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1 Evaluating scenarios of landscape change for Sunda clouded leopard connectivity in a human
2 dominated landscape

3

4 Short title: Assessing landscape change scenarios for Sunda clouded leopards

5 Keywords: Borneo; connectivity; scenarios; path selection function; resistant kernel; factorial
6 least cost path

7

8 **Abstract**

9

10 The forests of Borneo support some of the highest biodiversity in the world, yet have
11 experienced among the world's highest rates of deforestation. Such rapid forest loss and
12 associated fragmentation reduces the availability of suitable habitat for wildlife and creates
13 dispersion barriers. Understanding the prevalence and impacts of this anthropogenic
14 disturbance, and developing ways in which to mitigate such changes, is thus critical to the
15 conservation of Borneo's wildlife. Here, we applied a path selection function with conditional
16 logistic regression and used it to develop a resistance surface for a population of Sunda clouded
17 leopards (*Neofelis diardi*) residing within a fragmented and human dominated landscape in
18 Malaysian Borneo. We used cumulative resistant kernel and factorial least-cost path analysis
19 to predict how connectivity may change in response to four future scenarios involving
20 conversion of remaining unproductive forest to palm oil plantations, conversion of
21 unproductive palm oil back to forest, and restoration of a riparian buffer zone along the river,
22 and combination of the two forest restoration scenarios. We showed that Sunda clouded
23 leopard movement is facilitated by forest canopy cover and resisted by non-forest vegetation,
24 particularly recently cleared/planted and underproductive (flooded) plantation areas with low
25 canopy closure. By combining resistant kernel and factorial least-cost path modelling we

26 mapped core areas and the main linkages among them, and identified several key pinch points
27 that may limit regional connectivity of the population. We predict that Sunda clouded leopard
28 connectivity in the region can be greatly enhanced through the protection of privately owned
29 forest patches and the reforestation of underproductive oil palm plantation areas, and creation
30 of a forested buffer zone along the river. Conversely, we show that if the region's unprotected
31 forests were to be converted to plantations then connectivity across the Kinabatangan
32 floodplain would be significantly reduced.

33

34 **1. Introduction**

35

36 The island of Borneo is an evolutionary hotspot and centre of biodiversity and endemism
37 (Woodruff, 2010). Akin with much of Southeast Asia, however, Borneo's rich biological diversity
38 is increasingly threatened by a suite of anthropogenic disturbance, including selective logging
39 and deforestation (e.g., Meijaard et al., 2005; Wilcove et al., 2013), coupled with increased
40 pressures from hunting and poaching (e.g., Brodie et al., 2015a). In recent years, Borneo has
41 experienced some of the world's highest rates of deforestation, principally as a result of the
42 conversion to oil palm (*Elaeis guineensis*) plantations (Cushman et al., 2017). In 1973, an
43 estimated 76% (558,060 km²) of Borneo's land area (737,188 km²) remained under old-growth
44 forest cover (Gaveau et al., 2014). By 2010, Borneo's 1973 forest cover had declined by an
45 estimated 139,333 km² (25%), and by 2015 a further 47,174 km² (8.5%) was lost (Gaveau et
46 al., 2016). Such rapid habitat loss and associated fragmentation reduces the availability of
47 suitable habitat for wildlife and presents barriers to dispersion (Fahrig, 1997). Understanding
48 the prevalence and impacts of this rapid transition from a largely pristine landscape to a human
49 dominated one, is thus critical to the conservation of Borneo's wildlife.

50

51 The Sunda clouded leopard (*Neofelis diardi*) is an understudied, medium-sized Pantherine felid,
52 which inhabits the Sundaic islands of Borneo and Sumatra. This felid is currently listed as
53 Vulnerable on the IUCN Red List of Threatened Species as a result of a presumed small and
54 declining population size (Hearn et al. 2015). On Borneo, this felid appears to be relatively
55 resilient to forest disturbance (e.g., Wilting et al. 2012; Hearn et al. 2017), but intolerant of
56 deforestation. Thus, the island-wide expansion of oil palm plantations is likely resulting in a
57 decreasing extent and increasing fragmentation of Sunda clouded leopard habitat. To ensure
58 the conservation of this felid, it is essential to gain an understanding of the factors that
59 influence their movements and population connectivity (e.g., Taylor et al. 1993; Baguette et al.
60 2007), and to protect and/or restore potential movement corridors to maximise meta-
61 population connectivity (e.g., Chetkiewicz et al. 2006). Given the rapid land use change on
62 Borneo, it is particularly important to evaluate the impacts of realistic scenarios of landscape
63 change on this species.

64

65 Landscape resistance is the functional expression of those factors that mediate an organism's
66 movement within its environment (Spear et al., 2010). Landscape resistance is usually defined
67 as a function of environmental and anthropogenic variables across a resistance continuum, in
68 which landscape resistance represents the willingness of an organism to cross a particular
69 environment, or the physiological cost or reduction in survival for the organism moving
70 through a particular environment (Spear et al., 2010; Zeller et al., 2012). Reliable estimates of
71 landscape resistance are fundamental when attempting to understand underlying population-
72 level patterns of connectivity and their biological implications (e.g. Spear et al., 2010; Cushman
73 et al., 2006; Elliot et al., 2014).

