Royle and Nichols, 2003):

226     $$\Psi_{ij} \sim 1\text{-exp}(-\lambda ij)$$

227   in which occupancy Ψ_{ij} is defined as the probability of at least one individual occurring at a

228   given station. Throughout, we interpret occupancy as the probability that a species uses the

229   area around each camera (i.e. habitat, or space-use) as the assumption of spatial independence

230   between camera stations could not be met for wide-ranging species (Penjor et al., 2019).

231

232   **Model selection**

233   We implemented a robust model selection procedure to identify the most influential

234   environmental and anthropogenic determinants of mammal occurrence. Across all models,

235   we described abundance using a log link function and included study site identity as a

236   categorical fixed intercept term to account for spatial variation of species occurrence among

237   study sites and reduce bias from spatial autocorrelation due to clustered sampling design

238   (Fieberg et al., 2010; Rich et al, 2016). Initially, we constructed univariate, multi-species

239   occupancy models to identify the optimal spatial extent to extract predictor values to camera

240   localities (buffer radii: 250, 500, 750 and 1000 m). Scale-optimised predictors were

241   subjected to a second selection process, whereby highly intercorrelated predictors (Pearson's

242   correlation coefficient:|r| > 0.7; Variance Inflation Factors: VIF < 3) were removed.

243   Throughout, selection procedures were guided by the best-ranked model, according to

244   Watanabe–Akaike Information Criterion (WAIC; Watanabe, 2010), the number of species

245   demonstrating a statistical response to the scale/predictor (95% and 75% Bayesian credible

246   interval did not overlap zero) and the temporal scope of the predictor, with preference being

247   awarded to those that could be time-calibrated. The remaining covariates were used to build a

248   plausible model, i.e., its predictions and parameter estimates are biologically plausible

249   (Johnson and Omland, 2004). This resulted in abundance being defined as a function of site-

250   specific intercepts (Site) and four covariates (Table 2): poverty index (*Poverty*), distance to

251   primary roads (*Road*), proportion of forest cover (*Forest*) and forest biomass (*Biomass*):

252      $\log(\lambda_{ij}) = \alpha_{0i}Site_j + \alpha_{1i}Poverty_j + \alpha_{2i}Road_j + \alpha_{3i}Forest_j + \alpha_{4i}Biomass_j$

253   We describe detection using a logit link function as a linear combination of two

254   covariates, including a habitat-specific intercept (*Habitat*), comprising four factor levels

255   (lowland forest, upland forest, peat swamp forest and plantation) and survey effort (number

256   of camera trap nights; *CTN*). Camera model was strongly linked to site and thus excluded

257   from the detection model:

258      $\text{logit}(r_{ij}) = \beta_{0i}Habitat_j + \beta_{1i}CTN_j$

259   We conducted all analyses in JAGS version 4.3.0 through R version 4.1.0 using the

260   package jagsUI; see Supplementary Information S4 for further information on model

261   specification and predictive performance checks. We considered coefficients to have strong

262   support if the 95% Bayesian credible interval (95% BCI, the 2.5th and 97.5th percentiles of

263   the posterior distribution) did not overlap zero and moderate support if the 75% BCI did not

264   overlap zero. Unless stated otherwise, we summarise parameter estimates as the mean of the

265   posterior distribution and express uncertainty using 95% BCI.

266

267   **Spatial analysis of the impact of infrastructure development**

268 To explore impacts of the new capital city and road expansion on mammal communities, we

269 developed occurrence maps for each species using parameter estimates derived from the

270 occupancy model. We linked these with spatially explicit covariates from the most recent

271 year available (2018 for biomass; 2019 for all others) and masked these maps using the

272 observed range of covariate values across camera stations to prevent overprediction. This

273 resulted in occurrence maps for 20 species projected into a recent single time-point prior to

274 the expected infrastructure development associated with the capital. These maps were

275 summed across species to produce a count of species (i.e., a richness layer) corrected for

276 imperfect detection. A separate richness map was produced for high conservation value

