

20 **Abstract**

21 The islands of Borneo and Sumatra are strongholds for biodiversity and home for many
22 endemic species. They also have experienced among the highest deforestation rates globally. Both
23 islands are undergoing massive, rapid infrastructure development, leading to further deforestation
24 and habitat fragmentation. Here, we identify priority areas for continued functional forest
25 connectivity across Borneo and Sumatra, using spatial models of clouded leopard (*Neofelis diardi*, a
26 forest indicator species) movement, and impacts thereto from existing and future infrastructure
27 development. We specifically measure and map the anticipated impacts on forest functional
28 connectivity of three major infrastructure development projects (Pan Borneo Highway, Trans-
29 Sumatran Toll Road, and the new Indonesian capital city of Nusantara). We found that core clouded
30 leopard habitats are already highly fragmented in Sumatra, constituting only ~13% of the island,
31 with potential dispersal corridors still linking some habitat fragments. In Borneo, clouded leopard
32 core habitats cover 34% of the island, with one large central core area and several much smaller
33 satellite cores, which are largely unprotected (15% protected, compared to 42% in Sumatra). The
34 largest negative effect on habitat connectivity was predicted for Nusantara (66 % of the total
35 connectivity loss predicted for all three infrastructure projects), reverberating across the entirety of
36 Borneo with the strongest effects in East Kalimantan. The Pan Borneo Highway accounted for 28%
37 of the total connectivity loss, affecting every province in Borneo and Brunei, with 6% of this
38 decrease located within protected areas. The Trans-Sumatran Toll Road had the smallest negative
39 effect on connectivity (6%) but only when excluding the already built segments, which, when
40 included, produce a total negative impact similar to that of the Pan Borneo Highway.

41

42

43 1. Introduction

44 The islands of Borneo and Sumatra have experienced amongst the highest deforestation rates
45 globally over recent decades (Miettinen et al. 2011; Gaveau et al. 2014, 2016; Sloan et al. 2014),
46 while also hosting some of the most extensive and most biodiverse forest habitats remaining in
47 Southeast Asia (Alamgir et al. 2019). Sumatra, for example, is the only remaining place on Earth
48 where elephants, orangutans, rhinos, and tigers cooccur. The combination of rapid deforestation
49 and rich, unique biodiversity merits urgent attention to ensure persistent biodiversity.
50 Furthermore, it is important to resolve how the globally important biodiversity of both islands,
51 each under different governance, can be protected alongside the sustainable development
52 necessary to support the needs of their human populations. If development strategies are planned
53 in a forward-looking and sustainable manner, guided by scientific analyses and data-based
54 assessments, there is potential for the management of Sumatra and Borneo to be a paradigm for
55 building balanced human-wildlife coexistence.

56 Annual deforestation rates in Borneo and Sumatra reached as high as ~2.5% (Langner & Siegert
57 2009; Miettinen et al. 2011; Margono et al. 2012; Basyuni et al. 2018) over the last two decades.
58 Historically, the main drivers of deforestation were agricultural expansion (particularly for oil palm)
59 (Wijedasa et al. 2018; Sloan et al. 2019a), logging (legal and illegal) (Wijedasa et al. 2018; Sloan et
60 al. 2019a), forest fires (natural and human-induced) (Langner & Siegert 2009; Sloan et al. 2017) ,
61 and mining (mainly for coal and gold) (Alamgir et al. 2019). Such drivers were, however, widely
62 facilitated by infrastructure expansion (Sloan et al. 2019a; Alamgir et al. 2019) – largely highway,
63 road, and dam development. Recently, infrastructure development has accelerated to such a
64 degree as to constitute a major driver of deforestation by itself, as well as accelerating additional
65 landscape change and habitat fragmentation (Sloan et al. 2018a, 2019a; Alamgir et al. 2019).

66 Infrastructure development is difficult to predict and accommodate within conservation
67 designs. In response, conservation scientists are increasingly modelling potential spatio-ecological
68 impacts of planned infrastructure development to promote robust, pre-emptive conservation
69 design (or hedge against conservation failure) (Runting et al. 2015; Kaszta et al. 2019b, 2020b;
70 Sloan et al. 2019a; Ng et al. 2020) .

71 Three major infrastructure projects are presently under development in Borneo and Sumatra,
72 and are considered here with regard to their implications for landscape connectivity, namely:

73 THE PAN BORNEO HIGHWAY (PBH hereafter, also known as the Trans-Borneo Highway): The PHB will
74 increase connectivity between Malaysian Borneo (Sabah and Sarawak), Brunei, and
75 Indonesian Borneo (Kalimantan). The project will traverse and encircle Borneo via new roads
76 and road upgrades to facilitate the expansion of primary industries (e.g., coal mining, palm oil
77 and logging (Coordinating Ministry for Economic Affairs 2011; Sloan et al. 2019c; Alamgir et
78 al. 2019; Spencer et al. 2023). The Indonesian portion of PBH, known as the Trans-Kalimantan
79 Highway, is part of the Indonesian Master Plan for the Acceleration and Expansion of
80 Economic Development (2011-2025), which envisions the creation of six major Indonesian
81 economic corridors (Coordinating Ministry for Economic Affairs 2011). Many sections of the
82 PBH intersect or are very near protected areas (Alamgir et al. 2019), or otherwise fragment
83 large areas of intact forest (Sloan et al. 2019c).

84 TRANS-SUMATRAN TOLL ROAD (TTR hereafter, also known as Trans-Sumatra Highway): This 2,700 km
85 long economic-development corridor is intended to boost primary commodity exports (Sloan
86 et al. 2019b). In contrast to the PBH, much of the TTR intersects cleared lands and existing
87 roads. However, some segments are planned to traverse the last major Sumatran primary
88 forest remnants critical to the conservation of endangered fauna (Sloan et al. 2018b, 2019b).

89 CAPITAL CITY TRANSLOCATION: The most ambitious and expensive (US\$32 billion) project in the
90 region (Spencer et al. 2023) is the translocation of the Indonesian capital city from Jakarta to
91 Nusantara, Borneo, between the current cities of Balikpapan and Samarinda in East
92 Kalimantan province. Nusantara is promoted as a “smart, green, beautiful and sustainable
93 city”, with a projected population of 1.5 million (Teo et al. 2020). However, a large human-
94 economic footprint is still anticipated, as due to resource provision and waste disposal.
95 Conceivably, this could accelerate deforestation, resource extraction, and thus strongly affect
96 wildlife across the whole of Borneo (Teo et al. 2020; Spencer et al. 2023).

97 To anticipate the impacts of these development projects, it is necessary to, first, understand
98 current habitat potential, and, second, anticipate the likely impacts of infrastructure development
99 on core habitats, habitat connectivity, and thus ultimately on wildlife populations. To this end we
100 apply a spatial model of species movement to identify and prioritize habitat areas crucial for
101 functional forest connectivity across Borneo and Sumatra. We further measure and map likely
102 impacts on this connectivity due to the PBH, TTH, and Nusantara infrastructure projects. To model
103 functional forest connectivity and designate core habitats and dispersal corridors, we chose the
104 Sunda clouded leopard (*Neofelis diardi*) as a focal species due to its high charisma (Macdonald et al.
105 2015), vulnerability (Hearn et al. 2015) and forest-dependance (Hearn et al. 2017; Macdonald et al.
106 2018b; Haidir et al. 2021). Furthermore, studies of (Penjor et al. 2021; Chiaverini et al. 2022)
107 showed that clouded leopard is a good indicator of predicting habitats for wider mammalian
108 biodiversity.

109

110 2. Methods

111 Our methodology identified crucial habitats for maintaining functional forest connectivity and
112 modeled the potential impacts of major developments on these habitats. Specifically, we firstly
113 modelled clouded leopard habitat connectivity across Sumatra and Borneo, identifying core areas
114 (CAs) of high-density leopard movement and narrower corridors allowing long-distance dispersal
115 between core areas (following the methods of Cushman et al. (2018), Kaszta et al. (2020)). Secondly,
116 we ranked core areas and corridors per island in terms of their importance in supporting clouded
117 leopard population connectivity. Thirdly, we modelled the impact of planned and ongoing major
118 development projects (PHB, TTH, Nusantara) on clouded leopard landscape connectivity,
119 accounting for the effects of the existing road networks. Fourthly, we conducted a ‘gap analysis’ to
120 quantify the degree to which CAs and corridors are encompassed by the existing protected area
121 network in the context of infrastructure developments’ impact.

122 **2.1. Modelling current forest-habitat connectivity**

123 Rigorous spatial models of species landscape connectivity combine information on the number
124 and spatial distribution of individuals in the landscape (*source locations* from which species may
125 move/disperse) with spatial data quantifying the facility or *resistance* by which the species moves
126 through the landscape (Cushman et al. 2013, 2014). The best performing connectivity models are
127 usually based on known species distributions and movements or similarly on species’ particular
128 habitat use (Cushman et al. 2013a; Cushman et al. 2018; Mateo-Sánchez et al. 2015b; Zeller et al.
129 2018).

130 To model clouded leopard habitat connectivity across Borneo and Sumatra, we generated
131 clouded leopard source locations using existing and published information on their density and
132 habitat suitability in the islands (Hearn et al. 2017; Haidir et al. 2021). Similarly, since telemetry data
133 on clouded leopard movement are very sparse – the sole example (Hearn et al. 2018) was based on

134 only four individuals – we developed a resistance surface using the same published habitat suitability
135 models (Macdonald et al. 2018a).

136 Given these source locations and resistance surfaces, we applied two complementary
137 approaches modelling current leopard habitat connectivity: cumulative resistant kernels to identify
138 core habitat areas (Compton et al. 2007; Cushman et al. 2016), and factorial least-cost paths
139 (Cushman et al. 2009; Kaszta et al. 2020b) to identify dispersal corridors.

140 2.1.1. *Source locations*

141 To define number and distribution of Sunda clouded leopard source locations in the landscape, we
142 calculated the relationship between the known number of clouded leopard individuals (Hearn et al.
143 2017., Haidir et al. 2021) and habitat suitability (described in Appendix 1.1.). For both islands, we used
144 a Sunda clouded leopard habitat-suitability layer developed by Macdonald et al. (2018a) which is
145 based on an extensive dataset of ~1.5k camera-trap stations distributed across 22 camera grids (7 in
146 Sumatra, 15 in Borneo). In Borneo the cameras were distributed in the south and southeast of
147 Indonesian provinces of Kalimantan and in the south and east of the Malaysian state of Sabah. In
148 Sumatra the sampling effort was focused in the west and central part of the island (Macdonald et al.,
149 2018a). The Sunda clouded leopard source locations represented a pool of potential occurrence
150 points probabilistically distributed across the suitability surface (e.g., Cushman et al. 2017; see
151 Appendix 1.1 for details).

152 2.1.2. *Resistance surface*

153 To generate a resistance surface for habitat-connectivity modelling, we used a negative
154 exponential transformation of the leopard habitat suitability layers of Macdonald et al. (2018a) for
155 Borneo and Sumatra (Eqn 1).

156

$$157 \quad \text{Resistance surface} = 100\left(e^{-\frac{\text{Habitat suitability}}{0.2}}\right) \quad (1)$$

158

159 Exponential transformation of habitat suitability has been shown to explain the relationship
160 between a species' facility of movement across a landscape, that is, resistance to movement across
161 a landscape, and habitat suitability within the landscape (Mateo-Sánchez et al. 2015a; Keeley et al.
162 2016). We then rescaled these resistance surfaces between 1 and 200, with value 1 denoting pixels
163 of least resistance. The resistance surface has a pixel resolution of 250m.

164 It is important to note that the Sunda clouded leopard habitat suitability model developed by
165 Macdonald et al. (2018a) encompassed several variables linked to forest cover (extensiveness of
166 lowland forest, percent of lower montane forest and percent of forest loss), which stresses the
167 importance of forest habitat for Sunda clouded leopard and negative impact of deforestation on the
168 species occurrence. It also included two topographical variables, compound topographical index (CTI)
169 and slope position, which indicated that clouded leopards occur preferentially in rugged, upland
170 ridges.

