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Implications of large-scale infrastructure development for biodiversity in Indonesian Borneo

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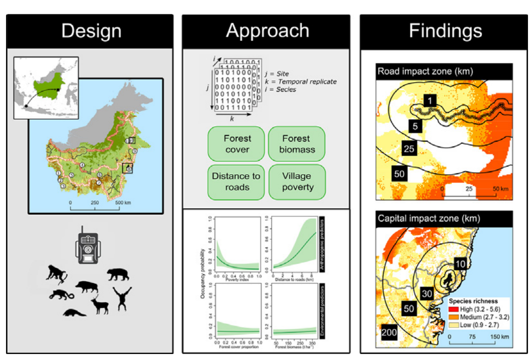
HIGHLIGHTS

- Infrastructure development influences wildlife at large spatial scales.
- We explored possible effects of Indonesia's new capital and roads using camera data.
- Mammal habitat-use was lowest near roads, degraded forest and poorer villages.
- Model projections revealed critical habitats to overlap with development zones.
- Without mitigation, regional development could affect critical wildlife habitat.

GRAPHICAL ABSTRACT



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ABSTRACT

Indonesia is embarking on an ambitious relocation of its capital city to Kalimantan, Borneo, bringing with it major urban and road infrastructure. Yet, despite being one of the world's most biologically diverse regions, the potential implications of this development for wildlife have yet to be fully assessed. We explored the potential impacts of the capital relocation, and road expansion and upgrades to critical habitat for medium-large mammals (>1 kg) using camera trap data from 11 forested landscapes. We applied Bayesian multi-species occupancy models to predict community and species-level responses to anthropogenic and environmental factors. We extrapolated spatial patterns of occupancy and species diversity across the forests of Kalimantan and identified "critical habitats" as the top 20th percentile of occupancy and species richness values. We subsequently overlapped these critical habitat layers with infrastructure

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impact zones to estimate the area that could potentially be affected by direct or secondary impacts. At both the community and species-level, distance to primary roads had the strongest negative influence on habitat-use. Occupancy was also influenced by forest quality and multidimensional poverty conditions in adjacent villages, demonstrating the sensitivity of biodiversity to socio-ecological pressures. Less than 1 % of the critical habitat for the threatened mammal community lay within the direct impact zone (30 km radius) of the capital relocation. However, approximately 16 % was located within 200 km and could potentially be affected by uncontrolled secondary impacts such as urban sprawl and associated regional development. The often-overlooked secondary implications of upgrading existing roads could also intersect a large amount of critical habitat for lowland species. Mitigating far-reaching secondary impacts of infrastructure development should be fully incorporated into environmental impact assessments. This will provide Indonesia with an opportunity to set an example of sustainable infrastructure development in the tropics.

1. Introduction

The tropics are experiencing a biodiversity crisis, with more threatened terrestrial mammals residing in Southeast Asia than other comparable regions (Schipper et al., 2008). With imminent large-scale infrastructure projects underway throughout Southeast Asia, it is important to assess potential implications these developments might have for biodiversity (Ng et al., 2020). Identifying these implications early in the development process allows for adjustments and safeguards to be put in place so that infrastructure can be expanded in a sustainable way (Garrard et al., 2018).

Declines in tropical biodiversity are driven by multiple interconnected ecological and anthropogenic factors (Gallego-Zamorano et al., 2020). Habitat loss and degradation influence animal communities through altered resource availability, reduced population connectivity (Kaszta et al., 2020) and increased contact with people, often leading to conflict and hunting (Azhar et al., 2013). Human-driven threats can be fuelled by demand for wild meat (Ripple et al., 2016), traditional medicine (Davis et al., 2020), illegal or legal trade (Symes et al., 2018), and negative human-wildlife interactions affecting people's livelihoods (Rode-Margono et al., 2016). These ecological and anthropogenic factors are pervasive in the tropics and can lead to defaunation even in intact or protected forests (Benitez-Lopez et al., 2019). Since the mid-20th century, Asia has experienced strong economic growth (Bloom and Finlay, 2009) and a tripling of its human population (Worldometer, 2022), which has exacerbated demand for wildlife products and subsequent declines in mammal populations (Linkie et al., 2018). For example, 79 % of primate species in this region are threatened with extinction (Schipper et al., 2008), and heavily traded and consumed species such as pangolin (*Manis* spp.), tiger (*Panthera tigris* spp.) and banteng (*Bos javanicus*) have been relisted as Endangered or Critically Endangered in recent years (Gardner et al., 2016; Challender et al., 2019; Goodrich et al., 2022). These biodiversity declines will likely continue as countries invest in large-scale infrastructure (Shira and Associates, 2011), unless well-planned mitigation strategies are put in place.

Infrastructure development and urban land expansion are major drivers of habitat disturbance and loss across the world (Laurance et al., 2015), but have received relatively little attention when compared with other drivers of biodiversity decline such as agriculture (Simkin et al., 2022). Asia is currently at the forefront of infrastructure development globally with the "Belt and Road Initiative" – the largest infrastructure programme in human history - passing through 72 countries and numerous fragile ecoregions and habitats (Ng et al., 2020). The initiative is bolstered by ambitious national targets and development plans which are already underway, including road and hydropower development in Myanmar (Kaszta et al., 2020) and Malaysia (Alamgir et al., 2020), and a 10-year master plan for economic development in Indonesia that aims to capitalise on natural resources and redistribute wealth across the archipelago (Shira and Associates, 2011).

Indonesia's most ambitious infrastructure project is the relocation of its capital city Jakarta, from Java to East Kalimantan (Indonesian Borneo). The new capital, "Nusantara", will house Indonesia's national government and administration, which are currently hindered by Jakarta's environmental and socio-economic issues arising from the rapidly growing human population (Van de Vuurst and Escobar, 2020). There are >30 million people residing in the Jakarta metropolitan area, with the inner city having an immensely high population density of 14,464 people/km^2 (World Population Review, 2022). Jakarta experiences problems with land subsidence, waste management, pollution and traffic congestion, and is increasingly faced with flooding and rising sea levels linked to climate change (Van de Vuurst and Escobar, 2020). The US$32 billion capital relocation project, originally planned for completion by 2024 but delayed during the pandemic, promotes upgrades of airports, seaports, and new access roads to transform the region into a low carbon superhub that facilitates economic development across the archipelago (Da Costa and Lamb, 2022). The relocation is expected to bring socioeconomic benefits and the government has pledged a "smart, green and clean" capital city (Adri, 2019). However, there remains some concern that the environmental and societal challenges experienced in Jakarta will be transferred to Borneo with potentially major repercussions for local wildlife and livelihoods (Mutaqin et al., 2021; Van de Vuurst and Escobar, 2020).