277 species (i.e., those listed as "Vulnerable" or higher by the IUCN Red List of Threatened

278 Species; bearded pig *Sus barbatus*, Sunda clouded leopard *Neofelis diardi*, Bornean

279 orangutan, long-tailed macaque *Macaca fascicilaris*, pig-tailed macaque *Macaca nemestrina*,

280 sambar deer *Rusa unicolor*, Bornean sun bear *Helarctos malayanus euryspilus* and Sunda

281 pangolin *Manis javanica*). We also provide estimates of uncertainty for our species richness

282 values with a map of posterior standard deviation in Fig. S2. To identify the most important

283 areas for each species across the projection region, we applied a fixed threshold to select the

284 top 20th percentile of cells with the highest occupancy probabilities (hereafter referred to as

285 "critical habitats").

286   We used overlapping buffer distances to represent ecological "impact zones" of the

287 roads and the new urban area for the capital (Teo *et al.* 2020; Ng *et al.* 2020). We applied

288 impact zone buffers to primary roads (*https://map.nusantara-atlas.org*) cross-referenced with

289 the locations of new and upgraded roads from Alamgir et al. (2019). Buffers of 1 km

290 represent immediate impacts (e.g., edge effects, vehicle-wildlife collisions) (Pfeifer et al.,

291 2017; Silva et al., 2020), 5 km represents direct deforestation and elevated hunting

292 opportunities (Barber et al., 2014) and the 25 km and 50 km zones reflecting broader

293   environmental changes to the landscape such as illegal logging, hunting or mining in distant

294   areas that become more accessible (Ng et al., 2020). Impact zones for the new capital were

295   based on previous research using night-lights to quantitatively assess the spatial growth of

296   previous capital cities (Teo et al., 2020). Therefore, zones of 10 km and 30 km were chosen

297   to represent direct impacts (e.g., immediate land destruction and resource extraction), and 50

298   km and 200 km to represent secondary impacts associated with expanding regional

299   development (e.g., urban sprawl, population expansion, deforestation, and mining or

300   agricultural activities) (Teo et al. 2020). We applied these impact zones to a map of the

301   planned Nusantara location geo-referenced from Indonesia's Ministry of National

302   Development Planning (Bappenas, 2021). Impact zones in closer vicinity to infrastructure

303   represent intense, but best-case scenario effects, whereas those further away assume the

304   worst-case scenario of uncontrolled secondary impacts.

305   We present results collectively across threatened mammal species as well as

306   individually for two focal taxa: the Bornean sun bear and Bornean orangutan. These species

307   were chosen as they are both highly threatened by human activities (Vulnerable and Critically

308   Endangered, respectively, according to the IUCN), but differ in their distributions and

309   ecology. For example, orangutans are found in higher densities in the lowland regions

310   compared to the higher elevation interior forests (Husson et al., 2009).

311

312   **Results**

313   Analysis of the 485 camera stations yielded 35,992 camera trap nights and 4,621 independent

314   detections of 20 medium-large mammal species (Table S5). Only three out of 20 species

315   (bearded pig, mouse-deer *spp*. and pig-tailed macaque) were detected at all 11 sites. Muntjac

316   *spp*. ($n = 1,105$) and bearded pig ($n = 810$) were the most detected taxa, while Sunda pangolin

317   (*n* = 11) and common palm civet *Paradoxurus hermaphroditus* (*n* =10) were detected the

318   least.

319

320   *Influence of anthropogenic and environmental variables on the mammal community*

321   Overall, the mammal community had a stronger response to anthropogenic rather than

322   environmental predictors. Distance to primary roads had the strongest negative response at

323   both the community (mean occupancy 0.64, 0.22 to 1.1) (Fig. 2), and species-level (12 of the

324   20 taxa) (Fig. 3). The strongest responses were demonstrated by Sunda clouded leopard

325   (*Neofelis diardi*; 1.69, 0.9 to 2.48), long-tailed porcupine (*Trichys fasciculata*; 1.47, 0.44 to

326   2.65) and mongoose species (*Herpestes spp*.; 1.35, 0.49 to 2.3) (Fig. 3). At the community-

327   level, poorer villages were associated with lower mammal habitat-use in nearby forests (-

328   0.41, 75% BCI: -0.67 to -0.15; Fig. 2). This was underpinned by a consistent moderate,

329   negative response by all observed mammals apart from leopard cat (*Prionailurus bengalensis*;

330   -0.32, 75% BCI -0.67 to 0.03) and sambar (*Rusa unicolor*; -0.22, 75% BCI: -0.60 to 0.18)

331   (Fig. 3).