171 *2.1.2. Connectivity model*

172 To define core habitat areas and dispersal corridors we adopted two different approaches. (1)
173 To calculate synoptic connectivity for each pixel in the landscape, a base for defining core areas, we
174 applied the cumulative resistant kernel method (Compton et al. 2007) in UNICOR software (Landguth
175 et al. 2012). The resistant kernels algorithm calculates least-cost distance from each Sunda clouded
176 leopard source location to every location in the landscape within a dispersal-distance threshold.
177 Here, cost was defined with respect to the cumulative resistance of Sunda clouded leopard

178 movement over space, and a dispersal-distance thresholds was set at 250,000 cost units, after
179 (Macdonald et al. 2018b; Kaszta et al. 2020a), which is effectively 250km dispersal ability through
180 minimally-resistant conditions (resistance=1). Next, the kernel surfaces were summed across every
181 source location, defined above, to generate a surface of a total expected movement density. Core
182 habitat areas are areas of high predicted density of Sunda clouded leopard movement (high
183 cumulative resistant kernels values). Therefore, we define these areas as areas with cumulative
184 resistance values greater than the 80th percentile (e.g., Macdonald et al. 2018b).

185 (2) To identify and map dispersal corridors between core areas, we adopted a factorial least-cost
186 path approach (FLCPs; Cushman et al. 2009), also using UNICOR. This approach is similar to the
187 traditional least-cost paths (LCPs) method, but is extended to calculate least-cost paths across all
188 combinations of source locations, resulting in a synoptic surface of least cost-path density. One of
189 the benefits of the FLCPs approach is that it accounts for a species' dispersal ability. Since we wanted
190 to model potentially long-distance dispersal and multi-generational movement, we set the dispersal
191 threshold for FLCP to five-times that used for the cumulative resistant-kernel analysis (*sensu*
192 (Macdonald et al. 2018c and Kaszta et al. 2020a). The raw FLCPs layer identified narrow pixel-wide
193 linkages between Sunda clouded leopards' source locations. To widen these narrow linkages, making
194 them more biologically realistic, we used a smoothing moving window of a 5km radius and calculated
195 focal mean over the FLCPs (e.g., Cushman et al. 2009, Kaszta et al. 2020a). To define dispersal
196 corridors, we first ran a smoothing function on the raw output layers of the FLCPs analyses. We then
197 applied a 30th percentile threshold to the smoothed paths. For further analyses we considered only
198 paths outside of the core areas.

199 **2.2. Ranking the importance of core areas and corridors**

200 To rank core areas in their importance for the Sunda clouded leopard population, we first
201 calculated the sum of resistant kernel values for each CA. We then ranked the CAs according to this
202 sum, which represents the total expected amount of Sunda clouded leopard movement within the
203 CA (sum of the kernel values) (Cushman et al. 2018; Kaszta et al. 2020a).

204 In the dispersal corridors ranking we only considered corridors (or network of corridors) linking
205 core areas. We ranked corridors based on their strength (sum of the LCP values) and the strength of
206 the core areas they connected (sum of the cumulative resistant kernels). More information on how
207 this ranking was performed is included in Appendix (Section A1.3).

208 **2.3. Defining infrastructure-development scenarios**

209 We quantified the impacts of future infrastructure development (PBH, TTR, Nusantara) as well
210 as existing road networks on functional habitat connectivity. To accomplish this, we first modelled
211 landscape accessibility of all locations across both islands for humans, given planned and existing
212 infrastructure. Next, we modulated our Sunda clouded leopard connectivity surfaces, given these
213 human accessibility surfaces, as detailed below.

214 **2.3.1. Accessibility from existing roads network**

215 The Sunda clouded leopard habitat suitability data (Macdonald et al. 2018a) on which our
216 connectivity models are based, did not account for the effects of existing infrastructure. To estimate
217 recent losses to connectivity due to road infrastructure development to date, we had to update our
218 understanding of current connectivity accordingly by incorporating effects of existing road network.
219 We, therefore, modeled human accessibility to all areas across each island as a function of
220 infrastructure using the same framework as for Sunda clouded leopard habitat connectivity. Source
221 locations were first defined, now with respect to potential human occupancy, i.e., human traffic;
222 then resistance surfaces were defined, now with respect to human dispersal, namely vehicular traffic

223 along roads and human ‘foot traffic’ from roads over the adjacent landscape. We defined existing
224 roads in Sumatra and Borneo as all motorways, trunk roads, primary roads, and secondary roads as
225 defined by the current version of the OpenStreetMap dataset (OSM) (OpenStreetMap contributors,
226 2022). Source locations were specified at differing densities for each of three road classes, with
227 higher (lower) densities ascribed to roads with higher (lower) capacity for human traffic, i.e., more
228 (less) lanes and higher (lower) speeds. This reflects the greater traffic and disturbance conduit
229 function of larger roads as compared to smaller less travelled roads. Specifically, we ascribed one
230 source location for every 2 km segment, 4km segment, and 8 km segment for motorways and trunk
231 roads, for primary roads, and for secondary roads, respectively (more information on the density of
232 source location is available in Appendix 1.3). All source locations were subsequently combined to run
233 a cumulative resistant kernels analysis in UNICOR, predicting human accessibility along and from the
234 road network, similar to the connectivity analysis run for Sunda clouded leopard habitat (Section
235 2.1.2)., but specifying dispersal distance threshold of 1,000,000 resistance units to reflect the high
236 mobility of humans assisted by motor vehicles.

237 Our resistance surface for modelling human accessibility incorporated two factors: road class,
238 being a proxy for traffic flow; and topographical slope, given that building additional roads or
239 accessing areas on foot is progressively limited by increasingly steeper terrain. We first defined a
240 slope surface at 90-m resolution, based on SRTM data (Jarvis et al. 2008) and rescaled to resistance
241 values of 100-1000. We then assigned nominal resistance values of 1, 20, and 40 to our three road
242 classes of motorways and trunk roads, primary roads, and secondary roads, respectively (the logic
243 behind choosing these resistance values is explained in Appendix 1.3). Finally, we combined the roads
244 layer with assigned resistance values with the slope resistance layer, and used this final resistance
245 surface for our modelling. Notably, in our final resistance layer, roads have lower resistance values
246 than surrounding flat areas, due to the rescaling of the input slope layer.

247 **2.3.2. Accessibility from the Trans-Sumatran Toll Road**

248 We digitized the planned segments of the Trans-Sumatran Toll Road (TTR) based on several
249 published maps (Sloan et al. 2019b), OpenStreetMap (OSM), and Google Earth. As with existing roads
250 (Section 2.4.1), we ascribed the TTR one source locations per 2km segment and a resistance values
251 of 1. These TTR source locations were then combined with the source locations defined for existing
252 roads, and the resistance of the TTR was similarly integrated into the final resistance surface of
253 existing roads (Section 2.3.1). Finally, using these updated data incorporating the TTR, we re-ran the
254 human accessibility analyses described for existing roads previously (Section 2.3.1).

255 **2.3.3. Accessibility from the Pan Borneo Highway**

256 There are several ongoing and planned road development projects of the Pan Borneo Highway
257 (PBH) network, namely the southern Trans-Kalimantan segments, the central part through Central
258 and West Kalimantan provinces, and the northern (Sarawak) segment and the Sabah highway
259 network (Sloan et al. 2019c; Alamgir et al. 2019). We defined these PBH segments here according to
260 spatial data provided by Alamgir et al (2019) for Kalimantan, and by Abram et al., 2022 for Sarawak
261 and Sabah. Human accessibility from these segments of the PBH was modelled otherwise as
262 described for the TTR above (Section 2.3.2).

263 **2.3.4. Accessibility and the Nusantara capital city**

264 To model the potential extent of the new capital city of Nusantara, as a base scenario we
265 generated a 50km circular buffer around its approximate proposed location. The size of the buffer
266 was determined based on a study of Pravitasari et al. (2015) analyzing urban expansion of Great
267 Jakarta. However, because we are uncertain about the size of future capital and its future rate of
268 urban expansion we also performed sensitivity analyses by applying three other scenarios of
269 potential urban expansion (buffer sizes: 30km, 40km and 60km). As with the major roadways above,

270 we ascribed this buffer area a resistance value of 1, and then integrated the corresponding resistance
271 layer with that defined for existing roadways previously (Section 2.3.1). The source locations for
272 vehicle and human traffic, were placed in the nominal location of the city plus random locations
273 within the surrounding buffer area. We then re-ran the modelled increased human accessibility due
274 to the city's planned development, as with the TTR and PBH developments above. Since the impact
275 of new capital city will presumably extend far beyond those of roads per se, as due to increased
276 regional economic activity, population size and resource extraction (Teo et al. 2020), we specified a
277 dispersal threshold four-times larger than for the TTR and PHN, i.e., 4,000,000 resistance units.

278 **2.3.5. Impact of development on Sunda clouded leopard connectivity**

279 To analyze how infrastructure may curtail Sunda clouded leopard habitat connectivity, we
280 defined a spatial *index of connectivity loss* (Eqn 2) on the basis of the spatial intersections between
281 our Sunda clouded leopard connectivity layer with the human accessibility layers for existing
282 roadways, the TTR, the PHB, and Nusantara city separately. In Equation 2, Sunda clouded leopard
283 connectivity was rescaled to between 0 (lowest connectivity) and 1 (highest connectivity), and
284 human accessibility was similarly rescaled and inverted to between 0 (most accessible) and 1 (least
285 accessible). Hence, index values approaching a minimum of -1 indicate losses of relatively connected
286 Sunda clouded leopard habitats due to relatively high human accessibility, while index values
287 approaching a maximum of 0 indicate smaller losses in connectivity due to either limited human
288 accessibility, initially low Sunda clouded leopard connectivity or high connectivity in areas with low
289 projected impact.

290

$$291 \quad \textit{Index of Connectivity Loss} = (\textit{Leopard Connectivity} * \textit{Human Accessibility}) -$$
$$292 \quad \textit{Leopard Connectivity} \tag{2}$$

293 **2.4 Identifying gaps in the protection of priority habitats**

294 We analyzed how thoroughly the existing protected area network encompasses our modelled
 295 CAs for population connectivity of the Sunda clouded leopard, taking into consideration the likely
 296 effects of future infrastructure. Protected areas (PAs hereafter) were defined as current official PAs
 297 of Management classes I-IV (Dudley 2008), delineated by IUCN (IUCN and UNEP-WCMC, 2021) as of
 298 April 2021. For each island, we then calculated several measures describing how, and how well, PAs
 299 encompass Sunda clouded leopard core habitats or dispersal corridors (Table 1).

300 *Table 1. Measures of protected areas coverage of Sunda clouded leopard habitat connectivity.*

| Measure | Description of Measure |
|---|---|
| Total protected connectivity | Summed resistant kernel values (unthresholded) within protected areas as a proportion of the total sum of resistant kernel values |
| Strength of the protected CAs | Summed resistant kernel values (thresholded, representing only core areas) within PAs as a proportion of the total sum of resistant kernel values within CAs |
| Percentage of core area protected | Percentage of the total size of CAs being protected |
| Strength of the protected dispersal corridors | Summed smoothed FLCPs values (thresholded and without CAs, representing dispersal corridors) within PAs as a proportion of the total sum of FLCPs values within the corridors |
| Percentage of corridors protected | Percentage of the total area of corridors within PAs |

301

302 To analyze the impact of the existing and future infrastructure on the current protected areas
303 network, we calculated the percent of connectivity lost within the PAs network as compared to the
304 total connectivity lost for each development scenario. This was done by summing up the Index of
305 Connectivity Loss for each scenario within PAs and across the landscape and then calculating the
306 percentage of that loss within the PAs network. Additionally, the percent loss in connectivity within
307 PAs for each development scenario was calculated in relation to loss of connectivity caused by the
308 existing road network.