The construction and expansion of urban centres and road networks across the world are associated with numerous direct and secondary environmental impacts (Bennett, 2017; Simkin et al., 2022). Construction and land clearance directly affect the surrounding environment, whereas uncontrolled extractive industries (i.e., agriculture, mining and logging), migration and urban sprawl also create secondary impacts that influence ecosystems much further away from infrastructural localities and can be worse than the initial development (Teo et al., 2020; Laurance et al., 2015). For example, the relocation of Brazil's capital city to Brasília in the 1950's facilitated widespread road construction and human intrusion in the Amazon rainforest, leading to deforestation in previously remote regions (Laurance et al., 2015). In Kalimantan, the direct expansion of Nusantara could exceed a 30 km radius by 2045 with associated regional development and deforestation affecting up to a 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 and Associates, 2011). In Borneo, roads are reported to be upgraded or expanded by >3300 km and 1920 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 implicated by uncontrolled direct and secondary impacts of infrastructure development; and 3) provide recommendations to minimise these impacts. Our study provides an important baseline from which mammal populations can be monitored in relation to continued infrastructural expansion, and an evidence-base to support actions to reduce habitat loss. The analytical framework could be readily applied to similar large-scale infrastructural assessments worldwide.

2. Methods and materials

2.1. Study region

Kalimantan encompasses 73 % of Borneo (533,400 km^2), approximately half of which is comprised of forest habitats, including lowland and hill dipterocarp forests, peatland and freshwater swamps in coastal and low-lying areas, and mountainous forests in the interior. Over 30 % of Kalimantan's

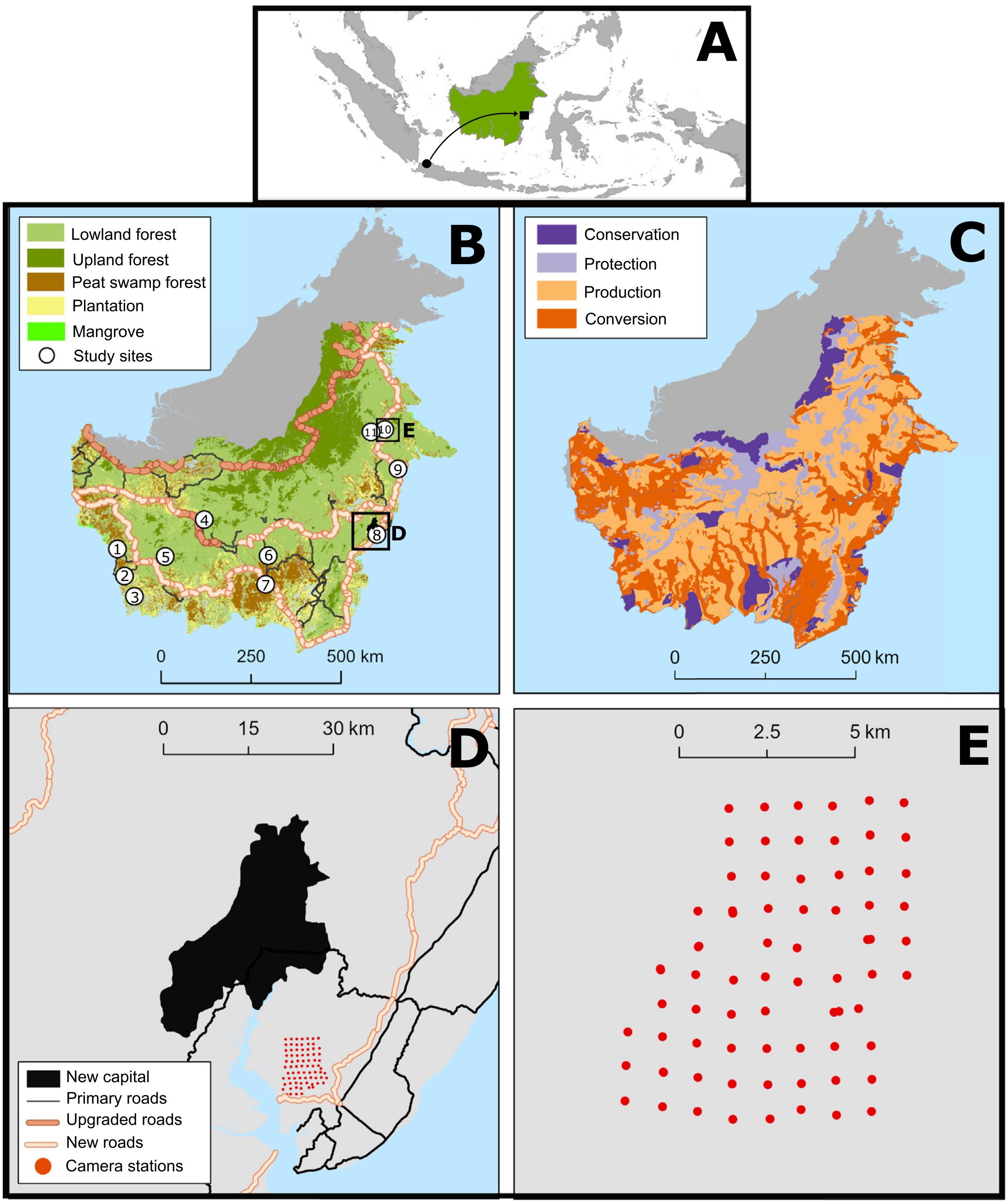

Fig. 1. A) Current capital city location, Jakarta (black circle) and proposed site (black square) of Nusantara in Kalimantan (green); B) Map of Kalimantan with broad habitat types and study sites: 1) Gunung Palung, 2) Pematang Gadung, 3) Muara Kendawangan, 4) Bukit Baka Bukit Raya, 5) Belantikan, 6) 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 conservation areas, protection forests, production forests and forest designated for conversion; D) Proposed location for the new capital; E) Lesan Protection Forest with typical survey design of camera-traps placed 1 km^2 apart. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

forests have been converted to other land-uses since the 1970s with <43 % intact forest cover and 26 % logged forest remaining (Gaveau et al., 2014). To date, deforestation has largely occurred in unprotected areas and in land gazetted for conversion to industrial plantations (Voigt et al., 2022). However, protected forests can also be subject to illegal logging, hunting, and small-scale conversion to plantations (Fawzi et al., 2018). Most development is concentrated on the coastal lowlands of the region's five provinces (Central, East, North, South, West), where plantation agriculture dominates. Urban areas and primary road networks are also predominantly located in these lowland regions, with East Kalimantan particularly influenced by infrastructure development and human population growth (Fuller et al., 2010).

2.2. Camera trap sampling of medium-large mammals

We collated camera trap data from 11 sites across West ($n = 4$), Central ($n = 3$) and East Kalimantan ($n = 4$) (Fig. 1) spanning a gradient of habitat (primarily lowland and hill dipterocarp forests, and peat swamp) and management types (Table 1). Surveys were implemented in forests allocated specifically for conservation ($n = 7$), watershed protection ($n = 3$) and logging ($n = 2$) (S1 and Table S1). Sites were sampled between 2012 and 2019, comprising an average of 44 camera stations per site (range: 19–79) separated by a mean inter-trap distance of 0.78 km. Cameras were positioned approximately 0.5 m from the ground and positioned on or near animal trails or key environmental resources (i.e., salt licks, water sources) to maximise detections. Length of camera deployment was variable between years, stations, and sites, therefore, to standardise sampling effort and meet assumptions of demographic closure for occupancy analysis we limited sampling periods to 90 consecutive nights per camera station per site. Camera data were pooled to make inferences at the landscape-level whilst accounting for site-level heterogeneity.