74

75 Here, we applied a multi-scale path selection function (e.g., Cushman et al. 2010; Cushman
76 and Lewis 2010) to parameterize a resistance surface and develop connectivity predictions for
77 a population of Sunda clouded leopards residing within a fragmented and human dominated
78 landscape in Sabah, Malaysian Borneo, the Lower Kinabatangan floodplain. We test the
79 hypothesis that forest, including highly disturbed forest types, would facilitate movement of
80 Sunda clouded leopards, while open canopy conditions, in particular recently established oil
81 palm plantations, would express high resistance to movement. We applied cumulative
82 resistant kernel and factorial least cost path modelling to predict how connectivity may change
83 in response to four potential future scenarios of land use change in the region. The scenarios
84 reflected ongoing landscape changes or future changes with a realistic chance of occurring,
85 and included (i) the establishment of a contiguous forested riparian buffer along the
86 Kinabatangan river, (ii) the conversion of non-productive oil palm to forest; both (i) and (ii) in
87 unison, and (iv) the conversion of all privately owned unprotected forest to oil palm.

88

89 **2. Material and methods**

90

91 *2.1 Study Area*

92

93 The study area consists of approximately 4,000 km² of the Lower Kinabatangan floodplain in
94 eastern Sabah, Malaysian Borneo (Figure 1). Much of the region's forests have been cleared
95 for oil palm and the remaining forests have been repeatedly logged over the past century,
96 resulting in a fragmented chain of forest patches along both banks of the Kinabatangan River
97 (Ancrenaz et al. 2004; Abram et al. 2014). These forests are characterised primarily by seasonal
98 freshwater swamp forest, freshwater swamp forest and severely degraded remnants of mixed

99 dipterocarp forest. Approximately 27,900 ha of the region's forests were gazetted as the Lower
100 Kinabatangan Wildlife Sanctuary (LKWS), which is composed of 10 'Lots' that provide a more
101 or less contiguous linkage to around 15,000 ha of protected commercial Forest Reserves. In
102 2010/11 the study area included around 30,000 ha of unprotected, privately owned forest,
103 much of which is currently allocated for future oil palm conversion (Abram et al. 2014). To the
104 west and south of the LKWS lie the Segaliud-Lokan, Malua, and Ulu Segama Forest Reserves,
105 which are all part of the largest contiguous area of forest in Sabah, and to the east lies an
106 extensive chain of protected coastal mangrove Forest Reserves. A sealed road (A6) runs
107 north/south through the study area, bisecting the two blocks of the Pin Supu Forest Reserve,
108 and another runs east/west to the north of the forested areas.

109

110 *2.2 Sunda clouded leopard telemetry data*

111

112 From 13 May 2013 to 28 September 2014, following a protocol developed by the Sabah
113 Wildlife Department and approved by the Sabah Biodiversity Centre (Nájera et al., 2017), we
114 deployed locally constructed, double ended, steel mesh box traps (1 x 1 x 3 m) in Lots 5 and 6
115 of the LKWS (Figure 1) to capture Sunda clouded leopards. We fitted captured animals with
116 GPS/GSM collars (Lotek WildCell SD, Lotek Wireless Inc., Ontario, Canada), which included an
117 automated drop-off device, scheduled to take a location fix every 20 minutes. We captured
118 five Sunda clouded leopards (three males, two females). One male (CLM4) was captured and
119 collared on three occasions, and one female (CLF3) was captured twice, but was deemed too
120 old (7-8 years) and underweight, and was released without collaring. Two additional males and
121 one female were captured and collared on one occasion. Physical examination, and earlier and
122 concurrent camera trapping efforts, suggest the collared animals were all adult, and likely

123 resident. Two of CLM4's collars failed without providing data. Three of the other four collars
124 failed prematurely, resulting in four usable data sets of varying durations (Table 1). To ensure
125 precision, we only retained location fixes with a Dilution of Precision <8 (e.g., Frair et al. 2010).
126 Final fix success rate was relatively high, and varied from 85 to 94% (Table 1). We subdivided
127 path data for each animal into lengths of 24 hour periods for further analysis (e.g., Zeller et al.
128 2015).

129

130 *2.3 Multiple Scale Path-level Modelling*

131

132 We applied a multiscale path selection function to model Sunda clouded leopard movement
133 as a function of landscape predictor variables. This approach employs conditional logistic
134 regression to compare landscape characteristics around paths used by an animal with those
135 from randomly generated available paths of identical length and topology, which are randomly
136 shifted and rotated around the observed paths (e.g., Cushman and Lewis 2010; Elliot et al.
137 2014). We selected potential predictor variables for the path selection function based on
138 existing knowledge of Sunda clouded leopard habitat associations (Hearn et al. 2015, 2016),
139 including land cover, canopy cover, carbon density, and road and river distribution (for full
140 details see Supplementary file S1). [All GIS layers were resampled to 15m pixel size for analysis.](#)

141 To explicitly account for spatial scale in our analysis (e.g. Zeller et al. 2017), for each used path,
142 we created 19 matched available paths, by shifting the x and y coordinates of the available
143 path by a random value (up to the maximum distance specified at each scale of shift), and
144 rotating its orientation by a random value between 0 and 360°. We used three spatial scales of
145 shift: (1) no shift, and distances between (2) 0-5 km, and (3) 0-10 km. Optimizing the scale of
146 the available neighbourhood in this way has been shown to be necessary to obtain correct

147 estimates of landscape resistance from path selection functions (Zeller et al. 2014; McGarigal
148 et al. 2016).