309 **3. Results**

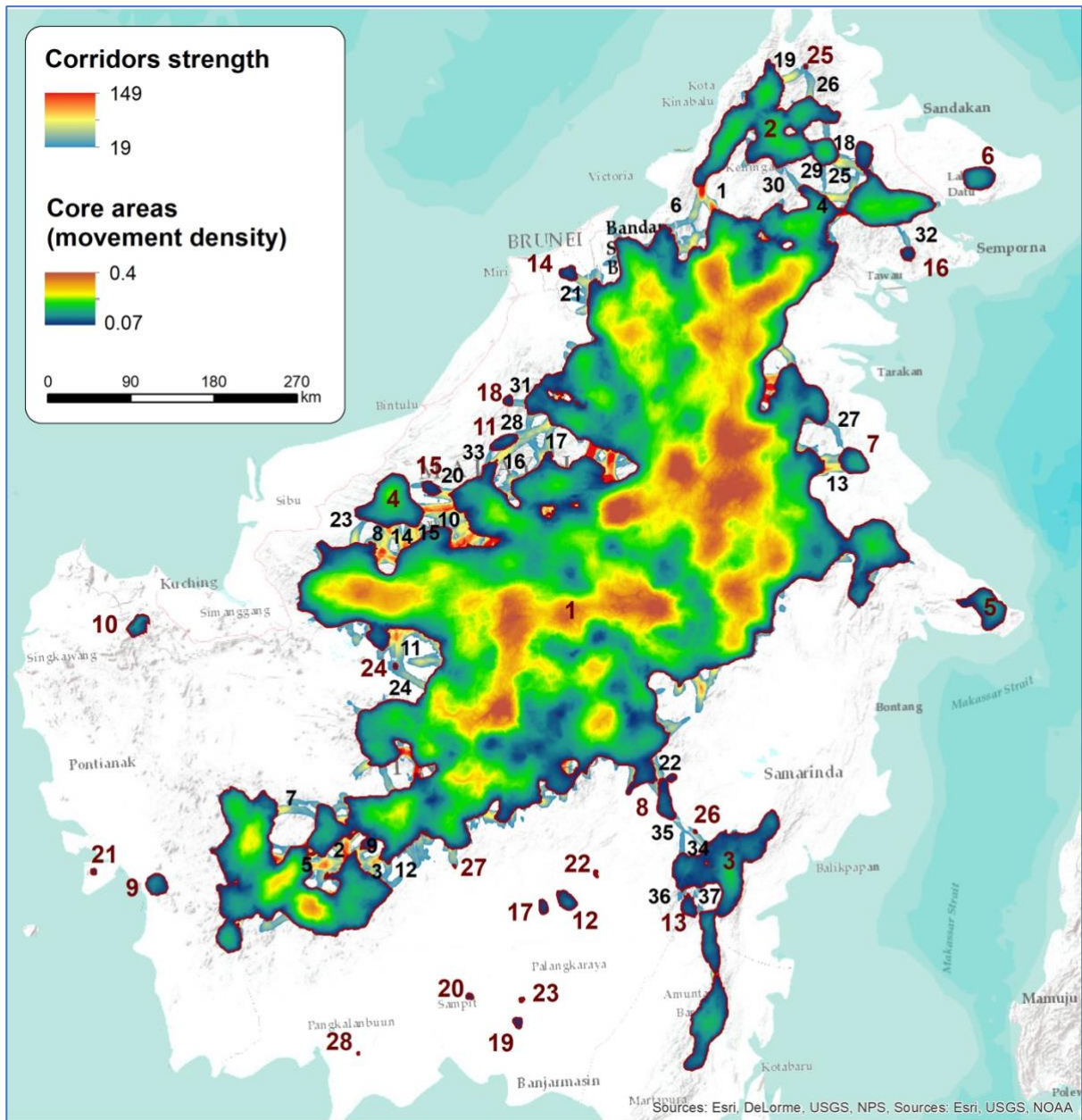
310 **3.1. Core areas and corridors**

311 We identified 28 CAs in Borneo and nine in Sumatra, ranked in Figure 1 and Figure 2,
312 respectively, according to their importance to Sunda clouded leopard population connectivity. These
313 CAs had highly disparate size distributions between the two islands. Borneo is characterized by one
314 large central CA in its highland region, with all other 'satellite' core areas being $<1/25$ the size. This
315 large central CA in Borneo is ~ 10 times larger than the largest CA in Sumatra (256,550 km² vs. 28,281
316 km²), while 65% of CAs in Borneo are smaller than the smallest Sumatran CA (Table A1 and Table A2).
317 Sumatra has a comparatively even distribution of CAs by area, with two relatively large CAs (above
318 18,000 km²) and seven CAs below 3,000 km², the smallest of which being 340 km². Sunda clouded
319 leopard CAs cover $\sim 34.2\%$ of Borneo and $\sim 12.9\%$ of Sumatra.

320 We further identified 37 dispersal corridors between CAs in Borneo (Table A3), and 22 and
321 Sumatra (Table A4), ranked in Figure 1 and Figure 2, respectively, by corridor strength. In general,
322 corridors in Sumatra linked relatively disjointed CAs. In Borneo, corridors typically linked the largest
323 central CA with proximate and much smaller satellite CAs. Borneo also has several isolated CAs, i.e.,

324 CAs not linked by any corridor, whereas in Sumatra all CAs are linked at the dispersal threshold
325 specified in this study.

326

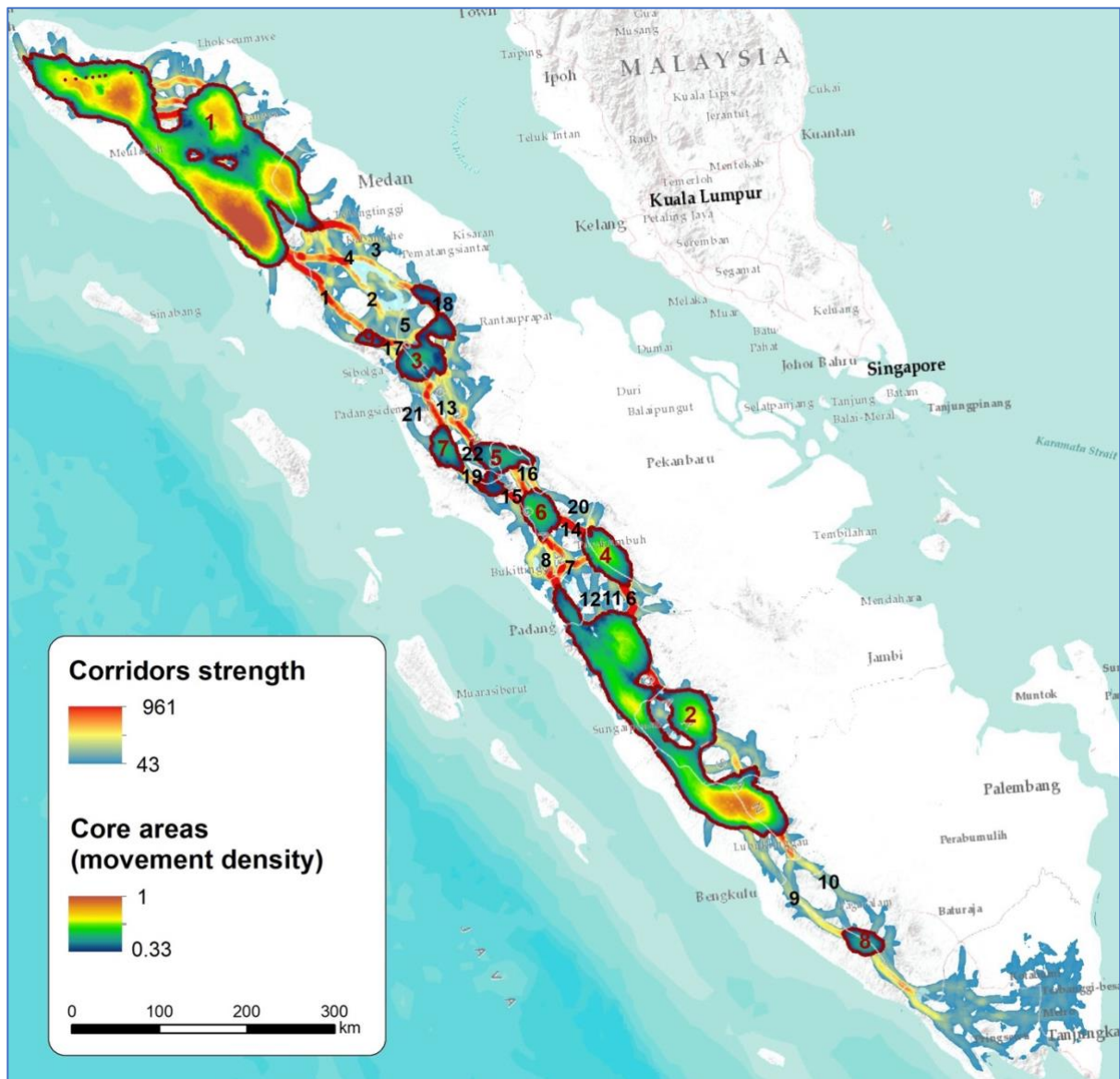


327

328 *Figure 1. Sunda clouded leopard core areas and corridors strength and ranking in Borneo. Red numbers - core areas ranking;*

329

Black numbers – corridors ranking.



330

331

Figure 2. Sunda clouded leopard core areas and corridors strength and ranking in Sumatra. Red numbers - core areas ranking;

332

Black numbers – corridors ranking.

333

334

3.2 Impact of infrastructure development on Sunda clouded leopard connectivity

335

3.2.1 Existing roadways in Borneo and Sumatra

336

As reported below, road development has affected all of the major CAs on both islands.

337

In Borneo, the greatest losses to connectivity occurred where roadways isolated large forest

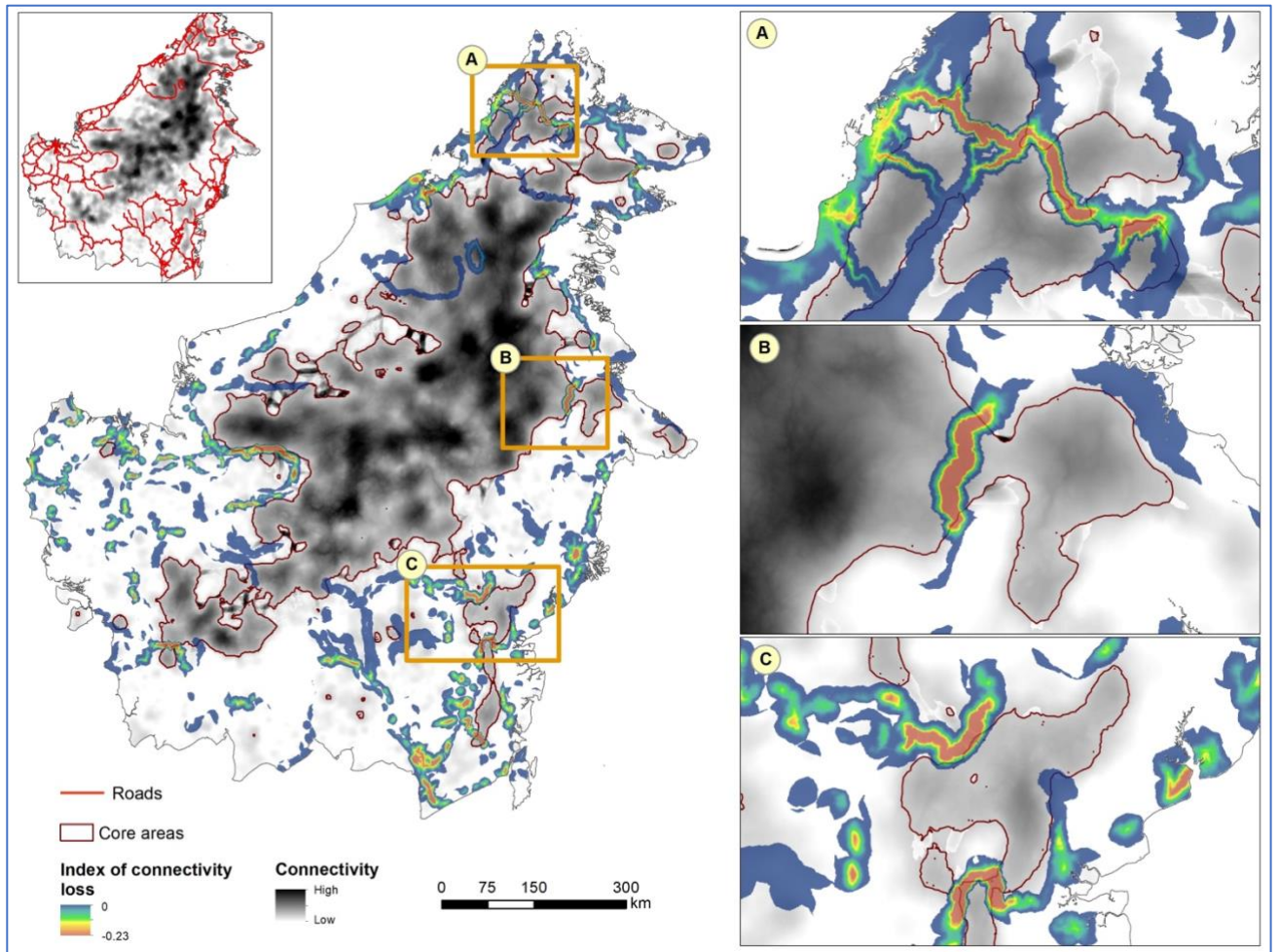
338

fragments from the second most important CA (Figure 3a) or from the most important, central CA