We define the mammal community as medium-large bodied (>1 kg), terrestrial species (Table S2). Taxonomically ambiguous species (e.g., lesser mouse deer *Tragulus kanchil*, and greater mouse deer *T. napu*; Bornean red muntjac *Muntiacus muntjac*, and Bornean yellow muntjac *M. atherodes*) were pooled into genus-level categories due to inconsistency in species identification among datasets. We excluded primarily arboreal species (e.g., red leaf monkey, *Presbytis rubicunda*) since these were unlikely to be reliably detected by cameras placed at ground-level. The Bornean orangutan *Pongo pygmaeus* was included since terrestrial activity is common for this species (Ancrenaz et al., 2014). Mammals <1 kg in size (e.g., murid rodents and squirrels) were discarded due to highly variable detection and species identification between study sites.

Prior to analysis, we developed a detection matrix for each of the remaining species, whereby 90-day sampling periods were divided into 5-day temporal replicates. Collapsing the survey period helps to reduce over-dispersion and increase temporal independence of detections (Penjor et al., 2019). Species with fewer than five detections in the detection matrix (banteng *Bos banteng*, flat-headed cat *Prionailurus planiceps*, bay cat *Catopuma badia*, Hose's palm civet *Diplogale hosei* and otter civet *Cynogale bennettii*) were removed from analysis because differences in detectability and occurrence cannot be reliably differentiated when observation data are sparse (Brodie et al., 2015b). Camera stations active for fewer than 10 days were also excluded, resulting in 485 stations each with four to 19 sampling occasions.

2.3. Covariates

We explored 10 anthropogenic and environmental covariates derived from remotely-sensed data based on their reported influence on mammalian habitat-use at either the community or species levels (e.g. Deere et al., 2020; Tilker et al., 2019b) (Table S3). Human disturbance and hunting patterns are difficult to quantify directly due to the complex nature of human behaviour but can be inferred over large spatial scales using established proxy variables from remote sensing (Tilker et al., 2019a). Therefore, we explored five such proxies to reflect anthropogenic disturbance ranging from traditional metrics (distance to primary roads and density of logging

Table 1
Details of the 11 study sites in Kalimantan, including forest classification, broad habitat type, sampling period, number of operational cameras and total number of camera trap nights (CTN) included in analysis.

Site	Forest land-use classification	Forest types	Total forest block size (km^2)	Sampling period start	Sampling period end	No. camera sites	CTN	Source
West Kalimantan								
Bukit Baka Bukit Raya	Conservation (National Park)	Lowland, Upland	1810	01/06/2019	30/08/2019	19	1642	Unpublished
Gunung Palung	Conservation (National Park)	Lowland, Peat swamp, Upland	1084	12/08/2015	10/11/2015	29	2569	Allen et al., 2016
Muara Kendawangan	Conservation (Nature Reserve)	Lowland, Peat swamp, Upland, Burnt	1490	01/06/2019	30/08/2019	20	744	Unpublished
Pematang Gadung	Conversion	Lowland, Peat swamp,	280	01/06/2019	30/08/2019	22	1980	Unpublished
Central Kalimantan								
Bawan	Production	Lowland	546	09/09/2012	26/11/2012	63	4060	Cheyne et al., 2016
Belantikan	Conservation & production	Lowland	5000	06/03/2014	04/06/2014	48	3519	Cheyne et al., 2016
Sebangau	Conservation (National Park)	Peat swamp	5700	01/09/2014	30/11/2014	20	2160	Cheyne et al., 2016
East Kalimantan								
Kutai	Conservation (National Park)	Lowland, Peat swamp,	2000	19/12/2012	19/03/2013	50	3053	Cheyne et al., 2016
Lesan	Watershed Protection	Lowland	110	20/09/2013	19/12/2013	79	6890	Cheyne et al., 2016
Sungai Wain	Watershed Protection	Lowland, Peat swamp	100	17/05/2012	09/08/2012	78	4729	Cheyne et al., 2016
Wehea	Watershed Protection	Lowland, Upland	380	07/07/2013	05/10/2013	54	4736	Wall et al., 2021

roads) to more bespoke measures: landscape accessibility, human population pressure, and a village-level multidimensional poverty index. We also explored five environmental covariates to capture local environmental conditions around camera traps, including percentage of forest cover (an indicator of habitat availability), aboveground biomass (an indicator of habitat quality), elevation, and characteristics of regional fire regimes (frequency and radiative power). All covariates were time-calibrated to the nearest year of data collection for each site reducing biases associated with different sampling years (Semper-Pascual et al., 2020), except for biomass which was only available for 2018. Further information regarding the source and processing of each covariate can be found in S2 and Table S3. Prior to analysis all continuous covariates were centred around their mean values and scaled to one-unit standard deviation to place the covariates on a comparable scale.

2.4. Modelling framework

We implemented Royle-Nichols multi-species occupancy models to estimate community and species-specific occurrence probabilities, whilst correcting for imperfect detection (Royle and Nichols, 2003). This model outperforms other analytical frameworks when variation in local abundance, non-random movement of animals or a biased sampling design induces high levels of heterogeneity in camera trap detection rates (Tobler et al., 2015). To account for overdispersion in the data, we modelled the local abundance a of species i at trapping station j, a_{ij}, as a realisation of a negative binomial process, governed by success parameter, λ_{ij}, representing the total number of individuals of each species using the habitat surrounding a camera station (Tobler et al., 2015), and a species-specific dispersion parameter, r_i, to explicitly model spatial variation in abundance:

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

Simulated assessments have found the negative binomial model specification to provide numerically unstable parameter estimates (Royle and Nichols, 2003). However, we found no evidence of this when applied to our data. As true abundance is imperfectly observed, summarised detection histories of species i at station j (y_{ij}) were described as realisations of a binomial process:

$$y_{ij} \sim Binomial\left(k_j, 1 - \left(1 - p_{ij}\right)^{aij}\right)$$

where k_j represents the number of temporal replicates at each station and p_{ij} denotes the probability of detecting species i at camera station j, which was specified to be functionally dependent on mean local abundance (a_{ij}). We estimate occupancy post-hoc, derived as a deterministic function of abundance (Royle and Nichols, 2003):

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

in which occupancy Ψ_{ij} is defined as the probability of at least one individual occurring at a given station. Throughout, we interpret occupancy as the probability that a species uses the area around each camera (i.e. habitat, or space-use) as the assumption of spatial independence between camera stations could not be met for wide-ranging species (Penjor et al., 2019).