149

150 We used ArcInfo Workstation (ESRI 2010) to derive the environmental predictor variables by
151 calculating the mean value for each GIS variable of all pixels that were aligned along the used
152 and available path trajectories (e.g., Cushman and Lewis 2010). We used the clogit function in
153 the Survival package of R (v3.1.2; R Development Team, 2014) to perform the conditional
154 logistic regression analyses, matching each used path with the 19 rotated and shifted available
155 paths at each scale. We performed the conditional logistic regression in three stages. First, we
156 determined the spatial scale at which each variable had the strongest relationship with Sunda
157 clouded leopard path selection by conducting a univariate scaling analysis (e.g. Zeller et al.
158 2017). We used Akaike Information Criterion corrected for small sample size (AICc) model
159 selection to identify the most supported scale for each variable, and retained the scale with
160 the lowest AICc ranking for the next step, so long as it had a Wald score p -value of <0.05 .
161 Second, we evaluated the correlation among the variables and dropped the variable with the
162 greater AICc value in each pair of variables that were correlated greater than Pearson $|r| =$
163 0.70. Third, we conducted an all-subsets analysis and model averaging of the 11 variables with
164 the strongest univariate relationship to Sunda clouded leopard path selection, based on Wald
165 Score (Table S1, Supplementary file), using the Dredge function in the R package MuMin,
166 version 1.15.6 (Barton, 2016). We judged the relative importance of each variable to the final
167 model based on the sum of Akaike weights of models where the variable was included (w_i).

168

169 *2.4 Resistance surface and connectivity modelling*

170

171 We produced a resistance surface for Sunda clouded leopard movement using ArcInfo
172 workstation (v10.2, ESRI 2010). This was done in two steps. First, we calculated the Z variable
173 for the path selection function: $z = \beta_1v_1 + \beta_2v_2 + \dots + \beta_nv_n$, where, β_i is the regression
174 coefficient for variable v_i . Second, we converted this to resistance by inverting and adding a
175 constant such that minimum resistance was given value 1. This produces a resistance surface
176 where resistance is inversely proportional to the path selection function, indicating high
177 resistance where there is low probability of path selection and low resistance where there is
178 high path selection probability.

179

180 We used cumulative resistant kernel (Compton et al. 2007; Cushman et al. 2010) and factorial
181 least-cost path approaches (e.g., Cushman et al. 2010) to predict Sunda clouded leopard
182 landscape connectivity using UNICOR v2.0 (Landguth et al. 2012). We chose to use both of
183 these methods because of their complementarity. Specifically, the resistant kernel model
184 produces a spatial incidence function of the expected frequency of an organism moving
185 through each cell of the landscape as a function of the distribution and density of source points
186 and the resistance of the landscape. This produces a synoptic picture of the total movement
187 density across the landscape and is useful to identify core areas and the main pattern of
188 synoptic connectivity. Conversely, the factorial least-cost path approach computes the
189 summed density of least cost paths between all source points. This highlights the main routes
190 of lowest cost linking the specific source points, which identifies and emphasizes areas where
191 the movement pattern is constrained, such as in narrow pinch points. The two together,
192 therefore, enable mapping the density of predicted movement synoptically (kernels) and also
193 to highlight the main linkages among the core areas (least-cost paths).

194

195 Both the resistant kernel and factorial least-cost path approaches include dispersal thresholds,
196 which limit the prediction of connectivity to a specified cost distance from the source points.
197 In this analysis, we chose thresholds of 25,000 cost units for the resistant kernel and 50,000
198 cost units for the factorial least cost path. We chose 25,000 cost units since it reflects the
199 potential radius of a Sunda clouded leopard home range (22.6 km², 95% Minimum Convex
200 Polygon (n=1); Hearn et al., 2013). Given that the analysis is conducted on adult animals that
201 are likely not in a dispersal stage, this threshold reflects connectivity of these individuals in
202 their life-stage. We chose a threshold for the factorial least-cost path that was twice this
203 because we wanted the analysis to reflect patterns of connectivity among adjacent home
204 ranges. This is typically achieved by having a larger threshold for paths (e.g., Cushman 2013).

205

206 *2.5 Future Scenarios*

207

208 We evaluated the impacts of four scenarios of possible future landscape change on the extent
209 and fragmentation of the landscape connected by animal movement. We selected future
210 scenarios which reflect changes that are either ongoing or stand a realistic chance of occurring,
211 and which present both potentially positive and negative implications for the Sunda clouded
212 leopard. The four scenarios were: S1 – deforested areas within 50 m of the Kinabatangan River
213 reverted back to forest cover; S2 – non-productive oil palm (identified in Abram et al. (2014))
214 converted to forest; S3 – both 50 m river buffer and non-productive oil palm converted to
215 forest; S4 – all privately owned unprotected forest converted to oil palm. For each scenario,
216 we created the resistant kernel and factorial least cost path maps using the same methods as
217 for the analyses described above, and we compared these maps with each other and with the
218 present condition in two ways. First, we calculated the average and standard deviation of pixel-

219 pixel differences in cumulative resistant kernel value among scenarios to gain an overall
220 quantitative measure of difference in connectivity across the study area. Second, for each
221 scenario, we used FRAGSTATS (v4; McGarigal et al. 2012) to calculate changes in the
222 percentage of the landscape and correlation length connected by movement (non-zero
223 cumulative kernel values) and correlation length (non-zero factorial least cost values) of the
224 factorial least cost path network, and compared these values with the present situation.

225

226 **3. Results**

227

228 *3.1 Visible inspection of movement paths*

229

230 Sunda clouded leopard movement paths were almost exclusively restricted to forest cover,
231 including a narrow section (130 m wide) of forest corridor (Figure 1). However, one male
232 (CLM3) traversed oil palm plantation and crossed a busy sealed road. Another male (CLM4)
233 crossed the relatively quiet, sealed access road in Gomantong Forest Reserve. No animals were
234 recorded crossing the Kinabatangan river.