339 (Figure 3b, 3c). In all cases, such isolation occurred where forest habitat was a narrow stretch or
340 'bottleneck' bridging expansive areas of forest habitat. Our results highlight the immediate
341 potential for similar major CA fragmentation at bottlenecks in the northeastern portion of the most
342 important, central CA, in Sabah, and at the southern extent of the third most important CA, in
343 South Kalimantan Province (Figure 1). Indeed, the latter is directly threatened by the PBH, as
344 discussed below.

345 In Sumatra, the greatest loss to Sunda clouded leopard connectivity occurred in the Leuser
346 Ecosystem (Figure 4a) (cf. Sloan et al. 2018a) with sum of the Index of Connectivity loss reaching
347 around 15,000 (North Sumatra Province, Figure 8). At the same time Leuser Ecosystem was also
348 ranked as the most important CA on the island (Figure 1). A newly built road has recently divided
349 the Leuser Ecosystem in half (Figure 4A) and potentially portends the isolation of Sunda clouded
350 leopards in the eastern and western halves of this CA. Similar, but lesser, losses occurred in the
351 second most important CA (cf. Sloan et al. 2019A) (Figure 4C) as well as amongst the fourth, fifth,
352 sixth and seventh most important CAs (Figure 2, Figure 4B). The third most important CA in
353 Sumatra was relatively less subject to connectivity losses due to its relative geographic isolation
354 from other CAs and its corresponding lesser potential for Sunda clouded leopard dispersal.

355

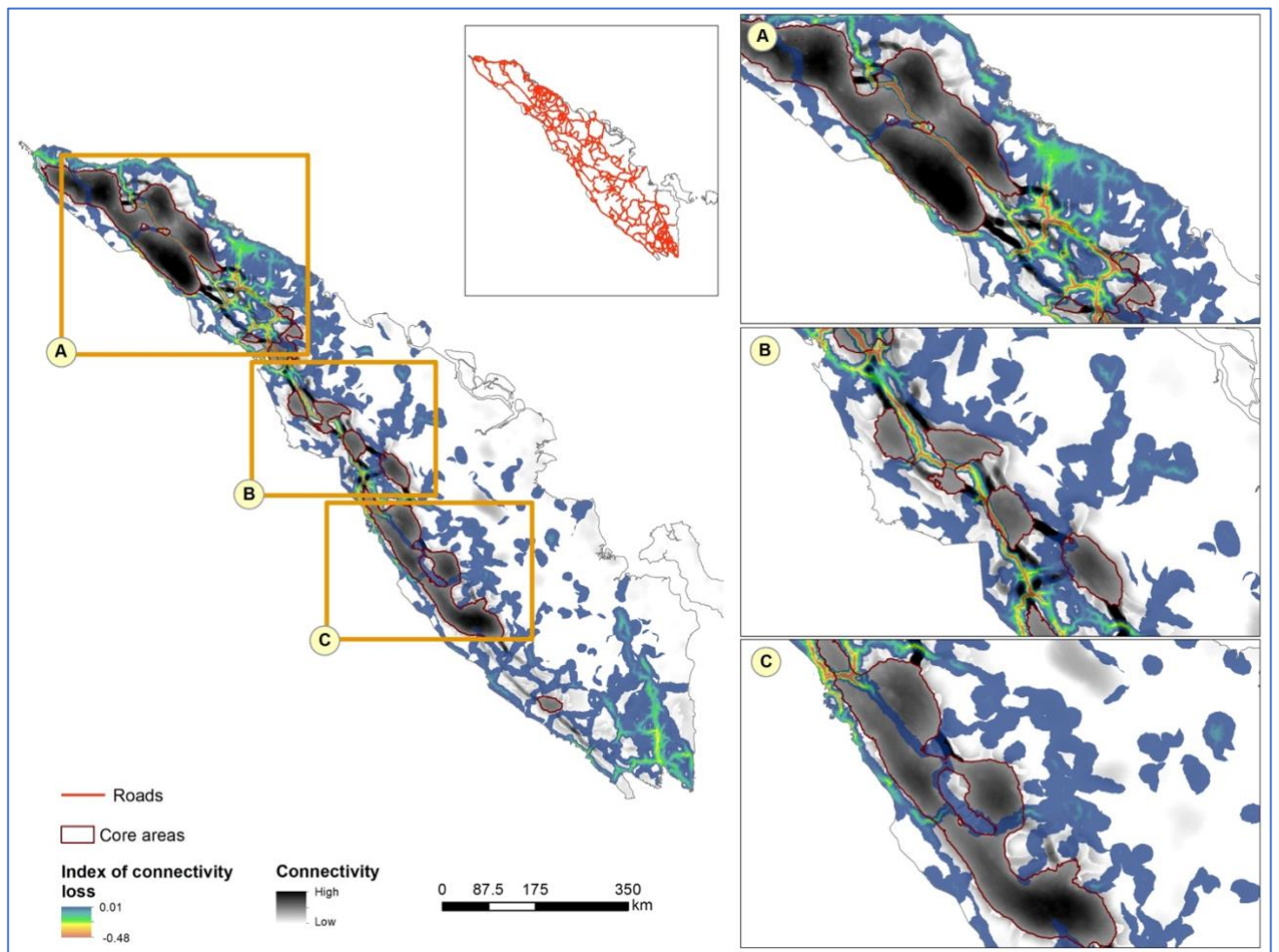


356

357

358

Figure 3. Recent historical losses to Sunda clouded leopard connectivity due to existing roadways in Borneo. A,B and C are areas of the highest impact.



359

360

361

Figure 4. Recent historical losses to Sunda clouded leopard connectivity due to existing roadways in Sumatra. A,B and C are areas of the highest impact.

362

3.2.3 Pan Borneo Highway

363

The anticipated impact of the Pan Borneo Highway on Sunda clouded leopard connectivity

364

accounted for 28% of the total modelled decrease in Sunda clouded leopard connectivity,

365

measured by the Index of Connectivity Loss, of the three future infrastructure projects (excluding

366

existing roads). Developing the PBH will likely result in 1.2% of total Sunda clouded leopard

367

connectivity loss across the entirety Borneo (Appendix Table A7). Several segments of the PBH will

368

traverse the largest, and modelled as most important, central CA (Figure 5A, 5B). The greatest

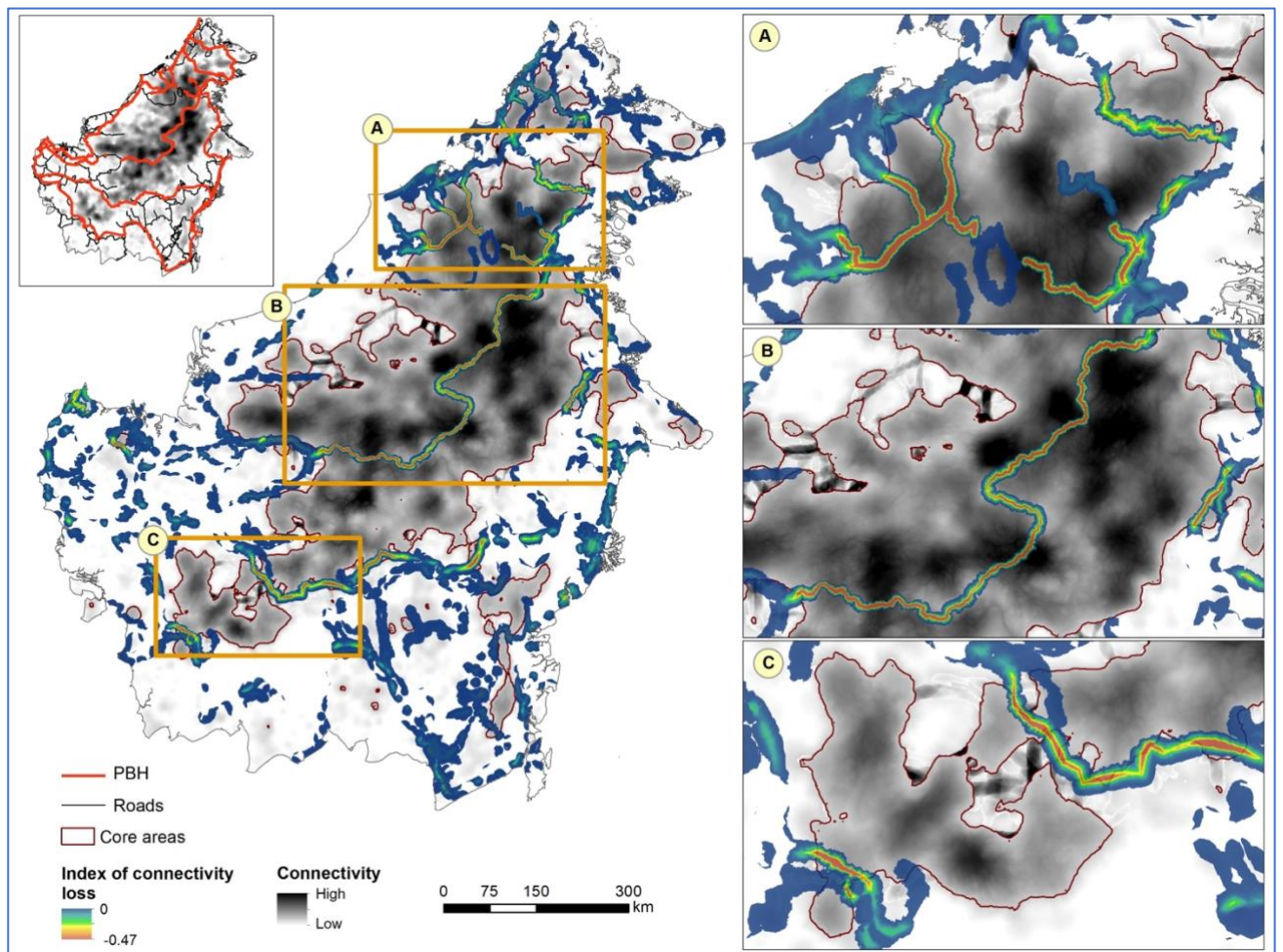
369

impact on Sunda clouded leopard connectivity is predicted in the northern segment of the Trans-

370

Kalimantan highway traversing the center of this CA (Figure 5B) with losses estimated by the sum of

371 the Index of connectivity loss of about 9,000 only in the North Kalimantan province (Figure 8). The
 372 entire northern reach of the PBH, in North Kalimantan Province and Sabah, will result in large
 373 losses to connectivity in the central CA and the potential disconnection of Sabah populations from
 374 the rest of Borneo (Figure 5A) (cf. Sloan et al. 2019A). A PBH segment traversing southern
 375 Kalimantan latitudinally will also fully isolate a major southwestern portion of the central CA
 376 (Figure 5C) and, further east, largely eradicate the eighth most important CA (Figure 5, Figure 1).