2.5. Model selection

We implemented a robust model selection procedure to identify the most influential environmental and anthropogenic determinants of mammal occurrence. Across all models, we described abundance using a log link function and included study site identity as a categorical fixed intercept term to account for spatial variation of species occurrence among study sites and reduce bias from spatial autocorrelation due to clustered sampling design (Fieberg et al., 2010). Initially, we constructed univariate, multi-species occupancy models to identify the optimal spatial extent to extract predictor values to camera localities (buffer radii: 250, 500, 750 and 1000 m). Scale-optimised predictors were subjected to a second selection process, whereby highly intercorrelated predictors (Pearson's correlation coefficient: $|r| > 0.7$; Variance Inflation Factors: VIF < 3) were removed. Throughout, selection procedures were guided by the best-ranked model, according to Watanabe–Akaike Information Criterion (WAIC; Watanabe, 2010), the number of species demonstrating a statistical response to the scale/predictor (95 % and 75 % Bayesian credible interval did not overlap zero) and the temporal scope of the predictor, with preference being awarded to those that could be time-calibrated. The remaining covariates were used to build a plausible model, i.e., its predictions and parameter estimates are biologically plausible (Johnson and Omland, 2004). This resulted in abundance being defined as a function of site-specific intercepts (Site) and four covariates (Table 2): poverty index (*Poverty*), distance to primary roads (*Road*), proportion of forest cover (*Forest*) and forest biomass (*Biomass*):

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

We describe detection using a logit link function as a linear combination of two covariates, including a habitat-specific intercept (*Habitat*), comprising four factor levels (lowland forest, upland forest, peat swamp forest and plantation) and survey effort (number of camera trap nights; *CTN*). Camera model was strongly linked to site and thus excluded from the detection model:

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

We conducted all analyses in JAGS version 4.3.0 through R version 4.1.0 using the package jagsUI; see Supplementary Information S4 for further information on model specification and predictive performance checks. We considered coefficients to have strong support if the 95 % Bayesian credible interval (95 % BCI, the 2.5th and 97.5th percentiles of the posterior distribution) did not overlap zero and moderate support if the 75 % BCI did not overlap zero. Unless stated otherwise, we summarise parameter estimates as the mean of the posterior distribution and express uncertainty using 95 % BCI.

Table 2
Predictors used in top-performing multispecies occupancy model, including their description, scale of extraction, year and source. Processing information can be found in Supplementary information S2 and Table S3.

Covariate	Description	Scale of extraction (meters)	Year	Source
Forest cover	Proportion (%) of forest cover within the immediate vicinity of the sampling location	250	2012, 2013, 2014, 2015, 2019	Hansen/UMD/Google/USGS/NASA
Forest biomass	Proxy for forest quality, quantified as aboveground biomass (t ha^{-1})	1000	2018	https://data.globalforestwatch.org/datasets/gfw::aboveground-live-woody-biomass-density/about
Distance to roads	Distance to primary roads in kilometres	500	2012, 2013, 2014, 2015, 2019	https://map.nusantara-atlas.org
Multidimensional poverty index (MPI)	Score between 0 and 1, where 0 reflects no deprivations and 1 reflects many	250	2011, 2014, 2018	Indonesian Central Agency on Statistics (Biro Pusat Statistiks: https://www.bps.go.id/)

2.6. Spatial analysis of the impact of infrastructure development

To explore impacts of the new capital city and road expansion on mammal communities, we developed occurrence maps for each species using parameter estimates derived from the occupancy model. We linked these with spatially explicit covariates from the most recent year available (2018 for biomass; 2019 for all others) and masked these maps using the observed range of covariate values across camera stations to prevent overprediction. This resulted in occurrence maps for 20 species projected into a recent single time-point prior to the expected infrastructure development associated with the capital. These maps were summed across species to produce a count of species (i.e., a richness layer) corrected for imperfect detection. A separate richness map was produced for high conservation value species (i.e., those listed as "Vulnerable" or higher by the IUCN Red List of Threatened Species; bearded pig *Sus barbatus*, Sunda clouded leopard *Neofelis diardi*, Bornean orangutan, long-tailed macaque *Macaca fascicilaris*, pig-tailed macaque *Macaca nemestrina*, sambar deer *Rusa unicolor*, Bornean sun bear *Helarctos malayanus euryspilus* and Sunda pangolin *Manis javanica*). We also provide estimates of uncertainty for our species richness values with a map of posterior standard deviation in Fig. S2. To identify the most important areas for each species across the projection region, we applied a fixed threshold to select the top 20th percentile of cells with the highest occupancy probabilities (hereafter referred to as "critical habitats").

We used overlapping buffer distances to represent ecological "impact zones" of the roads and the new urban area for the capital (Teo et al., 2020; Ng et al., 2020). We applied impact zone buffers to primary roads (https://map.nusantara-atlas.org) cross-referenced with the locations of new and upgraded roads from Alamgir et al. (2019). Buffers of 1 km represent immediate impacts (e.g., edge effects, vehicle-wildlife collisions) (Pfeifer et al., 2017; Silva et al., 2020), 5 km represents direct deforestation and elevated hunting opportunities (Barber et al., 2014) and the 25 km and 50 km zones reflecting broader environmental changes to the landscape such as illegal logging, hunting or mining in distant areas that become more accessible (Ng et al., 2020). Impact zones for the new capital were based on previous research using night-lights to quantitatively assess the spatial growth of previous capital cities (Teo et al., 2020). Therefore, zones of 10 km and 30 km were chosen to represent direct impacts (e.g., immediate land destruction and resource extraction), and 50 km and 200 km to represent secondary impacts associated with expanding regional development (e.g., urban sprawl, population expansion, deforestation, and mining or agricultural activities) (Teo et al., 2020). We applied these impact zones to a map of the planned Nusantara location georeferenced from Indonesia's Ministry of National Development Planning (Bappenas, 2021). Impact zones in closer vicinity to infrastructure represent intense, but best-case scenario effects, whereas those further away assume the worst-case scenario of uncontrolled secondary impacts.

We present results collectively across threatened mammal species as well as individually for two focal taxa: the Bornean sun bear and Bornean orangutan. These species were chosen as they are both highly threatened by human activities (Vulnerable and Critically Endangered, respectively, according to the IUCN), but differ in their distributions and ecology. For example, orangutans are found in higher densities in the lowland regions compared to the higher elevation interior forests (Husson et al., 2009).

3. Results

Analysis of the 485 camera stations yielded 35,992 camera trap nights and 4621 independent detections of 20 medium-large mammal species (Table S5). Only three out of 20 species (bearded pig, mouse-deer spp. and pig-tailed macaque) were detected at all 11 sites. Muntjac spp. (n = 1105) and bearded pig (n = 810) were the most detected taxa, whilst Sunda pangolin (n = 11) and common palm civet *Paradoxurus hermaphroditus* (n = 10) were detected the least.