235

236 *3.2 Multiple Scale Path-level Modelling*

237

238 The univariate scaling indicated that most variables had the strongest relationship with Sunda
239 clouded leopard path selection when shifted between 0-10 and 0-5 km; no variables had the
240 strongest relationship with no shift at all (Table S1, Supplementary file). Path selection was
241 positively related to Agroforest/forest regrowth, canopy cover and several closed forest
242 variables, and negatively related to the river and oil palm plantations (Table 1).

243

244 3.3 Resistance surface and connectivity modelling

245

246 Inspection of the resistance surface (Figure 2) revealed that areas with forest cover with high
247 canopy closure had the lowest resistance, while non-forest areas, such as severely degraded
248 areas and oil palm plantations, had high resistance. Areas of oil palm plantation that were
249 classified by Hansen et al (2013) as having low canopy cover, which were typically areas
250 classified as recently cleared/planted and underproductive (flooded) oil palm areas by Abram
251 et al. (2014), presented the highest levels of resistance.

252

253 The cumulative resistant kernel surface shows the expected density of clouded leopard
254 movement throughout the study extent (Figure 3a). The map shows two core areas of high
255 predicted internal connectivity, which correspond to the two large contiguous forest patches
256 along the Kinabatangan River. Three principal areas of attenuated connectivity are also shown:
257 (i) along the river in the west, between Lots 10 and 11, (ii) between the two core areas, where
258 Lot 5 is reduced to a narrow section of riverine forest, and (iii) where the forest is restricted to
259 a narrow band along the river in Lot 2. The model suggests that a low level of connectivity is
260 retained between the LKWS and the Segaliud-Lokan Forest Reserve and the extensive eastern
261 mangrove system, but no direct connectivity between the LKWS and Ulu Segama Forest
262 Reserve or Tabin Wildlife Reserve.

263

264 The factorial least cost path network map (Figure 3b) identifies the same two core areas of
265 high connectivity as the resistant kernel map. However, the least cost path model indicates
266 strong concentration of movement paths funnelled into the narrow bottleneck between these
267 two core patches, and also in the area of predicted low connectivity identified in the resistant

268 kernel in the far eastern part of the study area. The factorial least cost path analysis does,
269 however, match the resistant kernel analysis in identifying the reduced connectivity along the
270 river in the far western part of the study area, indicating that this area may be particularly
271 limiting.

272

273 *3.4 Future Scenarios*

274

275 Scenario 1 (Figures 4a, 5a; Table 3; Table S2, Supplementary file) was quite similar to the
276 pattern and strength of the connectivity predictions for the present landscape, indicating little
277 overall effect of adding a 50 m forest buffer to the rivers. In Scenario 2 (Figures 4b, 5b; Table
278 3; Table S2, Supplementary file) there was substantially higher connectivity than currently as a
279 result of conversion of non-productive palm oil plantation to forest. Scenario 3 (Figures 4c, 5c;
280 Table 3; Table S2, Supplementary file) was highly similar to Scenario 2, again indicating a
281 relatively small effect of the river buffer. While the establishment of a 50 m forested riverine
282 buffer in Scenario 1 had relatively little effect on the overall level of connectivity compared to
283 the impacts of a larger scale reforestation in Scenario 2, the percentage change to the
284 correlation length per unit area of reforestation was substantially greater in Scenario 1. The
285 resistant kernel Scenario 4 (Figures 4d, Table 3; Table S2, Supplementary file) showed large
286 reductions in connectivity as a result of conversion of private unprotected forest to oil palm,
287 with predicted breakage in connectivity in three places in the western part of the study
288 landscape. Similarly, the least cost Scenario 4 predicted breakage in connectivity at two places
289 in the western part of the study landscape (Figure 5d, Table 3; Table S2, Supplementary file).

290

291 **4. Discussion**

292
293 In this study, we present the first high-resolution data regarding the movements of an
294 understudied, threatened tropical forest felid, the Sunda clouded leopard, and develop the
295 first landscape resistance surface and connectivity models for this species based on empirical
296 movement data. Prior to this study, the only empirical movement data available for this species
297 were from a single collared female (Hearn et al., 2013), but these were too limited to yield
298 useful insights into connectivity. The only other published study of Sunda clouded leopard
299 connectivity stems from Brodie et al. (2015b), who used hierarchical modelling of camera-trap
300 data to develop a least-cost connectivity model to assess and identify dispersal and corridor
301 locations for Sunda clouded leopards within a transboundary network of protected areas in
302 Borneo.

303
304 Consistent with our hypothesis, we showed that Sunda clouded leopard movement is
305 facilitated by forest cover, including disturbed forest, so long as it had high canopy closure, but
306 resisted by non-forest vegetation. Recently cleared/planted and underproductive (flooded) oil
307 palm plantation areas with low canopy closure presented the highest resistance. The Sunda
308 clouded leopard has long been considered somewhat resilient to forest disturbance (e.g.,
309 Rabinowitz et al., 1987; Santiapillai and Ashby, 1988), and previous studies of this felid's
310 distribution (Hearn et al., 2016), density (e.g., Wilting et al., 2012) and population size (Hearn
311 et al., 2017) have suggested that they may avoid oil palm plantations. Prior to the current study,
312 however, no research had adequately investigated this presumed habitat association, although
313 two small-scale camera trapping studies in plantation habitats failed to detect this felid (Ross
314 et al., 2010; Yue et al., 2015). Our study thus provides strong support for the prediction that
315 Sunda clouded leopards are likely negatively impacted by deforestation and that the

316 conversion of forests to oil palm plantations present one of the greatest threats to Sunda
317 clouded leopards (e.g., Hearn et al., 2015).