377

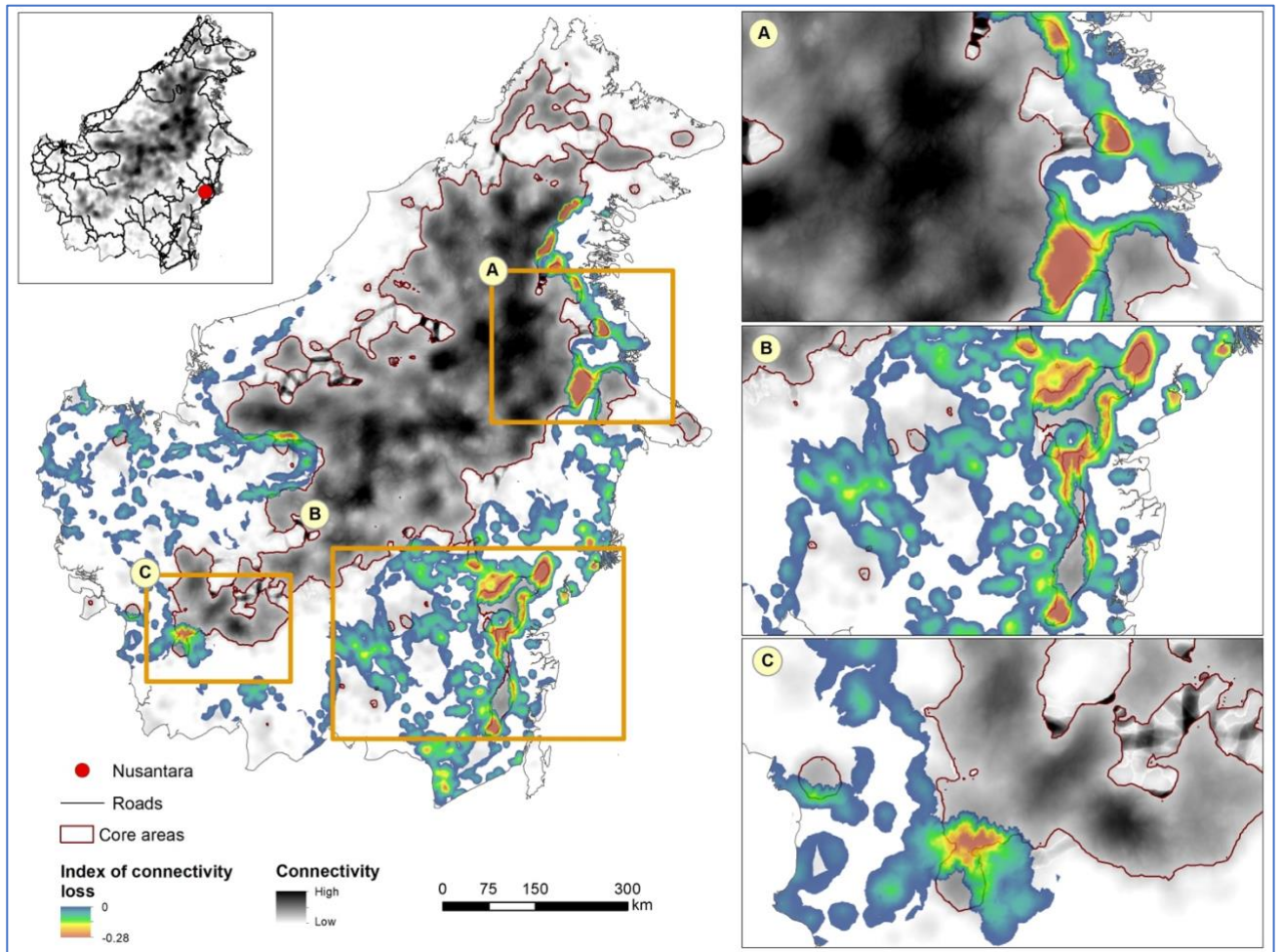
378 *Figure 5. Impact of Pan Borneo Highway on Sunda clouded leopard connectivity. A, B and C are areas of the highest impact.*

379

380 3.2.2 Nusantara Capital City

381 The new Indonesian capital of Nusantara in Eastern Kalimantan province poses the most
382 significant and extensive impact on Sunda clouded leopard connectivity amongst all future
383 infrastructure projects considered by far, accounting for 66% of the total modelled connectivity loss
384 across all three development projects. Depending on the rate of urban expansion and the size of
385 the megacity of Nusantara the loss in Sunda clouded leopard population connectivity in Borneo is
386 predicted to vary between 2.49% (30km buffer) and 3.16% (60km buffer) and is two to three times
387 greater than the connectivity loss potentially caused by PBH alone (Appendix Table A7). The impact
388 of the new capital is projected to cause the disintegration of many CAs across Borneo, particularly
389 in its southeast, including the third most important CA (Figure 6B, Figure 1). At best, this CA would
390 become disconnected from the central, most important CA and may struggle to maintain viable
391 Sunda clouded leopard populations, given its increasing isolation, elongated shape and bottlenecks,
392 which likely will reduce genetic exchange with the central CA, and growing human pressure from
393 the nearby new capital. Our analyses also project significant losses to connectivity along the entire
394 eastern flank of the central, most important CA (Figure 6), including major losses due to the
395 isolation of high-connectivity, large forest areas in Eastern Kalimantan (Figure 6A).

396



397

398

399

Figure 6. Impact of new Indonesian capital Nusantara on Sunda clouded leopard connectivity. A,B and C are areas of the highest impact.

400

3.2.4 Trans-Sumatran Toll Road

401

Since many segments of the TTR have been developed recently, the impact of this

402

infrastructure-development project on Sunda clouded leopard connectivity has largely been

403

accounted for by existing road infrastructure (4.6% of connectivity loss in Sumatra with existing

404

roads, 0.56% without existing roads; Appendix Table A7). When excluding the effects of existing

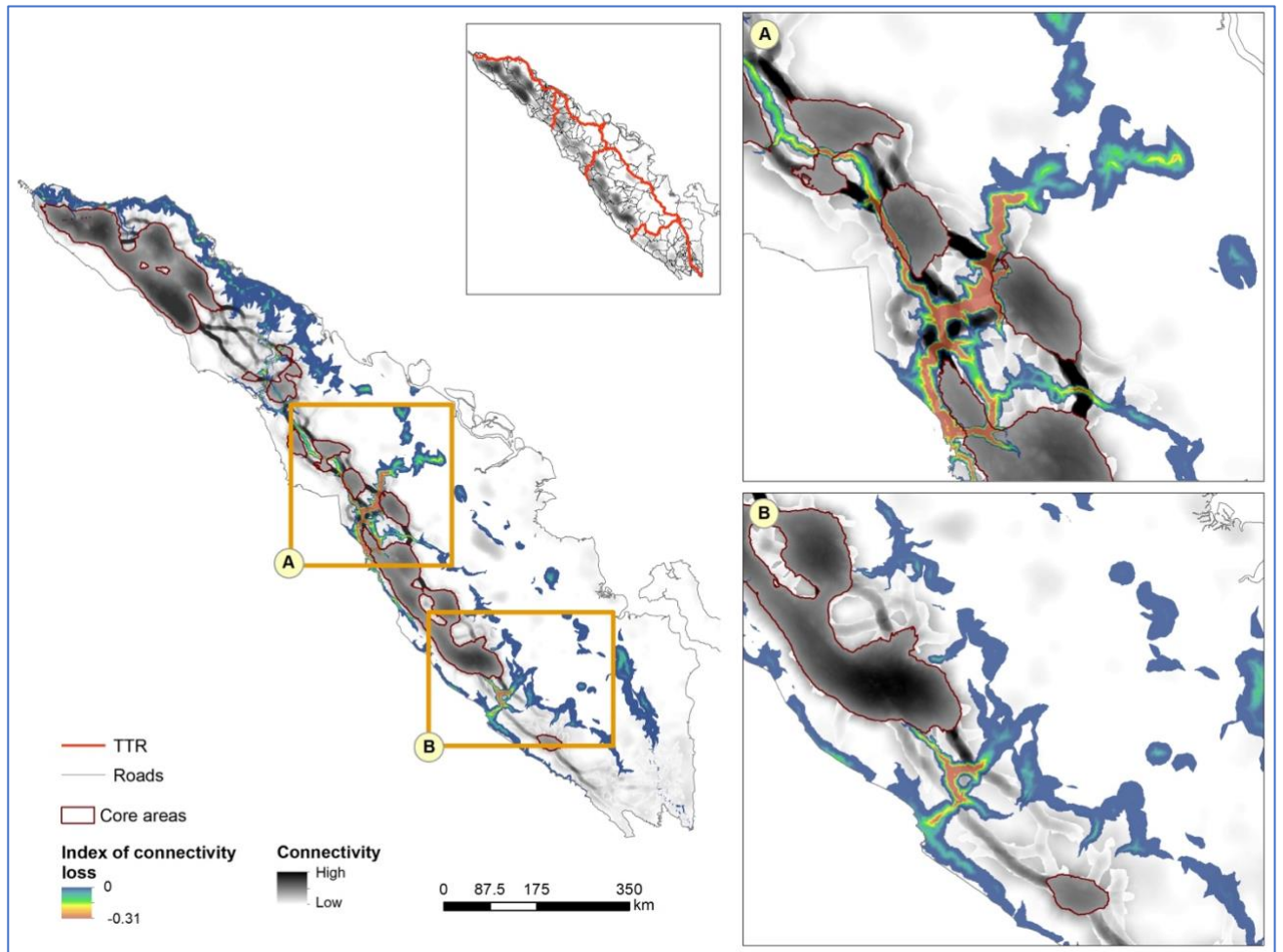
405

roads, the TTR was modelled to account for 5% of the total Index of Connectivity Loss across the

406

three infrastructure projects.