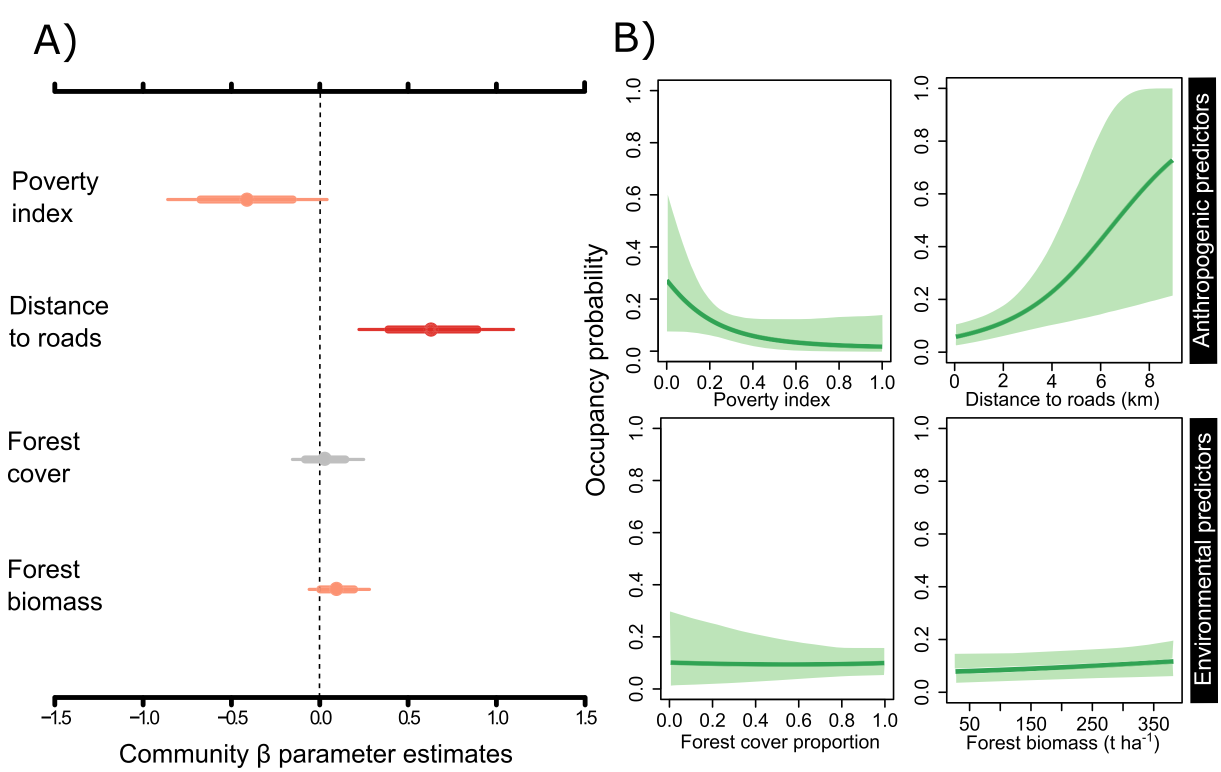

Fig. 2. Probability of habitat-use by the mammal community in relation to poverty in nearby villages (higher values indicate higher levels of poverty), distance to primary roads, and environmental predictors (proportion of forest cover and forest biomass); A) Standardized beta coefficients (mean, 95 % 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.1. Influence of anthropogenic and environmental variables on the mammal community

Overall, the mammal community had a stronger response to anthropogenic rather than environmental predictors. Distance to primary roads had the strongest negative response at both the community (mean occupancy 0.64, 0.22 to 1.1) (Fig. 2), and species-level (12 of the 20 taxa) (Fig. 3). The strongest responses were demonstrated by Sunda clouded leopard (*Neofelis diardi*; 1.69, 0.9 to 2.48), long-tailed porcupine (*Trichys fasciculata*; 1.47, 0.44 to 2.65) and mongoose species (*Herpestes* spp.; 1.35, 0.49 to 2.3) (Fig. 3). At the community-level, poorer villages were associated with lower mammal habitat-use in nearby forests (−0.41, 75 % BCI: −0.67 to −0.15; Fig. 2). This was underpinned by a consistent moderate, negative response by all observed mammals apart from leopard cat (*Prionailurus bengalensis*; −0.32, 75 % BCI -0.67 to 0.03) and sambar (*Rusa unicolor*; −0.22, 75 % BCI: −0.60 to 0.18) (Fig. 3).

Mammals were found to be less responsive to local environmental characteristics, suggesting a degree of tolerance towards habitat disturbance. Proportion of forest cover was not an influential predictor of habitat-use at the community level (Fig. 2), or for 17 of the 20 species (Fig. 3). However, two species had higher habitat-use in areas with reduced forest cover (bearded pig; −0.31, 95 % BCI: −0.61 to −0.03; long-tailed macaque *Macaca fascicularis;* −0.25, 75 % BCI: −0.47 to −0.03). Bornean sun bear was the only species to exhibit a preference for more forested habitats (0.31, 75 % BCI: 0.07 to 0.56). Habitat quality (biomass) had a moderately positive influence on community habitat-use (0.01, 75 % BCI: 0.04 to 0.19) (Fig. 2), which was predominantly driven by the habitat preferences of orangutans and sambar deer (Fig. 3).

3.2. Assessing the impact of infrastructure expansion

Across Kalimantan, model-predicted species richness at the camera station ranged from two to 14 for the observed mammal community and one to six when only threatened species were considered. Almost 18 % of the 247,257 km^2 projection region in Kalimantan was deemed critical habitat for threatened mammals overall (top 20th percentile of richness values: 3.2–5.6). The amount of land designated as critical habitat varied substantially among species. For sun bear, 47, 960 km^2 (19.4 % of suitable forest available) was deemed critical habitat based on the top 20th percentile (ψ: 0.56 to 0.99), whereas 8503 km^2 (3.4 % of suitable forest available) was deemed critical for the Bornean orangutan (ψ: 0.17 to 0.26).

a) Capital city relocation

The proportion of important habitat intersecting with the impact zones of the new capital city was variable between species. Direct impacts (within 30 km radius) intersected with little critical habitat for threatened mammals overall and sun bears specifically (<1 % of the total habitat), whereas secondary impacts (radiating up to 200 km away from the capital) intersected with up to 16.2 % of total critical habitat for threatened mammals (Fig. 5). However, critical habitats of orangutans and other lowland-dwelling species could be disproportionately affected by both direct and secondary impacts. For orangutans, this reflects up to 7.9 % of critical habitat within direct impacts zones of the new capital and up to 42.9 % within the secondary impact zones.

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 critical habitat. Additionally, 79 % of critical habitat for orangutans was predicted to be within the broader secondary impact zone (50 km) of upgraded roads.

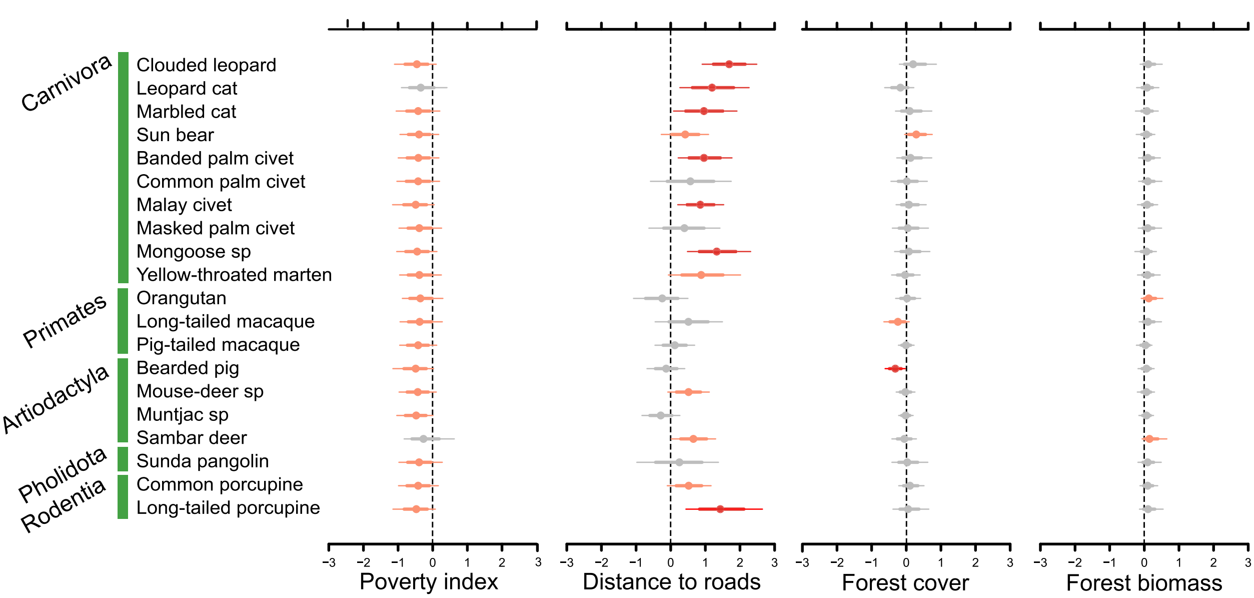

Fig. 3. Standardized beta coefficients (mean, 95 % BCI & 75 % BCI) showing covariate effects on species-specific habitat-use in Kalimantan. Grey bars indicate no relationship as BCI overlap zero, light red bars indicate moderate relationships with 75 % BCI not overlapping zero and dark red bars indicate strong relationships with 95 % BCI not overlapping. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