332   Mammals were found to be less responsive to local environmental characteristics,

333   suggesting a degree of tolerance towards habitat disturbance. Proportion of forest cover was

334   not an influential predictor of habitat-use at the community level (Fig. 2), or for 17 of the 20

335   species (Fig. 3). However, two species had higher habitat-use in areas with reduced forest

336   cover (bearded pig; -0.31, 95% BCI: -0.61 to -0.03; long-tailed macaque *Macaca*

337   *fascicularis;* -0.25, 75% BCI: -0.47 to -0.03). Bornean sun bear was the only species to

338   exhibit a preference for forested habitats (0.31, 75% BCI: 0.07 to 0.56). Habitat quality

339   (biomass) had a moderately positive influence on community habitat-use (0.01, 75% BCI:

340   0.04 to 0.19) (Fig. 2), which was predominantly driven by the habitat preferences of

341   orangutans and sambar deer (Fig. 3).

342

343   *Assessing the impact of infrastructure expansion*

344   Across Kalimantan, model-predicted species richness at the camera station ranged from two

345   to 14 for the observed mammal community and one to six when only threatened species were

346   considered. Almost 18% of the 247,257 km^2 projection region in Kalimantan was deemed

347   critical habitat for threatened mammals overall (top 20th percentile of richness values: 3.2-

348   5.6). The amount of land designated as critical habitat varied substantially among species. For

349   sun bear, 47, 960 km^2 (19.4% of suitable forest available) was deemed critical habitat based

350   on the top 20th percentile (ψ: 0.56 to 0.99), whereas 8,503 km^2 (3.4% of suitable forest

351   available) was deemed critical for the Bornean orangutan (ψ: 0.17 to 0.26).

352

353   a)   Capital city relocation

354   The proportion of important habitat intersecting with the impact zones of the new capital city

355   was variable between species. Direct impacts (within 30 km radius) intersected with little

356   critical habitat for threatened mammals overall and sun bears specifically (< 1% of the total

357   habitat), whereas secondary impacts (radiating up to 200 km away from the capital)

358   intersected with up to 16.2% of total critical habitat for threatened mammals (Fig. 5).

359   However, critical habitats of orangutans and other lowland-dwelling species could be

360   disproportionately affected by both direct and secondary impacts. For orangutans, this

361   reflects up to 7.9% of critical habitat within direct impacts zones of the new capital and up to

362   42.9% within the secondary impact zones.

363

b) New roads

Though much of the forest surrounding the new northern link of the Trans-Kalimantan highway was beyond the bounds of our data, initial findings suggest these new roads will impact a greater proportion of critical habitat for threatened species overall, and specifically for sun bear compared to orangutan. For new roads, 12.3% of the direct impact zone (within 5 km) and 15.0% of the secondary impact zone (within 50 km) contained critical habitat for threatened mammals, representing 1.8% and 15.5% of the entire forest within the top 20th percentile for mammal richness (Fig. 5). In contrast, just 1.0% of direct impact zones were critical habitat for orangutans, and 1.5% of secondary impacts zones – approximately 0.1% and 8.2% of this species' total critical habitat.

c) Upgraded roads

Conversely, the direct impact zone of upgraded roads, which were primarily in the lowlands, did not overlap the critical habitat for threatened species. However, these species could be affected by sprawling secondary impacts, which intersect with up to 14.1% of critical habitat for threatened mammals across the Kalimantan region. Nearly 12% of the 5 km impact zone contained critical habitat for orangutan, reflecting up to 26.4% of the total habitat. Additionally, 79% of critical habitat for orangutans was predicted to be within the broader secondary impact zone (50 km) of upgraded roads.