318

319 Our connectivity modelling and land use change scenarios provide a useful basis on which to
320 develop future conservation management strategies for the Sunda clouded leopard in the
321 Lower Kinabatangan. Our connectivity models suggest that, in the present landscape, all the
322 protected forest blocks in the Lower Kinabatangan region remain functionally connected with
323 each other, with the eastern coastal mangroves and, crucially, with the largest contiguous
324 forest block in Sabah, via the Segaliud-Lokan Forest Reserve. The model also predicts three key
325 pinch points to movement: (i) along the river in the west, between Lots 10a and 10b,c, (ii)
326 between the two core areas, where Lot 5 is reduced to a narrow section of riverine forest, and
327 (iii) where the forest is restricted to a narrow band along the river in Lot 2. The model predicts
328 that these pinch points are expected to have attenuated frequency of clouded leopard
329 movement in them (resistant kernel analysis results), but also form the main potential linkages
330 between core areas (factorial least cost path results) to maintain broad-scale connectivity in
331 this landscape for Sunda clouded leopard. These pinch points are therefore a priority for
332 protection and or restoration.

333

334 Given the Kinabatangan's limited forest cover and the Sunda clouded leopard's low local
335 population density (1.5 individuals per 100 km²; Hearn et al., 2017) it is essential to maintain
336 and/or enhance this broad-scale connectivity through the retention and expansion of forest
337 cover. However, around 30,000 ha, or 40% of the Kinabatangan's forests lie outside of the
338 protected areas, and at least 64% of these unprotected forests have been allocated for future
339 oil palm cultivation (Abram et al., 2014). We predicted that conversion of these forests to oil

340 palm plantations would not only significantly reduce the amount of available Sunda clouded
341 leopard habitat, but would also result in a substantial reduction in connectivity in the western
342 part of the study landscape, in the same region where we have shown there to be a pinch point
343 to movement, and which, critically, provides linkage to the largest contiguous forest block in
344 Sabah. Abram et al (2014) estimated that a minimum of 54% of these unprotected forests
345 earmarked for conversion are unsuitable for oil palm cultivation due to the likelihood of
346 flooding. Thus, the conversion of existing underproductive plantations to forest would bring
347 large benefits to Sunda clouded leopards, whilst minimising impacts to the plantation industry.
348 We predicted that the reforestation of riparian forest close to the river resulted in the highest
349 gains to connectivity per unit area of forest converted, which suggests that narrow riparian
350 corridors may be an important and cost-effective conservation tool for this species.
351 Furthermore, riparian areas offer much to the prevention of bank erosion and existing
352 legislation is already in place to reinstate such buffers. In addition, the riparian restoration
353 scenario is predicted to have the biggest effects in the most important locations in this
354 landscape, e.g. the pinch points and potential breakages.

355

356 *Scope and limitations*

357

358 An animal's behavioural state (e.g., resident individuals within home ranges vs. exploring or
359 dispersing individuals outside their home ranges) can be a significant determinant of resource
360 selection patterns, and thus failure to recognize this distinction may lead to misidentification
361 of animal movement corridors and ineffective use of limited conservation resources (e.g.,
362 Abrahms et al. 2017). Habitat selection during the dispersal phase differed greatly to that
363 within the home-range in studies of elk (*Cervus elaphus*, Killeen et al. 2014), lions (*Panthera*

364 *leo*, Elliot et al. 2014), cougars (*Puma concolor*, Morrison et al. 2015), Iberian lynx (*Lynx*
365 *pardinus*, Blazquez-Cabrera et al. 2016), red wolves (*Canis rufus*, Hinton et al. 2016), and
366 African wild dogs (*Lycaon pictus*, Abrahms et al. 2017). This pattern may not be universal,
367 however. Fattebert et al. (2015) showed that juvenile African leopards (*Panthera pardus*) use
368 resident adult suitable habitats during dispersal, regardless of their behavioural state, and
369 Masenga et al. (2015) found that African wild dogs disperse through suitable habitat with
370 adequate prey.

371

372 Our models of Sunda clouded leopard movement were developed from adult animals, with
373 established home ranges, and so our results may be limited to predicting the connectivity of
374 adults in this landscape. Our study is therefore relevant for the survival and reproduction of
375 adults, but our understanding of juvenile dispersal in this landscape remains limited. In
376 addition, our model of Sunda clouded leopard landscape resistance and connectivity was
377 developed from the movement data of just four animals, with two animals providing over 97%
378 of information, and from a single population, in a specific region of Sabah. Consequently, the
379 model may not necessarily reflect the behavioural ecology of the species elsewhere. Future
380 efforts should thus strive to refine these models of landscape connectivity by obtaining data
381 from a diverse range of locations from across the island. Efforts should also be made to include
382 as many demographic classes as possible, and ideally from dispersing animals (presumably
383 young males).

384

385 6. Conclusions

386

387 Path selection functions enabled us to produce the first empirical movement based resistance
388 models for the Sunda clouded leopard. Sunda clouded leopard movement through the
389 Kinabatangan landscape is facilitated by forest canopy cover and resisted by non-forest
390 vegetation, particularly recently cleared/planted and underproductive (flooded) plantation
391 areas with low canopy closure. By combining resistant kernel and factorial least-cost path
392 modelling we mapped core areas and the main linkages among them, and identified several
393 key pinch points that may limit regional connectivity of the population. We predict that clouded
394 leopard connectivity in the region can be greatly enhanced through the protection of privately
395 owned forest patches and the reforestation of underproductive oil palm plantation areas, and
396 creation of a forested buffer zone along the river. Conversely, we show that if the region's
397 unprotected forests were to be converted to plantations then connectivity across the
398 Kinabatangan floodplain would be significantly reduced. Future work should focus on obtaining
399 larger sample sizes of multiple demographic categories of animals, including dispersers, to
400 strengthen our understanding of how landscape factors affect movement of clouded leopards
401 across their full life-cycle.