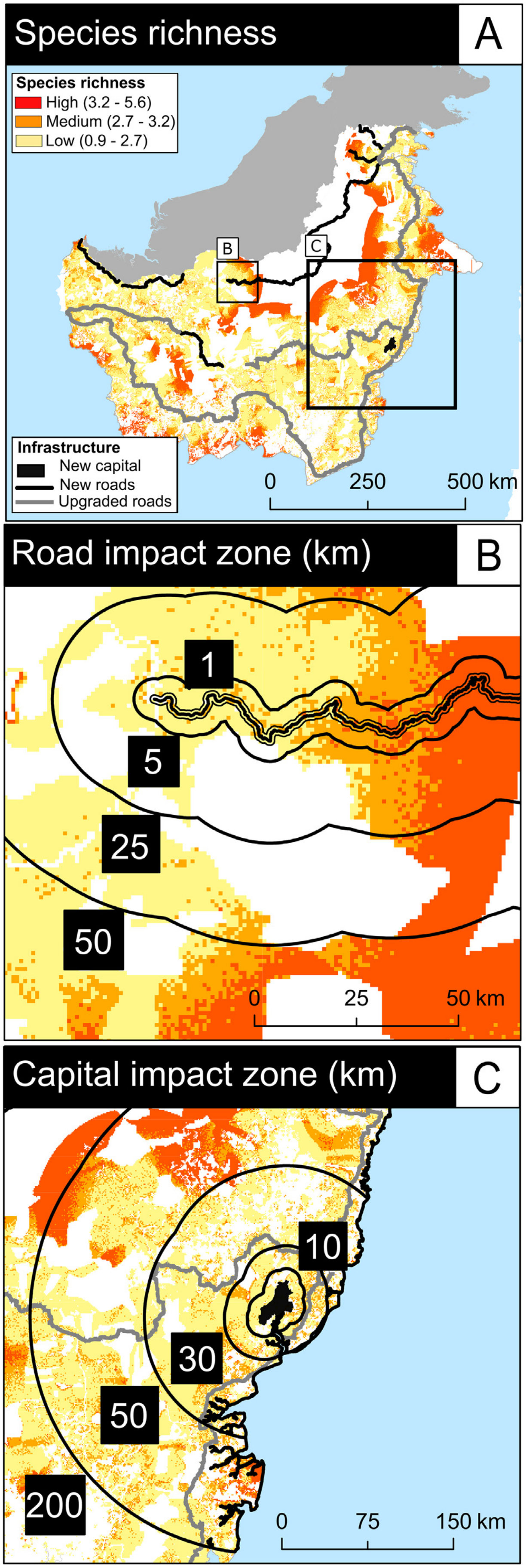

Fig. 4. A) Predicted threatened species richness (number of mammals classified as IUCN Vulnerable or higher) across Kalimantan derived from the top-performing occupancy model. Values are reclassified as: 'low' representing 60 % of the predictions; 'medium' represents 60–80 %; and 'high' representing the top 20 %); B) Impact zones surrounding the new roads through the *Kapuas Hulu* region of West Kalimantan (1, 5, 25, 50 km); C) Impact zones surrounding the proposed location of the new capital city in East Kalimantan (10, 30, 50, 200 km).

4. Discussion

Consistent with other tropical regions, Borneo has experienced significant deforestation and biodiversity loss since the latter half of the 20th century (Gaveau et al., 2014), a trend that could continue with planned infrastructure expansion. Combining camera trap data from 11 landscapes in Kalimantan, we found anthropogenic, rather than environmental, predictors had the strongest influence on mammal communities. We demonstrate that proximity to road already has a significant influence on mammal habitat-use, and that the further expansion of infrastructure could intersect with critical wildlife habitat. The extent of these impacts will vary considerably between species, infrastructure type and locality but mitigation could reduce the area of habitat implicated.

Distance to primary roads was one of the strongest predictors of mammal occupancy (Fig. 2), which mirrors more localised studies undertaken elsewhere in Borneo (Evans et al., 2020; Mohd-Azlan et al., 2020b; Tee et al., 2021). Distance to roads reflects the multitude of direct and secondary disturbances radiating from roads, which alter the physical environment, decrease population connectivity (Kaszta et al., 2019) and increase mortality for many vertebrate species (Healey et al., 2020). Roads can also create population sinks (Carter et al., 2020) and skew mammal community compositions towards generalist species (Mohd-Azlan et al., 2020b). Moreover, human encroachment into previously remote areas facilitates widespread secondary disturbances such as hunting, habitat degradation and urbanisation, which radiate much further than the linear clearing itself (Laurance et al., 2009). For example, increased accessibility into forests via new roads and settlements was linked to significant declines of jaguar and their prey in the Amazon (Espinosa et al., 2018). Similarly, the largest felid in Borneo (Sunda clouded leopard) exhibited the strongest negative response to roads in our study (Fig. 3).

We found mammal habitat-use was lower in forests neighbouring villages with higher levels of poverty, determined by our multidimensional poverty index (Santika et al., 2019). Although the relationship between poverty and biodiversity is nuanced, a shared dependence between people and wildlife on limited resources, degraded ecosystems and/or vulnerabilities to environmental disasters such as fires and floods could explain this finding (Barrett et al., 2011). Infrastructure development could influence human wellbeing and poverty in surrounding communities both positively (i.e. improved electricity and water supplies) (Shin et al., 2022), and/or negatively (i.e. environmental degradation) (Barrett et al., 2011), and therefore warrants further research.

The limited influence of forest extent on mammal occupancy and richness is counterintuitive given the levels of deforestation reported for Borneo during the study period (Gaveau et al., 2014), but is likely due to most cameras being placed within forests. Across the tropics there is ample evidence of wildlife tolerating logging disturbance, but conversion to other land-uses severely diminishing biodiversity (Yue et al., 2015; Oakley and Bicknell, 2021). We also found forest quality to influence the mammal community, supporting findings at the global scale (Pillay et al., 2022). We advocate further biodiversity studies in more degraded forests to better capture the impact of forest loss and habitat quality on faunal communities.