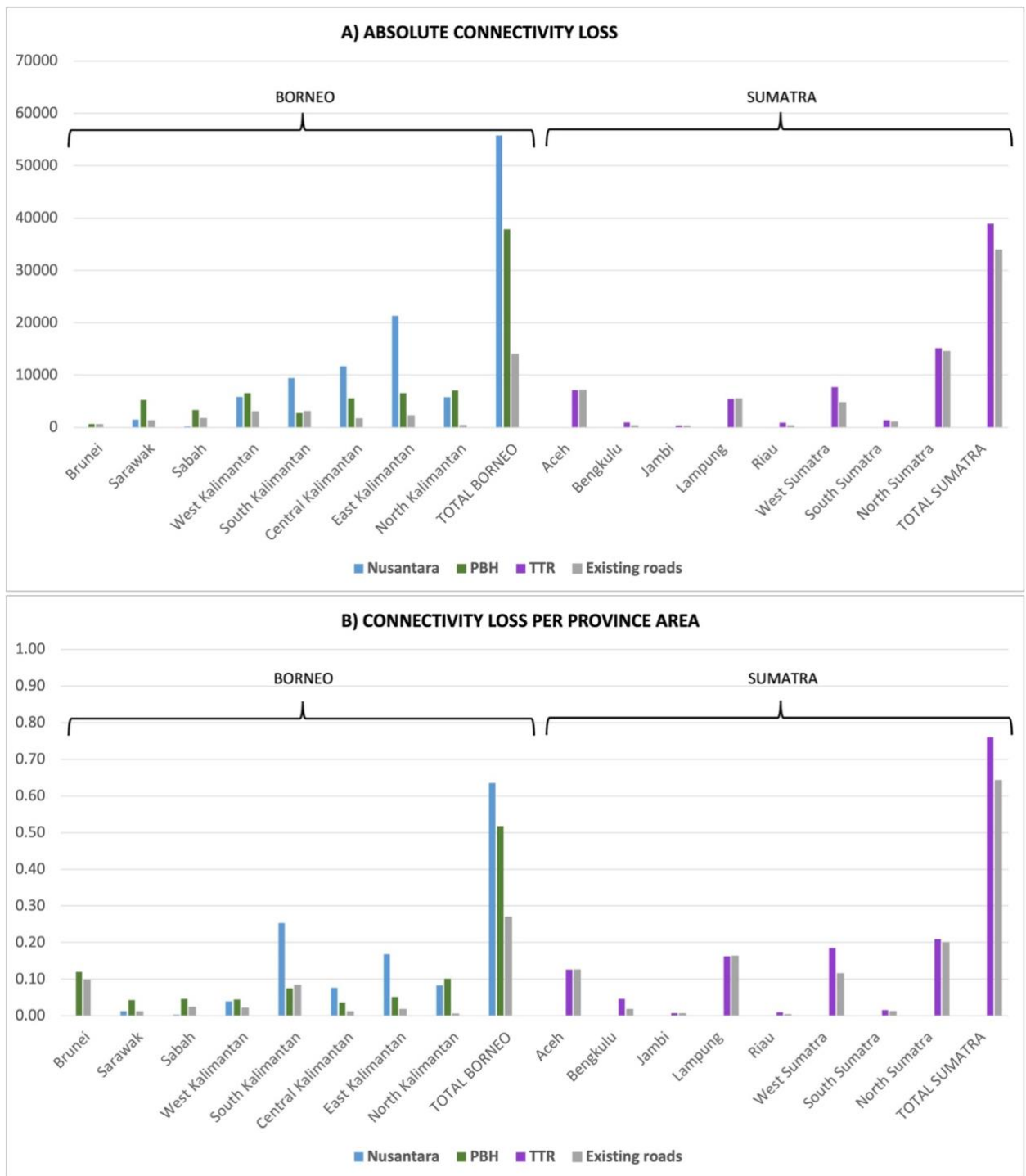
407 Amongst pending TTR segments, the most significant impacts are anticipated in central
408 Sumatra (Figure 7A), where the TTR will further and fully isolate several CAs, breaking up some of
409 the most important Sunda clouded leopard dispersal corridors (Figure 7A). Similar, but lesser,
410 impacts are also anticipated in the connectivity network of corridors connecting the CA host to
411 Kerinci Seblat National Park with smaller forest areas in southern Sumatra (Figure 7B).



412
413 *Figure 7. Impact of Trans-Sumatran Toll Road on Sunda clouded leopard connectivity. A,B and C are areas of the highest*
414 *impact.*

415
416 **3.2.5. Comparison of impacts across projects and provinces**

417 Upon comparing the impact of infrastructure developments across both islands and their
418 provinces/states, total losses to connectivity (excluding the impact of existing infrastructure) were
419 consistently greatest for the new capital Nusantara of and accordingly for Borneo overall (absolute
420 connectivity loss calculated by the Index of connectivity loss of 55,806; and Figure 8 and Appendix
421 Table A7). The anticipated impact on connectivity due to the new capital was many times greater
422 than for the PBH in three provinces of Kalimantan (Figure 8). It is worth noting that the negative
423 impact of the PBH in Borneo on Sunda clouded leopard connectivity, excluding the effects of the
424 existing road network, was much higher than the impact of the TTR in Sumatra (absolute
425 connectivity loss of 23,851 for PBH versus 4,866 for TTR; Figure 8 and Appendix Table A7).



426

427

428

Figure 8. Index of connectivity loss across provinces in Borneo and Sumatra (A- the sum of the index of connectivity loss in each province; B- the sum of the index of connectivity loss standardized by province area).

429

430

3.3 Clouded leopard habitat connectivity protection amidst infrastructure development

431 Core areas in Borneo constitute 34.2 % of the island. In comparison, protected areas cover only
432 9.4% of Borneo. In Sumatra CAs cover 12.8% of the island while PAs constitute 11.2% of the island.

433 Within Borneo 15% of CAs extent and 17.7% of their strength (sum of kernel values) are currently
434 protected (Table A5, Figure A1A). In the case of dispersal corridors in Borneo, 3.3% their strength
435 (sum of LCP values) and 3.5% of their areas lies within PAs (Table A4, Figure A1A).

436 In Sumatra, the strength of the protected CAs (44.9%) and the extent of all CAs within the PAs
437 network (41.7%) is much higher as compared to Borneo. In the case of dispersal corridors in Sumatra,
438 17.9% of their strength and 12.9% of their total area is under protection (Table A5, Figure A1B). In
439 Sumatra, almost all CAs with the highest modelled density of movement are within protected areas.
440 This is not the case in Borneo, where only very small proportion of the high movement density CAs
441 is protected (Figure A1A).

442 Overall, across the three modeled development projects, the impact on Sunda clouded leopard
443 connectivity in PAs was the strongest for the PBH, where ~5% of the total connectivity loss was
444 modelled to occur directly within the existing PAs network (Table A6). As a comparison, this
445 constitutes 15% of the total connectivity loss caused by the existing road network in Borneo. In
446 Sumatra, ~4% of the total connectivity loss due to the TTR development was predicted to occur
447 within PAs (Table A6).

448 **4. Discussion**

449 In this paper, we used the Sunda clouded leopard as a charismatic forest indicator species
450 (Macdonald et al. 2017) to investigate the existing functional forest connectivity across both islands.
451 We ranked the most important core habitats and dispersal corridors, and we quantified the impact
452 of existing, planned and ongoing roads development projects, as well as potential effects of
453 relocation of the new Indonesian capital – Nusantara.

454 We found that core Sunda clouded leopard habitats are already largely fragmented in Sumatra,
455 with some existing dispersal corridors still linking this highly fragmented landscape. The effects of
456 forest fragmentation and habitat loss was found to be different in Borneo, with one large central
457 core area, a few much smaller and still connected satellite core areas, and many very small and
458 already fully isolated fragments.

459 Our results stress the strong negative effects of all the considered already vulnerable existing
460 forest functional connectivity. The PBH cuts through the identified by our analyses most important
461 Bornean core area in several crucial places supporting high density of Sunda clouded leopard
462 movement. Furthermore, the projected impact of the new Indonesian capital was modelled to
463 significantly decrease forest connectivity not only in the near proximity of the capital but almost
464 across the entire island. Finally, the negative effects of TTR (the second most impactful
465 infrastructure project after Nusantara) are already visible and accounted for by the existing road
466 network since the project is largely completed.

467 **4.1. Clouded leopard habitat connectivity and prioritization**

468 Our connectivity model identified a much higher number of CAs in Borneo compared to
469 Sumatra. However, nearly half of these CAs are very small ($< 200\text{km}^2$; as comparison all CAs in
470 Sumatra are $> 300\text{km}^2$) and fully isolated. Most of them are probably not providing conditions for
471 viable Sunda clouded leopard populations.

472 Our results reveal the extensive fragmentation of Sunda clouded leopard core habitats in
473 Sumatra. Although nearly 42% of these areas are currently under protection, except for the
474 relatively large CAs in Gunung Leuser NP and Kerinci Seblat NP, remaining Sunda clouded leopard
475 core population areas in Sumatra are relatively small. Not only is the small size of CAs in Sumatra
476 worrying, our results indicate the urgency of protecting the linkages between these CAs to allow

477 demographic exchange and gene flow between them. Small habitats without the possibility of
478 movement between them expose the species to elevated risk of local extinctions. Although all
479 Sunda clouded leopard CAs in Sumatra are still connected by dispersal corridors, only 13% of these
480 corridors are protected. The northeast side of the CA within the Kerinci Seblat NP is already highly
481 vulnerable, with a relatively narrow connection to the rest of that second most important core
482 area. The existing roads traversing this narrow connecting zone not only increase the risk of
483 wildlife-vehicle collisions (Alamgir et al. 2019; Silva et al. 2020) but in the long term may lead to
484 fragmentation of this part of the second most important CA.

485 We found the habitat connectivity of the Sunda clouded leopard population in Borneo has a
486 dramatically different pattern to that in Sumatra. Although Sunda clouded leopard CAs cover about
487 34% of Borneo, only 15% of those areas and 3.4% of dispersal corridors are currently protected.
488 Furthermore, according to our results, the parts of the main CA supporting a high density of Sunda
489 clouded leopard movement are currently not protected. Furthermore, there are several vulnerable
490 areas within the central CA. Without formal protection, and even with current slowing rates of
491 deforestation (Gaveau et al. 2022), these areas will likely become detached from the central CA
492 (e.g. the most southwestern and northeastern parts of that CA).

493 **4.2. Infrastructure developments and connectivity**

494 Out of all the development scenarios we investigated, the new Indonesian capital Nusantara
495 poses by far the highest threat to Sunda clouded leopard connectivity. The modelled negative
496 impact of the capital reverberated across the entirety of Borneo, except Brunei, with especially
497 high negative effects in South and East Kalimantan. Spencer et al. (2023) predicted that, within an
498 estimated 200km impact zone of the new capital, 16% of critical habitats for biodiversity and more
499 than 40% of the critical orangutan habitat will be affected. According to our results, the capital will

500 especially affect the 3rd and 8th most important Sunda clouded leopard CAs, causing their
501 degradation and disconnection from the central core area (Figure 1). This is worrying considering
502 that Sunda clouded leopards are a barometer of likely change of wider biodiversity (Chiaverini et al.
503 2022).

504 The Pan Borneo Highway is another potential development that is predicted to drive major
505 declines in Sunda clouded leopard connectivity across all Bornean provinces. Many segments of the
506 PBH intersect the most important Sunda clouded leopard CA located in the heart of the island. The
507 Trans-Kalimantan part of the PBH, traversing the central part of this CA, including areas supporting
508 the highest modelled Sunda clouded leopard density of movement, showed the greatest negative
509 impact on connectivity. Spencer et al. (2023) found that the Trans-Kalimantan highway is planned
510 to cross important hotspots of biodiversity, potentially causing large negative impacts on wildlife.
511 For example, Spencer et al. (2023) reported that 12.3 % of the area within 5km of the new roads in
512 Kalimantan and 15.0 % of the area within 50km from the new roads contains critical habitat for
513 threatened mammals. Similarly, Alamgir et al. (2019) reported that planned and ongoing
514 infrastructure-expansion networks in Kalimantan, including the PBH, would decrease structural
515 forest connectivity in this region from 89% to 55%. Our results show very strong negative impacts
516 of the PBH especially in East, North and West Kalimantan provinces, as well as in Sarawak.
517 Although, in our analyses Sabah was not predicted to be the most affected province by the PBH
518 development, Kaszta et al. (2019) have previously predicted that effects of all potentially planned
519 infrastructure developments in this state could result in a 23% loss of Sunda clouded leopard
520 connectivity, 40-63% decrease in Sunda clouded leopard population size and significant reduction
521 in its genetic diversity. Moreover, the negative impact of the PBH development will also affect
522 protected areas. Our results shows that the PBH had the highest modelled negative effect on Sunda
523 clouded leopard habitat connectivity within protected areas amongst all the considered

524 infrastructure developments. According to Alamgir et al. (2019) the PBH is planned to intersect 25
525 PAs in Kalimantan alone, including Kayan Mentarang NPK, which is one of the largest relatively
526 intact NP in Indonesian Borneo.

527 In Sumatra, the Trans-Sumatran Toll Road was also modelled to have a negative effect on
528 Sunda clouded leopard habitat connectivity, especially in the province of West Sumatra. The total
529 negative effects of the TTR are probably much higher, however, because many segments of this
530 highway have already been constructed, with the consequence that their existing impact (e.g. in
531 Aceh and North Sumatra provinces) was incorporated in our analysis of existing (rather than future)
532 road impacts. Sloan et al (2019) discussed these potential negative effects of the TTR on remnant-
533 forests of the Leuser Ecosystem, Kerinci-Seblat NP and Batang Toru. The authors envisaged that,
534 without legal protection, the highway would promote human incursions into the fringes of these
535 protected areas.