402

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404

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411

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413

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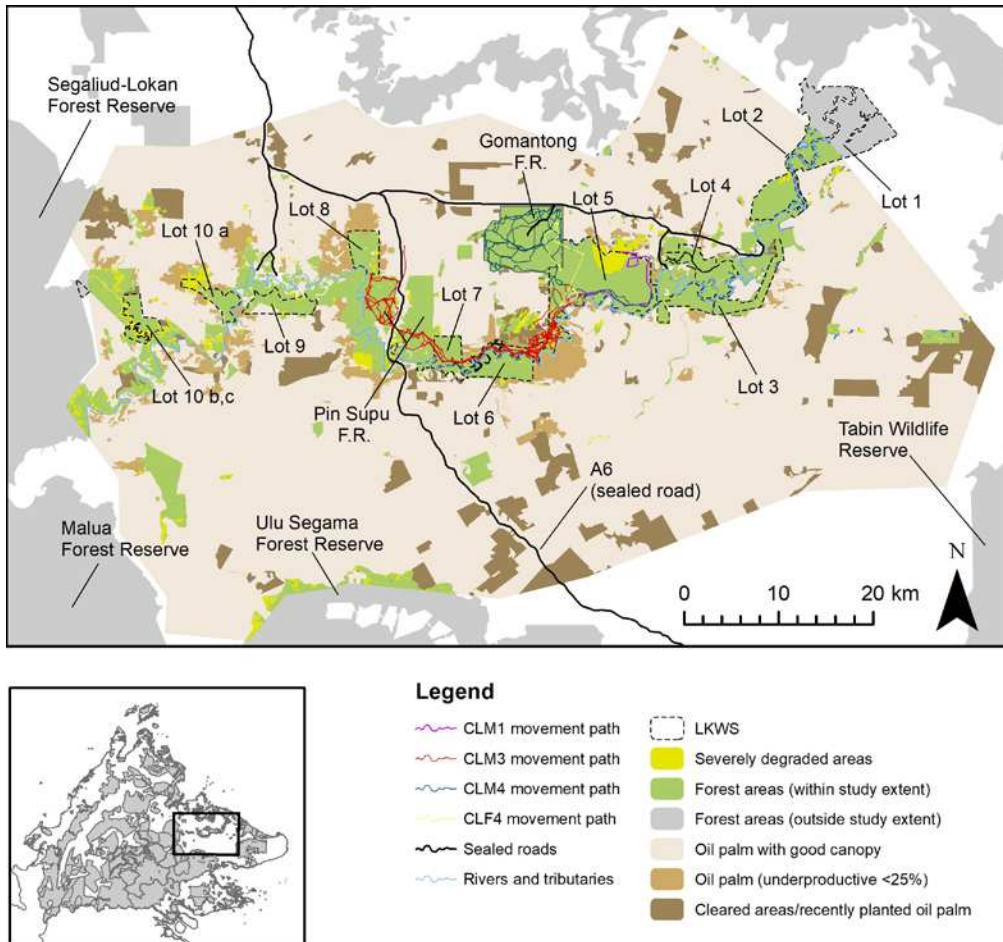
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635 **Figures**

636



637

638 **Figure 1.** Map of the Lower Kinabatangan floodplain, showing the study extent and land use. Inset map shows the
 639 Malaysian state of Sabah, and bounding box shows location of the Kinabatangan floodplain. Land cover data
 640 modified from Abram et al. (2014).