4. Discussion

386   Consistent with other tropical regions, Borneo has experienced significant deforestation and

387   biodiversity loss since the latter half of the 20th century (Gaveau et al., 2014), a trend that

388   could continue with planned infrastructure expansion. Combining camera trap data from 11

389   landscapes in Kalimantan, we found anthropogenic, rather than environmental, predictors had

390   the strongest influence on mammal communities. We demonstrate that proximity to road

391   already has a significant influence on mammal habitat-use, and that the further expansion of

392   infrastructure could intersect with critical wildlife habitat. The extent of these impacts will

393   vary considerably between species, infrastructure type and locality but mitigation could

394   reduce the area of habitat implicated.

395   Distance to primary roads was one of the strongest predictors of mammal occupancy

396   (Fig. 2), which mirrors more localised studies undertaken elsewhere in Borneo (Evans et al.,

397   2020; Mohd-Azlan et al., 2020b; Tee et al., 2021). Distance to roads reflects the multitude of

398   direct and secondary disturbances radiating from roads, which alter the physical environment,

399   decrease population connectivity (Kaszta et al., 2019) and increase mortality for many

400   vertebrate species (Healey et al., 2020). Roads can also create population sinks (Carter et al.,

401   2020) and skew mammal community compositions towards generalist species (Mohd-Azlan

402   et al., 2020b). Moreover, human encroachment into previously remote areas facilitates

403   widespread secondary disturbances such as hunting, habitat degradation and urbanisation,

404   which radiate much further than the linear clearing itself (Laurance et al., 2009). For

405   example, increased accessibility into forests via new roads and settlements was linked to

406   significant declines of jaguar and their prey in the Amazon (Espinosa et al., 2018). Similarly,

407   the largest felid in Kalimantan (Sunda clouded leopard) exhibited the strongest negative

408   response to roads in our study (Fig. 3).

409   We found mammal habitat-use was lower in forests neighbouring villages with higher

410   levels of deprivation, determined by our multidimensional poverty index (Santika et al.,

411 2019). Although the relationship between poverty and biodiversity is nuanced, a shared

412 dependence between people and wildlife on limited resources, degraded ecosystems and/or

413 vulnerabilities to environmental disasters such as fires and floods could explain this finding

414 (Barrett et al., 2011). Infrastructure development could influence human wellbeing and

415 poverty in surrounding communities both positively (i.e. improved electricity and water

416 supplies) (Shin et al., 2022), and/or negatively (i.e. environmental degradation) (Barrett et al.

417 2011), and therefore warrants further research.

418 The limited influence of forest extent on mammal occupancy and richness is

419 counterintuitive given the levels of deforestation reported for Borneo during the study period

420 (Gaveau et al., 2014), but is likely due to most cameras being placed within forests. Across

421 the tropics there is ample evidence of wildlife tolerating logging disturbance, but conversion

422 to other land-uses severely diminishing biodiversity (Yue et al., 2015; Oakley and Bicknell,

423 2022). We also found forest quality to influence the mammal community, supporting findings

424 at the global scale (Pillay et al., 2022). We advocate further biodiversity studies in more

425 degraded forests to better capture the impact of forest loss on faunal communities.

426

Implications of Indonesia's capital relocation

428 Whilst the capital relocation will have environmental consequences for surrounding land

429 (Teo et al., 2020), direct impacts (i.e. immediate land conversion within 30 km) to critical

430 habitats of threatened species will be minimal due to the placement of the capital in a region

431 near other substantially developed cities (e.g. Balikpapan and Samarinda) (Farida, 2021).

432 However, species found in higher densities in Kalimantan's lowlands could be

433 disproportionately affected within impact zones of the capital relocation. For example,

434 Bornean orangutan was predicted to have approximately 8% and 43% of its total critical

435   habitat intersected with direct and secondary impacts zones of the capital respectively,

436   compared to < 1% and 16% for sun bears. Therefore, minimising further human

437   encroachment into lowland forest surrounding infrastructure should be a priority to safeguard

438   threatened species restricted to these regions.