4.1. Implications of Indonesia's capital relocation

Whilst the capital relocation will have environmental consequences for surrounding land (Teo et al., 2020), direct impacts (i.e. immediate land conversion within 30 km) to critical habitats of threatened species will be minimal due to the placement of the capital in a region near other substantially developed cities (e.g. Balikpapan and Samarinda) (Farida, 2021). However, species found in higher densities in Kalimantan's lowlands could be disproportionately affected within impact zones of the capital relocation. For example, Bornean orangutan was predicted to have approximately 8 % and 43 % of its total critical habitat intersected with direct and secondary impacts zones of the capital respectively, compared to <1 % and 16 % for sun bears (Fig. 5D). Therefore, minimizing further human encroachment into lowland forest surrounding infrastructure should be a priority to safeguard threatened species restricted to these regions.

Our model prediction of lower values for species richness and sun bear occupancy within 30 km of the new capital site reflects the anthropogenic disturbances already influencing biodiversity in East Kalimantan. Human population growth and annual deforestation rates have been higher in this province than elsewhere in Kalimantan, with much of the lowlands subject to habitat degradation and infrastructure development (Rustam et al., 2012). Therefore, species not restricted to the lowlands (i.e. sun bear and Sunda clouded leopard) are increasingly associated with the interior regions at higher elevation, and further from human settlements (Brodie et al., 2015a; Tee et al., 2021). Importantly, for all threatened species assessed, secondary impacts overlapped a larger proportion of critical habitat than the direct impacts (Fig. 5). Capital cities have large ecological footprints and urban land expansion is a major driver of habitat loss (Simkin et al., 2022). The secondary impact zones represent proliferating extractive industries (i.e., mining and timber), land conversion and urban sprawl radiating from the city core (Teo et al., 2020; Muhtar et al., 2021). Whilst this reflects a possible worst-case scenario whereby such actions are uncontrolled, especially at the broader level (200 km), they are arguably more difficult to plan for and prevent (Laurance et al., 2015). Given the environmental problems triggered by overpopulation in Indonesia's current capital Jakarta, limiting urban sprawl and migration will be an important challenge for the new capital (Mutaqin et al., 2021). For instance, the capital relocation is set to bring another 1.5 million federal workers from Jakarta to Kalimantan by 2024 alone (Watts, 2019), which will require resources from surrounding land (Puppim de Oliveira et al., 2011). Additionally, human encroachment may exacerbate negative human-wildlife interactions in the region (Fredriksson, 2005; Meijaard et al., 2011) or give rise to new urban markets for wildlife products (Corlett, 2007; Linkie et al., 2018). This is particularly concerning for species already threatened by illegal wildlife trade e.g., sun bear and pangolin (Gomez and Shepherd, 2019; Nash et al., 2018).

4.2. Implications of road development

New roads (e.g., the northern link of the Trans-Kalimantan highway) are being constructed in the more remote interior of Borneo, which to date has experienced less disturbance than lowland regions and therefore harbours some of the highest biodiversity levels in Kalimantan. Whilst our estimates are conservative given portions of the new road transverse areas outside the limits of our data within the Heart of Borneo region, and also have higher uncertainty (Fig. 4; Fig. S1), approximately 12 % of the direct impact zone of new roads could intersect with these important habitats (Fig. 5B), pre-disposing wildlife populations with a greater risk of vehicle collision (Silva et al., 2020), edge-effects (Pfeifer et al., 2017) and habitat fragmentation (Alamgir et al., 2019). This has been demonstrated in Malaysian Borneo, where the newly constructed Pan-Borneo highway reduced mean species richness and increased the presence of generalist species within 1 km (Mohd-Azlan et al., 2020b). Furthermore, new roads in this region could be a catalyst for wider human accessibility and habitat degradation (Laurance et al., 2015), overlapping with 15 % of the total area deemed highest in threatened mammal richness in the worst-case scenario of secondary impacts sprawling up to 50 km either side of the roads (Fig. 5E).

In contrast, the impacts of roads planned for upgrade were of greater concern to species typically found in higher densities in the lowlands. The negative effects of road upgrades are often overlooked (Laurance et al., 2015), yet our analysis predicted over a quarter of critical habitat for orangutans could be within direct impact zones and, in the worse-case scenario, over three-quarters within secondary impact zones of upgraded roads (Fig. 5F) . That said, there appeared no discernible effect of distance to road on orangutan habitat-use in our occupancy analysis (Fig. 3), which may provide some optimism for this adaptable species if human-induced mortality and sprawling land conversion can be prevented (Voigt et al., 2018).

Considering the primary goal of road expansion is to increase commercial connectivity and facilitate extractive industries (Shira and Associates, 2011), and the current level of unmapped roads and extractive activities operational in Kalimantan (Hughes, 2018), these secondary impacts should be anticipated and prevented. Conservation attention should be paid to species particularly sensitive to infrastructure, such as the Sunda clouded leopard which we found to exhibit the strongest negative response to roads (Fig. 3). Research in Sabah predicted a 23 % reduction in population connectivity and subsequent population declines for this species in response to the development of highways and railroads (Kaszta et al., 2019).

4.3. Conservation and management implications

Our findings indicate up to 46 % of critical habitat for threatened mammals could intersect with combined impact zones of road development and the capital relocation. Importantly, however, this represents the worst-case scenario of uncontrolled secondary impacts. Therefore, there is opportunity to significantly reduce the amount of important habitat affected by new and ongoing development. This should be proactively managed by ensuring any environmental impact assessments (EIAs) and ongoing conservation strategies are not limited to the direct vicinity of infrastructure itself, but also include an appraisal of magnitude, direction and patterns of secondary impacts that radiate far beyond the infrastructure core. Secondary impacts are often excluded from the remit of EIAs, severely underestimating surrounding deforestation (Ritter et al., 2017).

More localised research in human-modified landscapes is needed to understand specifically where and how infrastructure will have the severest direct impacts to mammal populations. For road development, this could include longitudinal biodiversity and roadkill surveys (Healey et al., 2020) in critical-habitat areas to inform key locations for interventions including (but not limited to) wildlife crossings, culverts, fencing and traffic control (Bennett, 2017). Planners should look to other Southeast Asian countries investing in green road infrastructure; for example, the Eco-Link bridge in Singapore that reconnects nature reserves either side of a major expressway (NParks, 2014). There are also smaller-scale, cheaper alternatives, demonstrated by Malaysia's first urban canopy bridge, which successfully aided crossings of long-tailed macaques (*Macaca fascicularis*) and squirrel species within three months of installation (Yap and Ruppert, 2019). However, the success of such initiatives is varied and requires thorough planning (Bennett, 2017).

For Indonesia's Nusantara capital, studies elsewhere imply that the proposed green infrastructure in the core zone should have a lesser impact on biodiversity than conventional equivalents, whilst also benefiting city inhabitants through improved flood management, reduced urban heat and increased human wellbeing (Filazzola et al., 2019; Garrard et al., 2018). There are emerging frameworks to incorporate ecological knowledge into urban planning, which include maintaining and introducing wildlife habitat, aiding habitat connectivity, minimizing anthropogenic disturbances and facilitating positive human-nature interactions (Garrard et al., 2018).