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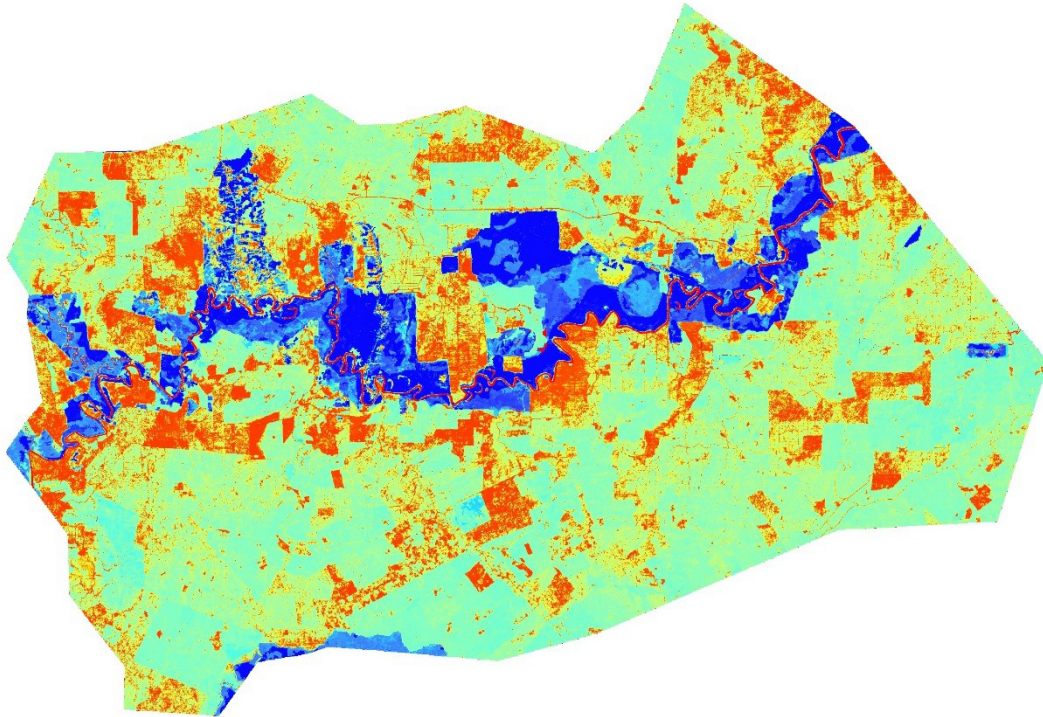
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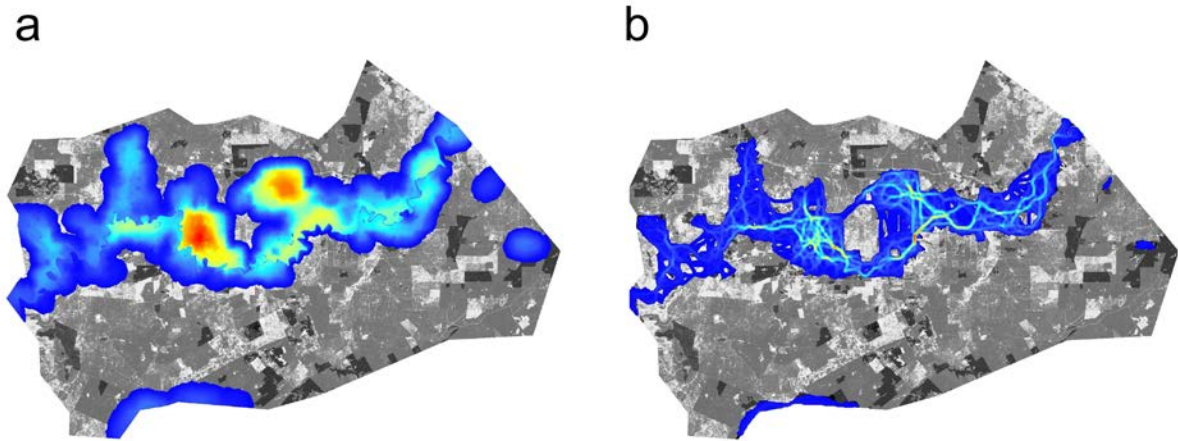
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648 **Figure 2.** Resistance surface derived from the path selection function, applied to the extent of the Kinabatangan
649 study area. Low resistance is shown in dark blue (forest with high canopy closure) and high resistance in bright
650 red (oil palm plantations with low canopy closure).

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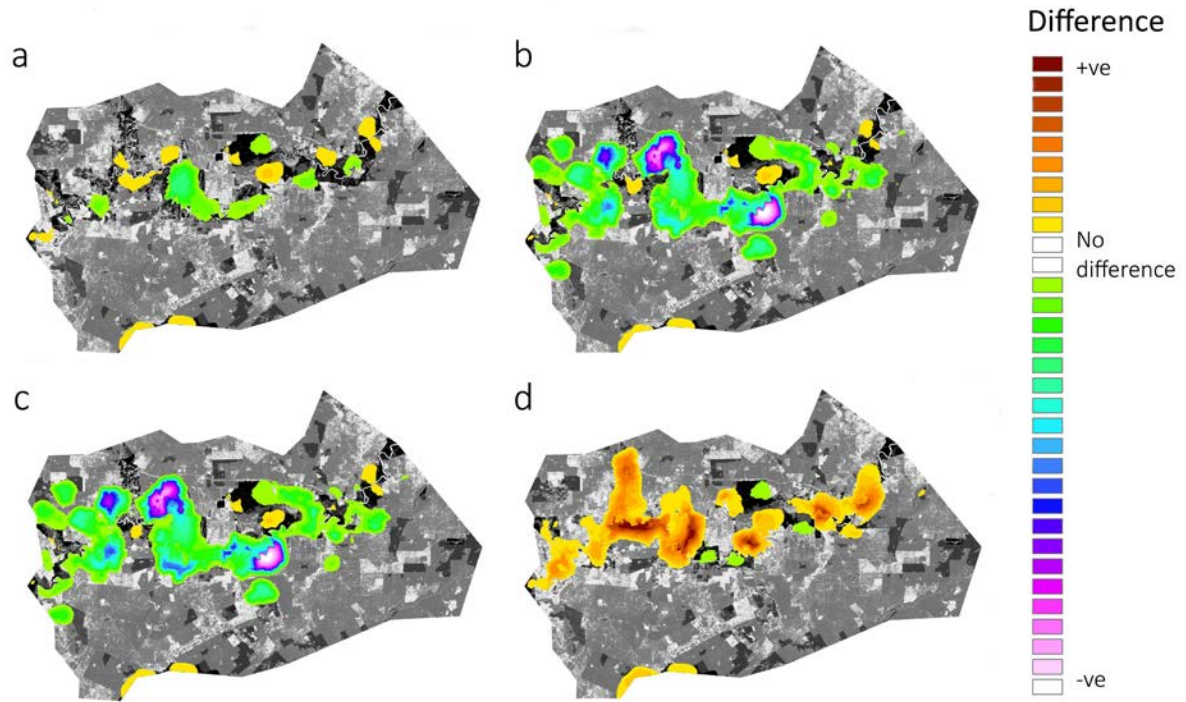
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Figure 3. Cumulative resistant kernel surface (a) and Factorial least cost path density (b) networks for the Kinabatangan study area. The maps show predictions of Sunda clouded leopard connectivity for the present condition of the landscape. The colour ramps are scaled linearly from min to max (dark blue to red) and range from 0 to 135 for the kernel surface and 0 to 1883 for the factorial least cost path surface.