439   Our model prediction of lower values for species richness and sun bear occupancy

440   within 30 km of the new capital site reflects the anthropogenic disturbances already

441   influencing biodiversity in East Kalimantan. Human population growth and annual

442   deforestation rates are higher in this province than elsewhere in Kalimantan, with much of the

443   lowlands subject to habitat degradation and infrastructure development (Rustam et al., 2012).

444   Therefore, species not restricted to the lowlands (i.e. sun bear and Sunda clouded leopard) are

445   increasingly associated with the interior regions with higher elevations, further from human

446   settlements (Brodie et al., 2015; Tee et al., 2021). Importantly, for all threatened species

447   assessed, secondary impacts overlapped a larger proportion of critical habitat than the direct

448   impacts (Fig. 5). Capital cities have large ecological footprints and urban land expansion is a

449   major driver of habitat loss (Simkin et al., 2022). The secondary impact zones represent

450   proliferating extractive industries (i.e., mining and timber), land conversion and urban sprawl

451   radiating from the city core (Teo et al. 2020; Muhtar et al., 2021). Whilst this reflects a

452   possible worst-case scenario whereby such actions are uncontrolled, especially at the broader

453   level (200 km), they are arguably more difficult to plan for and prevent (Laurance et al.,

454   2015). Given the environmental problems triggered by overpopulation in Indonesia's current

455   capital city, limiting urban sprawl and migration will be a challenge for the new capital

456   (Mutaqin et al., 2021). For instance, the capital relocation is set to bring another 1.5 million

457   federal workers from Jakarta to Kalimantan by 2024 alone (Watts, 2019), which will require

458   resources from surrounding land (Puppim de Oliveira et al., 2011). Additionally, human

459   encroachment may exacerbate negative human-wildlife interactions in the region

460   (Fredriksson, 2005; Meijaard et al., 2011) or give rise to new urban markets for wildlife

461   products (Corlett, 2007; Linkie et al., 2018). This is particularly concerning for species

462   already threatened by illegal wildlife trade e.g., sun bear and pangolin (Gomez and Shepherd,

463   2019; Nash et al., 2018).

464

Implications of road development

466   New roads (e.g., the northern link of the Trans-Kalimantan highway) are being constructed in

467   the more remote interior of Borneo, which to date has experienced less disturbance than

468   lowland regions and therefore harbours some of the highest biodiversity levels in Kalimantan.

469   Whilst our estimates are conservative given portions of the new road transverse areas outside

470   the limits of our data within the Heart of Borneo region, and also have higher uncertainty (Fig

471   4; Fig. S1), approximately 12% of the direct impact zone of new roads could intersect with

472   these important habitats, pre-disposing populations with a greater risk of vehicle collision

473   (Silva et al., 2020), edge-effects (Pfeifer et al., 2017) and habitat fragmentation (Alamgir et

474   al., 2019). This has been demonstrated in Malaysian Borneo, where the newly constructed

475   Pan-Borneo highway reduced mean species richness and increased the presence of generalist

476   species within 1 km (Mohd-Azlan et al., 2020b). Furthermore, new roads in this region could

477   be a catalyst for wider human accessibility and habitat degradation (Laurance et al., 2015),

478   overlapping with 15% of the total area deemed highest in threatened mammal richness in the

479   worst-case scenario of secondary impacts sprawling up to 50 km either side of the roads.

480   In contrast, the impacts of roads planned for upgrade were of greater concern to

481   species typically found in higher densities in the lowlands. The negative effects of road

482   upgrades are often overlooked (Laurance et al., 2015), yet our analysis predicted over a

483   quarter of critical habitat for orangutans could be within direct impact zones and, in the

484   worse-case scenario, over three-quarters within secondary impact zones of upgraded roads.

485   That said, there appeared no discernible effect of distance to road on orangutan habitat-use in

486   our occupancy analysis (Fig. 3), which may provide some optimism for this adaptable species

487   if human-induced mortality and sprawling land conversion can be prevented (Voigt et al.,

488   2018).