536 Although in this paper we were not investigating and predicting indirect effects of road
537 developments, it is well documented that roads significantly increase detrimental human access to
538 forest. This in turn increases logging (Laurance et al. 2009; Teo et al. 2020), hunting pressure
539 (Deere et al. 2020), edge effects (Pfeifer et al. 2017) as well as fire risk and further degradation of
540 primary forest (Nikonovas et al. 2020). Based on the Tesso Nilo NP (Riau Province of Sumatra)
541 example, Poor et al. (2019) reported a proliferation of small roads sprawling from the larger
542 highways which greatly increased forest loss and fragmentation. The authors found that previously
543 unmapped smaller roads created an edge effect covering 82-99% of the forest within the Tesso Nilo
544 NP.

545 **4.3. Scope and limitations**

546 In this work we used data from camera traps across Borneo and Sumatra to understand Sunda
547 clouded leopard movement-habitat relationships and to model the species habitat connectivity.
548 Habitat-based estimates of landscape resistance are often inferior to those produced from
549 telemetry or genetic methods (e.g., Mateo-Sanchez et al. 2015; Wasserman et al. 2012; Sartor et al.
550 2022). Furthermore, our assumptions on road resistance are untested due to lack of empirical data
551 on clouded leopard movement across a wide range of landscape conditions. As the availability of
552 Sunda clouded leopard telemetry or genetic data increases, we recommend that the connectivity
553 models be updated and validated based on this information.

554 It is important to acknowledge that both the density calculations and the habitat suitability
555 model are based on models, which inherently carry a degree of uncertainty, often of considerable
556 magnitude. Therefore, future research should validate and improve understanding of the key
557 parameters used in this study including density, movement ability, resistance, and habitat
558 suitability. This study used the most complete information currently available and given the
559 urgency represented by rapid habitat loss and fragmentation in the system it is important to
560 present the most complete knowledge we have currently. Future work can improve estimation of
561 these parameters through empirical research on movement behavior of GPS monitored individuals,
562 landscape genetics, and continued camera trap studies to document changes in distribution and
563 estimate density through capture-recapture methods.

564 We used the Sunda clouded leopard as a focal species, given it is highly mobile, wide-ranging
565 and it is closely associated with forest ecosystems. Thus, it can potentially serve as an umbrella
566 species for other forest dependent species (e.g., Dickman et al. 2015; Macdonald et al. 2017;
567 Chiaverini et al. 2022). However, to fully investigate effects of current and future infrastructure

568 projects on wildlife, habitats, landscape integrity and population connectivity in Borneo and
569 Sumatra more species with different levels of sensitivity to fragmentation, should be investigated.

570 Furthermore, in this work we did not model any indirect and longer-term effects of road
571 expansion and development of the new capital, as those can be highly unpredictable. Therefore,
572 we believe that probably the effects of the investigated infrastructure developments will be far
573 more detrimental to Sunda clouded leopards, and other wildlife, than our conservative modelled
574 predictions.

575 **4.4. Conservation implications**

576 This work identified, mapped and ranked the most important core habitats and dispersal
577 corridors for Sunda clouded leopard, and potentially other forest-dependent species, across
578 Borneo and Sumatra to inform conservation priorities. The top priority is protecting the existing
579 core areas and, secondly, protecting also the highly ranked dispersal corridors between them.
580 Based on the predicted maps of Sunda clouded leopard habitat connectivity, we recommend
581 expansion of the existing protected areas to cover larger parts of the two most important core
582 areas and also protection of the smaller core area between them which might act as
583 steppingstones linking the two large expanses of core habitat.

584 Our results suggest that both Borneo and Sumatra need dramatic conservation action to
585 safeguard clouded leopard connectivity. In Borneo only a very small proportion of Sunda clouded
586 leopard core habitats are protected and with a probable increase in development driven by
587 expanding infrastructure and the relocation of the Indonesian capital. Without legal protection the
588 large central core area in the heart of Borneo might soon become dismembered and its fragments
589 isolated. We advocate prioritizing protection of the central part of the main core area, which we
590 predict supports a high density of Sunda clouded leopard movement. In Sumatra, in contrast,

591 extensive past habitat loss has highly reduced and fragmented clouded leopard core habitats.
592 These remaining core habitats are relatively well protected by existing PAs; in Sumatra, therefore,
593 the conservation focus must be on safeguarding these last core populations and ensuring their
594 functional connectivity by protecting the priority corridors identified in this analysis.

595 According to our predictions, in Borneo the added effects of the new capital and all segments
596 of the PBH, if not properly mitigated, will likely greatly decrease connectivity of Sunda clouded
597 leopard populations and forest integrity in general. We recommend rerouting the North
598 Kalimantan segment of the TTR (*sensu* Kaszta et al. 2019), which was modelled as the segment
599 likely to be most detrimental to Sunda clouded leopard connectivity, and is currently planned to
600 run through the primary forest in the heart of Borneo. In case of the approval of the TTR project,
601 we strongly advocate to integrate multiple strategically located and well-designed wildlife under-
602 or over-passes into the TTR development plans, allowing at least minimal mitigation (Bennett
603 2017). This construction should be placed especially in the areas modelled here as important core
604 habitats/corridors supporting high-density movement. Although there are speculations over the
605 effectiveness of under- or over-passes, several studies have shown that even if the structures are
606 not frequently used they still may be sufficient to facilitate population connectivity and allow gene
607 flow (Clevenger 2013; Zimmermann Teixeira et al. 2013). Furthermore, additional fencing along
608 roadsides can be effective in preventing wildlife from crossing a road or directing them towards the
609 crossing structures (Bennett 2017).

610 The relocation of the Indonesian capital to Nusantara, which is already underway, was
611 revealed by our models to be the most impactful development of all those we analyzed. The
612 predicted impacts affected almost the entirety of Borneo, making it difficult to mitigate. However,
613 since the new capital is designed and built from a blank slate it is crucial to incorporate an effective

614 and strategically placed green infrastructure to create biodiversity sensitive urban design (Garrard
615 et al. 2018). One of the best examples of such design could be a Fishermans Bend (Melbourne) -
616 the largest urban renewal project in Australia explicitly including biodiversity targets (Kirk et al.
617 2021).

618 Overall, our core areas and corridors prioritization and assessment of potential effects of three
619 major development projects provide an important foundation to develop conservation actions and
620 land use planning to minimize the impact of future developments planning on habitats of forest
621 dependent species across Borneo and Sumatra. This paper did not explore alternative development
622 scenarios or evaluate modifications of development and conservation plans (as was done in
623 Cushman et al. 2016 and Kaszta et al 2019, 2021 for example). However, analyzing the current state
624 of connectivity for Sunda clouded leopard and projected impacts of three major development
625 projects provides a critical baseline to assess ongoing habitat loss and fragmentation, a benchmark
626 for comparing future changes, and a foundation on which future collaborative research should co-
627 develop optimized conservation and development scenarios.

628

629 **Acknowledgements**

630 We thank the Robertson Foundation for granting this project. This work builds on the large-
631 scale camera-trapping effort, published by Macdonald et al. (2019) co-authored Helen M. Bothwell,
632 Susan M. Cheyne, Iding Haidir, Luke T.B. Hunter, Matthew Linkie, Ewan A. Macdonald, and Joanna
633 Ross, all of whom we gratefully acknowledge. We also acknowledge map data copyrighted
634 OpenStreetMap contributors and available from <https://www.openstreetmap.org>.

635

636 **References**

- 637 Abram, Nicola; Lim, Hong Ye; Ng, Casey Keat-Chuan; Yorath, Sylvia; Razi, Mohamed Haleem
638 Mohamed; Ong, Cynthia Gaik Suan; et al. (2022). Data_Dwellings.zip. figshare. Dataset.
639 <https://doi.org/10.6084/m9.figshare.19299689.v1>
- 640 Alamgir M, Campbell MJ, Sloan S, Suhardiman A, Supriatna J, Laurance WF. 2019. High-risk
641 infrastructure projects pose imminent threats to forests in Indonesian Borneo. *Scientific*
642 *Reports* **9**. Nature Research.
- 643 Basyuni M, Sulistiyono N, Wati R, Hayati R. 2018. Deforestation trend in North Sumatra over
644 1990-2015. Page IOP Conference Series: Earth and Environmental Science. Institute of
645 Physics Publishing.
- 646 Bennett VJ. 2017. Effects of Road Density and Pattern on the Conservation of Species and
647 Biodiversity. *Current Landscape Ecology Reports* **2**:1–11. Springer Science and Business
648 Media LLC.
- 649 Chiaverini L et al. 2022. Multi-scale, multivariate community models improve designation of
650 biodiversity hotspots in the Sunda Islands. *Animal Conservation* **25**:660–679. John Wiley
651 and Sons Inc.
- 652 Clevenger AP. 2013. Mitigating Highways for a Ghost: Data Collection Challenges and
653 Implications for Managing Wolverines and Transportation Corridors. *Northwest Science*
654 **87**:257 – 264. Northwest Scientific Association. Available from
655 <https://doi.org/10.3955/046.087.0307>.
- 656 Compton BW, McGarigal K, Cushman SA, Gamble LR. 2007. A resistant-kernel model of
657 connectivity for amphibians that breed in vernal pools. *Conservation Biology* **21**:788–799.
- 658 Coordinating Ministry for Economic Affairs. 2011. Master Plan: Acceleration and Expansion of
659 Indonesia Economic Development 2011-2025. Jakarta.
- 660 Cushman SA, Elliot NB, Bauer D, Kesch K, Bahaa-el-din L, Bothwell H, Flyman M, Mtare G,
661 Macdonald DW, Loveridge AJ. 2018. Prioritizing core areas, corridors and conflict
662 hotspots for lion conservation in southern Africa. *PLoS ONE* **13**. Public Library of Science.

663 Cushman SA, Elliot NB, Macdonald DW, Loveridge AJ. 2016. A multi-scale assessment of
664 population connectivity in African lions (*Panthera leo*) in response to landscape change.
665 *Landscape Ecology* **31**:1337–1353. Springer Netherlands.

666 Cushman SA, Landguth EL, Flather CH. 2013. Evaluating population connectivity for species of
667 conservation concern in the American Great Plains. *Biodiversity and Conservation*
668 **22**:2583–2605.

669 Cushman SA, McKelvey KS, Schwartz MK. 2009. Use of Empirically Derived Source-Destination
670 Models to Map Regional Conservation Corridors. *Conservation Biology* **23**:368–376.

671 Deere NJ et al. 2020, May 1. Implications of zero-deforestation commitments: Forest quality
672 and hunting pressure limit mammal persistence in fragmented tropical landscapes. Wiley-
673 Blackwell.

674 Dickman AJ, Hinks AE, Macdonald EA, Burnham D, Macdonald DW. 2015. Priorities for Global
675 Felid Conservation. *Conservation Biology* **29**:854–864.

676 Dudley N. 2008. Guidelines for applying protected area management categories. Iucn.

677 Garrard GE, Williams NSG, Mata L, Thomas J, Bekessy SA. 2018. Biodiversity Sensitive Urban
678 Design. *Conservation Letters* **11**:e12411. Available from
679 <https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/conl.12411>.

680 Gaveau DLA, Locatelli B, Salim MA, Husnayaen, Manurung T, Descals A, Angelsen A, Meijaard
681 E, Sheil D. 2022. Slowing deforestation in Indonesia follows declining oil palm expansion
682 and lower oil prices. *PLoS ONE* **17**. Public Library of Science.

683 Gaveau DLA, Sheil D, Husnayaen, Salim MA, Arjasakusuma S, Ancrenaz M, Pacheco P, Meijaard
684 E. 2016. Rapid conversions and avoided deforestation: Examining four decades of
685 industrial plantation expansion in Borneo. *Scientific Reports* **6**. Nature Publishing Group.

686 Gaveau DLA, Sloan S, Molidena M, Wijaya A, Ancrenaz M, Nasi R, Wielaard N, Meijaard E,
687 others. 2014. Four decades of forest loss and degradation in Borneo. *PLoS One*
688 **9**:e101654.