Green infrastructure, however, is not a replacement for natural ecosystems (Filazzola et al., 2019). For all infrastructure types, mitigating human encroachment and secondary impacts such as illegal logging, mining and deforestation should be prioritised as these factors already pose a considerable economic cost to Indonesia (Khan, 2014). Additionally, illegal wildlife trade networks should be tackled with stronger enforcement given that roads can enable a shift from subsistence to market-based hunting patterns (Pattiselanno and Krockenberger, 2021) and new transportation links under the Belt and Road Initiative could facilitate trade networks with mainland Asia (Farhadinia et al., 2019).

Finally, we stress that our analysis prioritised forest within the top 20th percentile of occupancy and richness values as critical, but viable populations require well-connected habitats. Ensuring connectivity between

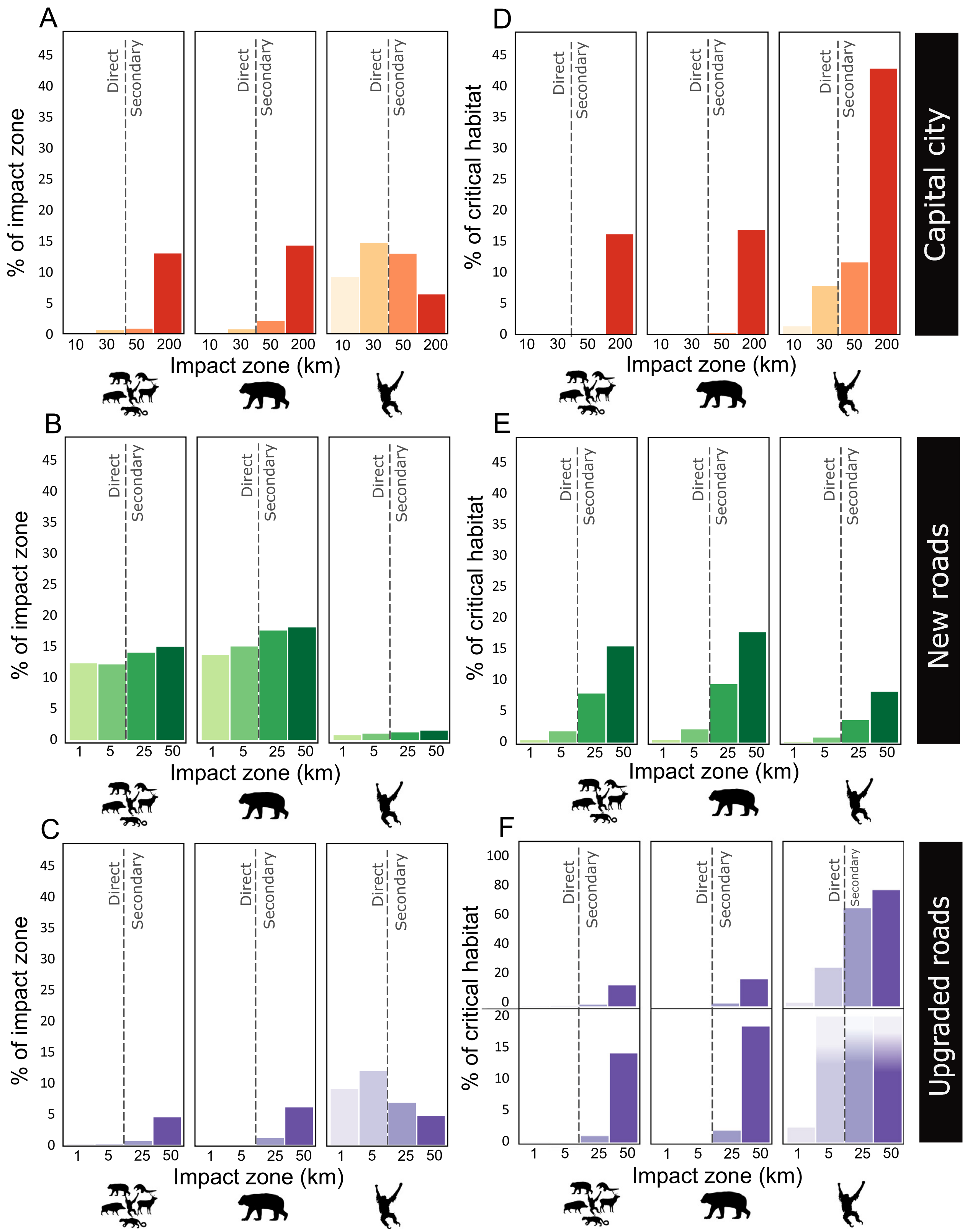

Fig. 5. The potential impact of infrastructure development to critical habitat for threatened species richness, sun bear and orangutan. For the new capital city, direct impacts are represented by 10 km and 30 km and secondary impacts by 50 km and 200 km. For roads, direct impacts are represented by 1 km and 5 km, and secondary impacts are represented by 25 km and 50 km. Panels A, B and C represent the percentage of each impact zone considered to be critical habitat for each species based on the top-performing multi-species occupancy model. Panels D, E and F represent the percentage of total critical habitat for each species that could be implicated by each impact zone. The y-axis for panel F is split to represent both 0 to 20 %, and 0 to 100 %, due to orangutan having disproportionately higher values.

human-dominated landscapes is vital for threatened and low-density species such as orangutan, sun bear and clouded leopard (Mohd-Azlan et al., 2020a; Seaman et al., 2021). This requires extending protected area networks, wildlife corridors and riparian buffers (Mohd-Azlan et al., 2020a; Yaap et al., 2016), but also preventing further degradation forests gazetted for timber and oil palm which still harbour high densities of threatened species (Voigt et al., 2022).

5. Conclusion

Our work highlights that the often overlooked but far-reaching secondary impacts of infrastructure development should be fully assessed and proactively planned for to minimise the impacts of urbanisation, anthropogenic disturbance, and land-use change in some of the most important habitats for threatened mammals. With this level of planning, Indonesia has a unique opportunity to pave the way for more green and sustainable infrastructural development that provides a strong example to other tropical countries in pursuit of economic and infrastructural development whilst simultaneously protecting the country's rich biological diversity.

CRediT authorship contribution statement

Katie L. Spencer: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Project administration, Funding acquisition. **Nicolas J. Deere:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Supervision. **Muhammad Aini:** Investigation, Resources. **Ryan Avriandy:** Investigation, Resources. **Gail Campbell-Smith:** Investigation, Resources, Writing – review & editing. **Susan M. Cheyne:** Investigation, Resources, Writing – review & editing. **David L.A. Gaveau:** Resources, Writing – review & editing. **Tatyana Humle:** Supervision, Writing – review & editing. **Joseph Hutabarat:** Investigation, Resources. **Brent Loken:** Investigation, Resources. **David W. Macdonald:** Funding acquisition, Writing – review & editing. **Andrew J. Marshall:** Investigation, Resources, Writing – review & editing. **Courtney Morgans:** Resources, Supervision, Writing – review & editing. **Yaya Rayadin:** Investigation, Resources. **Karmele L. Sanchez:** Investigation, Resources. **Stephanie Spehar:** Investigation, Resources. **Suanto:** Investigation, Resources. **Jito Sugardjito:** Supervision, Project administration. **Heiko U. Wittmer:** Investigation, Resources, Writing – review & editing. **Jatna Supriatna:** Supervision, Project administration, Writing – review & editing. **Matthew Struebig:** Conceptualization, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Data availability

The authors do not have permission to share data.

Declaration of competing interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.161075.

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