489   Considering the primary goal of road expansion is to increase commercial

490   connectivity and facilitate extractive industries (Shira et al., 2011), and the current level of

491   unmapped roads and extractive activities operational in Kalimantan (Hughes, 2018), these

492   secondary impacts should be anticipated and prevented. Conservation attention should be

493   paid to species particularly sensitive to infrastructure, such as the Sunda clouded leopard

494   which we found to exhibit the strongest negative response to roads (Fig. 3). Research in

495   Sabah predicted a 23% reduction in population connectivity and subsequent population

496   declines for this species in response to the development of highways and railroads (Kaszta et

497   al., 2019).

498

499   **Conservation and management implications**

500   Our findings indicate up to 46% of critical habitat for threatened mammals could intersect

501   with combined impact zones of road expansion and the capital relocation. Importantly,

502   however, this represents the worst-case scenario of uncontrolled secondary impacts.

503   Therefore, there is opportunity to significantly reduce the amount of important habitat

504   affected by new and ongoing development. This should be proactively managed by ensuring

505   any environmental impact assessments (EIAs) and ongoing conservation strategies are not

506   limited to the direct vicinity of infrastructure itself, but also include an appraisal of

507   magnitude, direction and patterns of secondary impacts that radiate far beyond the

508 infrastructure core. Secondary impacts are often excluded from the remit of EIAs, severely

509 underestimating surrounding deforestation (Ritter et al., 2017).

510   More localised research in human-modified landscapes is needed to understand

511 specifically where and how infrastructure will have the severest direct impacts to mammal

512 populations. For road development, this could include longitudinal biodiversity and roadkill

513 surveys (Healey et al., 2020) in critical-habitat areas to inform key locations for interventions

514 including (but not limited to) wildlife crossings, culverts, fencing and traffic control (Bennett,

515 2017). Planners should look to other Southeast Asian countries investing in green road

516 infrastructure; for example, the Eco-Link bridge in Singapore that reconnects nature reserves

517 either side of a major expressway (NParks, 2014). There are also smaller-scale, cheaper

518 alternatives, demonstrated by Malaysia's first urban canopy bridge, which successfully aided

519 crossings of long-tailed macaques (*Macaca fascicularis*) and squirrel species within three

520 months of installation (Yap and Ruppert, 2019). However, the success of such initiatives is

521 varied and requires thorough planning (Bennett, 2017).

522   For Indonesia's Nusantara capital, studies elsewhere imply that the proposed green

523 infrastructure in the core zone should have a lesser impact on biodiversity than conventional

524 equivalents, whilst also benefiting city inhabitants through improved flood management,

525 reduced urban heat and increased human wellbeing (Filazzola et al., 2019; Garrard et al.,

526 2018). There are emerging frameworks to incorporate ecological knowledge into urban

527 planning, which include maintaining and introducing wildlife habitat, aiding habitat

528 connectivity, minimizing anthropogenic disturbances and facilitating positive human-nature

529 interactions (Garrard et al., 2018).

530   Green infrastructure, however, is not a replacement for natural ecosystems (Filazzola

531 et al., 2019). For all infrastructure types, mitigating human encroachment and secondary

532   impacts such as illegal logging, mining and deforestation should be prioritised as these

533   factors already pose a considerable economic cost to Indonesia (Khan, 2014). Additionally,

534   illegal wildlife trade networks should be tackled with stronger enforcement given that roads

535   can enable a shift from subsistence to market-based hunting patterns (Pattiselanno and

536   Krockenberger, 2021) and new transportation links under the Belt and Road Initiative could

537   facilitate trade networks with mainland Asia (Farhadinia et al., 2019).