689 Haidir I, Macdonald DW, Linkie M. 2021. Sunda clouded leopard *Neofelis diardi* densities and
690 human activities in the humid evergreen rainforests of Sumatra. *Oryx* **55**:189–196.

691 Hearn A, Ross J, Brodie J, Cheyne S, Haidir IA, Loken B, Mathai J, Wilting A, McCarthy J. 2015.
692 *Neofelis diardi*. The IUCN Red List of Threatened Species 2015.

693 Hearn AJ, Cushman SA, Goossens B, Macdonald E, Ross J, Hunter LTB, Abram NK, Macdonald
694 DW. 2018. Evaluating scenarios of landscape change for Sunda clouded leopard
695 connectivity in a human dominated landscape. *Biological Conservation* **222**:232–240.
696 Elsevier Ltd.

697 Hearn AJ, Ross J, Bernard H, Baker SA, Gossens B, Hunter LTB, Macdonald DW. 2017.
698 Responses of Sunda clouded leopard *Neofelis diardi* population density to anthropogenic
699 disturbance: refining estimates of its conservation status in Sabah. *Oryx*:1–11.

700 Jarvis A, Reuter HI, Nelson A, Guevara E. 2008. Hole-filled SRTM for the globe Version 4.
701 available from the CGIAR-CSI SRTM 90m Database (<http://srtm.csi.cgiar.org>).

702 Kaszta, Cushman SA, Hearn AJ, Burnham D, Macdonald EA, Goossens B, Nathan SKSS,
703 Macdonald DW. 2019a. Integrating Sunda clouded leopard (*Neofelis diardi*) conservation
704 into development and restoration planning in Sabah (Borneo). *Biological Conservation*
705 **235**.

706 Kaszta, Cushman SA, Macdonald DW. 2020a. Prioritizing habitat core areas and corridors for a
707 large carnivore across its range. *Animal Conservation* **23**:607–616. Blackwell Publishing
708 Ltd.

709 Kaszta Ż, Cushman SA, Hearn AJ, Burnham D, Macdonald EA, Goossens B, Nathan SKSS,
710 Macdonald DW. 2019b. Integrating Sunda clouded leopard (*Neofelis diardi*) conservation
711 into development and restoration planning in Sabah (Borneo). *Biological Conservation*
712 **235**:63–76. Available from
713 <https://linkinghub.elsevier.com/retrieve/pii/S0006320718309480>.

714 Kaszta Ż, Cushman SA, Htun S, Naing H, Burnham D, Macdonald DW. 2020b. Simulating the
715 impact of Belt and Road initiative and other major developments in Myanmar on an
716 ambassador felid , the clouded leopard , *Neofelis nebulosa*. *Landscape Ecology*
717 **0123456789**.

718 Kaszta Ż, Cushman SA, Macdonald DW. 2020c. Prioritizing habitat core areas and corridors for
719 a large carnivore across its range. *Animal Conservation*:(In press).

720 Keeley ATH, Beier P, Gagnon JW. 2016. Estimating landscape resistance from habitat
721 suitability: effects of data source and nonlinearities. *Landscape Ecology* **31**:2151–2162.
722 Springer Netherlands.

723 Kirk H, Garrard GE, Croeser T, Backstrom A, Berthon K, Furlong C, Hurley J, Thomas F, Webb A,
724 Bekessy SA. 2021. Building biodiversity into the urban fabric: A case study in applying
725 Biodiversity Sensitive Urban Design (BSUD). *Urban Forestry and Urban Greening* **62**.
726 Elsevier GmbH.

727 Landguth EL, Hand BK, Glassy J, Cushman SA, Sawaya MA. 2012. UNICOR: A species
728 connectivity and corridor network simulator. *Ecography* **35**:9–14.

729 Langner A, Siegert F. 2009. Spatiotemporal fire occurrence in Borneo over a period of 10 years.
730 *Global Change Biology* **15**:48–62.

731 Laurance WF, Goosem M, Laurance SGW. 2009, December. Impacts of roads and linear
732 clearings on tropical forests.

733 Macdonald DW et al. 2018a. Multi-scale habitat selection modeling identifies threats and
734 conservation opportunities for the Sunda clouded leopard (*Neofelis diardi*). *Biological*
735 *Conservation* **227**:92–103. Available from
736 <https://linkinghub.elsevier.com/retrieve/pii/S0006320718303549>.

737 Macdonald EA, Burnham D, Hinks AE, Dickman AJ, Malhi Y, Macdonald DW. 2015.
738 Conservation inequality and the charismatic cat: *Felis felis*. *Global Ecology and*
739 *Conservation* **3**:851–866. Elsevier. Available from
740 <https://www.sciencedirect.com/science/article/pii/S2351989415000426> (accessed
741 January 28, 2019).

742 Macdonald EA, Cushman SA, Landguth EL, Hearn AJ, Malhi Y, Macdonald DW. 2018b.
743 Simulating impacts of rapid forest loss on population size, connectivity and genetic
744 diversity of Sunda clouded leopards (*Neofelis diardi*) in Borneo. *PLOS ONE* **13**:1–22. Public
745 Library of Science. Available from <https://doi.org/10.1371/journal.pone.0196974>.

746 Macdonald EA, Hinks A, Weiss DJ, Dickman A, Burnham D, Sandom CJ, Malhi Y, Macdonald
747 DW. 2017. Identifying ambassador species for conservation marketing. *Global Ecology*

748 and Conservation **12**:204–214. Elsevier Ltd. Available from
749 <https://doi.org/10.1016/j.gecco.2017.11.006>.

750 Margono BA, Turubanova S, Zhuravleva I, Potapov P, Tyukavina A, Baccini A, Goetz S, Hansen
751 MC. 2012. Mapping and monitoring deforestation and forest degradation in Sumatra
752 (Indonesia) using Landsat time series data sets from 1990 to 2010. *Environmental*
753 *Research Letters* **7**. Institute of Physics Publishing.

754 Mateo-Sánchez MC, Balkenhol N, Cushman S, Pérez T, Domínguez A, Saura S. 2015a. A
755 comparative framework to infer landscape effects on population genetic structure: are
756 habitat suitability models effective in explaining gene flow? *Landscape Ecology* **30**:1405–
757 1420.

758 Mateo-Sánchez MC, Balkenhol N, Cushman SA, Perez T, Domínguez A, Saura S. 2015b.
759 Estimating effective landscape distances and movement corridors : comparison of habitat
760 and genetic data. *Ecosphere* **6**:1–16.

761 Miettinen J, Shi C, Liew SC. 2011. Deforestation rates in insular Southeast Asia between 2000
762 and 2010. *Global Change Biology* **17**:2261–2270.

763 Ng LS, Campos-Arceiz A, Sloan S, Hughes AC, Tiang DCF, Li B V., Lechner AM. 2020. The scale of
764 biodiversity impacts of the Belt and Road Initiative in Southeast Asia. *Biological*
765 *Conservation* **248**. Elsevier Ltd.

766 Nikonovas T, Spessa A, Doerr SH, Clay GD, Mezbahuddin S. 2020. Near-complete loss of fire-
767 resistant primary tropical forest cover in Sumatra and Kalimantan. *Communications Earth*
768 *and Environment* **1**. Nature Publishing Group.

769 Penjor U, Kaszta Ż, Macdonald DW, Cushman SA. 2021. Prioritizing areas for conservation
770 outside the existing protected area network in Bhutan: the use of multi-species, multi-
771 scale habitat suitability models. *Landscape Ecology* **36**:1281–1309. Springer Netherlands.

772 Pfeifer M et al. 2017. Creation of forest edges has a global impact on forest vertebrates.
773 *Nature* **551**:187–191. Nature Publishing Group.

774 Poor EE, Jati VIM, Imron MA, Kelly MJ. 2019. The road to deforestation: Edge effects in an
775 endemic ecosystem in Sumatra, Indonesia. *PLoS ONE* **14**. Public Library of Science.

776 Runting RK et al. 2015. Alternative futures for Borneo show the value of integrating economic
777 and conservation targets across borders. *Nature Communications* **6**. Nature Publishing
778 Group.

779 Silva I, Crane M, Savini T. 2020. High roadkill rates in the Dong Phrayayen-Khao Yai World
780 Heritage Site: conservation implications of a rising threat to wildlife. *Animal Conservation*
781 **23**:466–478. Blackwell Publishing Ltd.

782 Sloan S, Alamgir M, Campbell MJ, Setyawati T, Laurance WF. 2019a. Development Corridors
783 and Remnant-Forest Conservation in Sumatra, Indonesia. *Tropical Conservation Science*
784 **12**. SAGE Publications Inc.

785 Sloan S, Alamgir M, Campbell MJ, Setyawati T, Laurance WF. 2019b. Development Corridors
786 and Remnant-Forest Conservation in Sumatra, Indonesia. *Tropical Conservation Science*
787 **12**. SAGE Publications Inc.

788 Sloan S, Campbell MJ, Alamgir M, Collier-Baker E, Nowak MG, Usher G, Laurance WF. 2018a.
789 Infrastructure development and contested forest governance threaten the Leuser
790 Ecosystem, Indonesia. *Land Use Policy* **77**:298–309. Elsevier. Available from
791 <https://doi.org/10.1016/j.landusepol.2018.05.043>.

792 Sloan S, Campbell MJ, Alamgir M, Lechner AM, Engert J, Laurance WF. 2019c. Trans-national
793 conservation and infrastructure development in the Heart of Borneo. *PLoS ONE* **14**. Public
794 Library of Science.

795 Sloan S, Jenkins CN, Joppa LN, Gaveau DLA, Laurance WF. 2014. Remaining natural vegetation
796 in the global biodiversity hotspots. *Biological Conservation* **177**:12–24. Elsevier Ltd.

797 Sloan S, Locatelli B, Wooster MJ, Gaveau DLA. 2017. Fire activity in Borneo driven by industrial
798 land conversion and drought during El Niño periods, 1982–2010. *Global Environmental*
799 *Change* **47**:95–109. Elsevier Ltd.

800 Sloan S, Supriatna J, Campbell MJ, Alamgir M, Laurance WF. 2018b, June 4. Newly discovered
801 orangutan species requires urgent habitat protection. Cell Press.

802 Spencer KL et al. 2023. Implications of large-scale infrastructure development for biodiversity
803 in Indonesian Borneo. *Science of the Total Environment* **866**. Elsevier B.V.

804 Teo HC, Lechner AM, Sagala S, Campos-Arceiz A. 2020. Environmental impacts of planned
805 capitals and lessons for Indonesia's new capital. *Land* **9**:1–17. MDPI AG.

806 Wijedasa LS, Sloan S, Page SE, Clements GR, Lupascu M, Evans TA. 2018. Carbon emissions
807 from South-East Asian peatlands will increase despite emission-reduction schemes.
808 *Global Change Biology* **24**:4598–4613. Blackwell Publishing Ltd.

809 Zeller KA, Jennings MK, Vickers TW, Ernest HB, Cushman SA, Boyce WM. 2018. Are all data
810 types and connectivity models created equal? Validating common connectivity
811 approaches with dispersal data. *Diversity and Distributions* **24**:868–879.

812 Zimmermann Teixeira F, Cambará Printes R, Cláudio Godoy Fagundes J, Chein Alonso A, Kindel
813 A. 2013. Canopy bridges as road overpasses for wildlife in urban fragmented landscapes.
814 *Biota Neotrop* **13**:117–123. Available from
815 <http://www.biotaneotropica.org.br/v13n1/en/abstract?article+bn02713012013><http://www.biotaneotropica.org.br>
816 <http://www.ecologia.ufrgs.br/ppgeco/><http://www.ufrgs.br/m>
817 [acacosurbanoshttp://www.biotaneotropica.org.br/v13n1/en/abstract?article+bn027130](http://www.biotaneotropica.org.br/v13n1/en/abstract?article+bn02713012013)
818 [12013](http://www.biotaneotropica.org.br/v13n1/en/abstract?article+bn02713012013).

819

820

821