538   Finally, we stress that our analysis prioritised forest within the top 20th percentile of

539   occupancy and richness values as critical, but viable populations require well-connected

540   habitats. Ensuring connectivity between human-dominated landscapes is vital for threatened

541   and low-density species such as orangutan, sun bear and clouded leopard (Mohd-Azlan et al.,

542   2020a; Seaman et al., 2021). This requires extending protected area networks, wildlife

543   corridors and riparian buffers (Mohd-Azlan et al., 2020a; Yaap et al., 2016), but also

544   preventing further degradation forests gazetted for timber and oil palm which still harbour

545   high densities of threatened species (Voigt et al., 2022).

546

547   **Conclusion**

548   Our work highlights that the often over-looked but far-reaching secondary impacts of

549   infrastructure development should be fully assessed and proactively planned for to minimise

550   the impacts of urbanisation, anthropogenic disturbance, and land-use change in some of the

551   most important habitats for threatened mammals. With this level of planning, Indonesia has a

552   unique opportunity to pave the way for more green and sustainable infrastructural

553   development that provides a strong example to other tropical countries in pursuit of economic

554   and infrastructural development whilst simultaneously protecting their rich biological

555   diversity.

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Figure legends

Figure 1. A) Current capital city location, Jakarta (black circle) and proposed site (black

square) in Kalimantan (green); B) Map of Kalimantan with broad habitat types and study

sites: 1) Gunung Palung, 2) Pematang Gadung, 3) Muara Kendawangan, 4) Bukit Baka Bukit

Raya, 5) Belantikan, 6) Bawan, 7) Sebangau), 8) Sungai Wain, 9) Kutai, 10) Lesan, and 11)

Wehea. Existing primary roads and planned infrastructure expansion are shown including

upgraded roads, planned roads and location for the relocated capital; C) Broad forest

classifications comprise of conservation areas, protection forests, production forests and

forest designated for conversion; D) Proposed location for new capital. E) Lesan Protection

Forest with typical survey design of camera-traps placed 1 km^2 apart.

Figure 2. Probability of habitat-use by the mammal community in relation to poverty in

nearby villages (higher values have more deprivations), distance to primary roads, and

environmental predictors (proportion of forest cover and forest biomass); A) Standardized

beta coefficients (mean, 95% BCI, 75% BCI) showing covariate effects on community

habitat-use; grey bars indicate no relationship as BCI's overlap zero, light red bars indicate

moderate relationships with the 75% BCI not overlapping zero and dark red bars indicate

strong relationships with 95% BCI not overlapping zero; B) Predicted mean posterior

distribution values presented in dark green and the 95% BCI in light green.

Figure 3. Standardised beta coefficients (mean, 95% BCI & 75% BCI) showing covariate

effects on species-specific habitat-use in Kalimantan. Grey bars indicate no relationship as

950 BCI overlap zero, light red bars indicate moderate relationships with 75% BCI not

951 overlapping zero and dark red bars indicate strong relationships with 95% BCI not

952 overlapping

953 Figure 4. A) Predicted threatened species richness (number of mammals classified as IUCN

954 Vulnerable or higher) across Kalimantan derived from the top-performing occupancy model.

955 Values reclassified as: 'low' representing 60% of the predictions; 'medium' represents 60-

956 80%; and 'high' representing the top 20%); B) Impact zones surrounding the new roads

957 through the *Kapuas Hulu* region of West Kalimantan (1, 5, 25, 50 km); C) Impact zones

958 surrounding the proposed location of the new capital city in East Kalimantan (10, 30, 50, 200

959 km).

960 Figure 5. The potential impact of infrastructure development to critical habitat for threatened

961 species richness, sun bear and orangutan. For the new capital city, direct impacts are

962 represented by 10 km and 30 km and secondary impacts by 50 km and 200 km. For roads,

963 direct impacts are represented by 1 km and 5 km, and secondary impacts are represented by

964 25 km and 50 km. Panels A, B and C represent the percentage of each impact zone

965 considered to be critical habitat for each species based on the top-performing multi-species

966 occupancy model. Panels D, E and F represent the percentage of total critical habitat for each

967 species that could be implicated by each impact zone. The y-axis for panel F is split to

968 represent both 0 to 20%, and 0 to 100%, due to orangutan having disproportionately higher

969 values.