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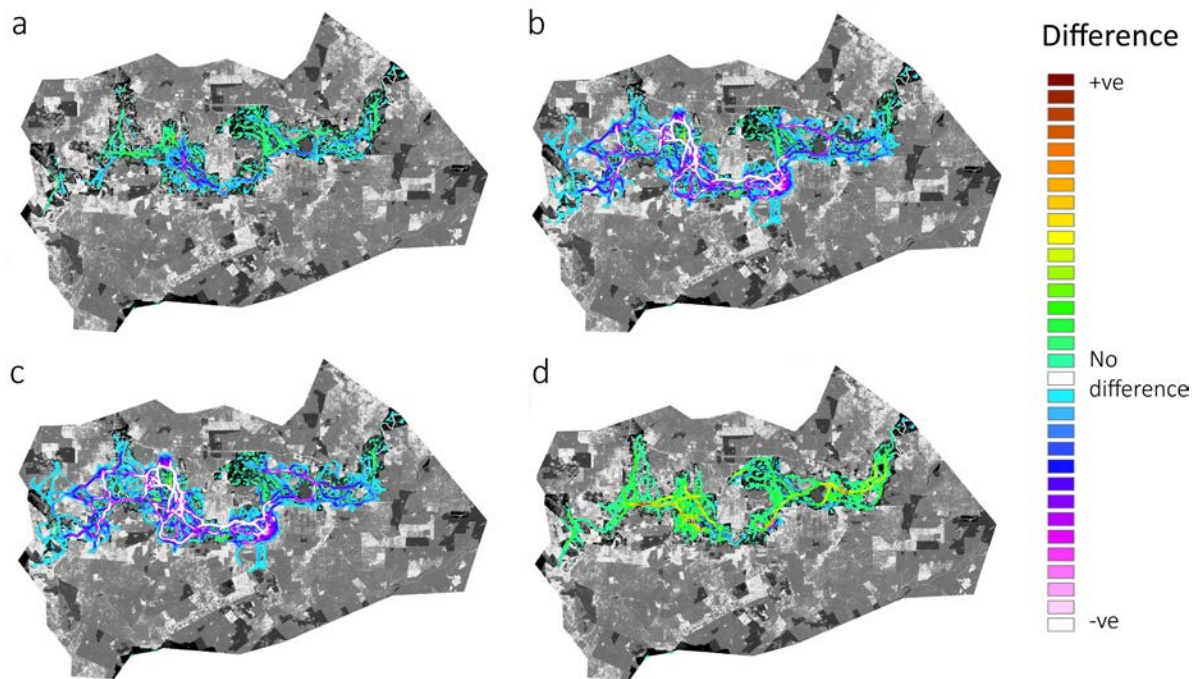
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Figure 4. Maps showing the differences between the cumulative kernel surface for the present condition of the landscape and four scenarios of future landscape change. The difference is present surface - scenario surface and positive values indicate areas where the present landscape has higher kernel connectivity than the scenario landscape. The scenarios are (a) S1: riparian restoration, (b) S2: restoring unproductive oil palm, (c) S3: both a and b, (d) S4: conversion of unprotected forest to oil palm.



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Figure 5. Maps showing the differences between the factorial least cost path surface for the present condition of the landscape and four scenarios of future landscape change. The difference is present surface - scenario surface and positive values indicate areas where the present landscape has higher least cost path density than the scenario landscape. The scenarios are (a) S1: riparian restoration, (b) S2: restoring unproductive oil palm, (c) S3: both a and b, (d) S4: conversion of unprotected forest to oil palm.

676 **Tables**

677

678 **Table 1.** Telemetry data from Sunda clouded leopards captured and tagged within the Lower Kinabatangan
 679 Wildlife Sanctuary, Sabah, Malaysian Borneo.

680

Animal ID	Sex	Estimated age	Duration of collar data		No. fixes DOP <8 (% success rate)	No. used paths
			Dates	No. days		
CLM3	Male	5–6	15/09/2013 – 27/12/2013	103	5618 (85)	96
CLM4	Male	2–3	01/02/2014 – 11/3/2014	38	2497 (92)	39
CLM1	Male	3–4	22/03/2014 – 27/03/2014	5	70 (92)	6
CLF4	Female	7–8	16/08/2014 – 06/10/2014	51	158 (94)	17

681

682 **Table 2.** Regression coefficients (β) and AICc importance for the 11 variables with the strongest univariate
 683 relationship to clouded leopard path selection for the path selection function. SE β : standard error of
 684 regression coefficient. Final model AICc: 700.56. ¹ The location of the river was obtained using a handheld
 685 GPS unit; ²Gaveau et al., 2014; ³Abram et al., 2016; ⁴Miettinen et al., 2012; ⁵Hansen et al., 2013.
 686

Variable		β	SE β	AICc <i>importance</i>	z-score	p-value
Source	Name					
NA ¹	River	-12.11	4.85	1.00	2.50	0.013
Gaveau ²	Agroforest/forest regrowth	3.60	0.86	1.00	4.21	0.000
SFD ³	Lowland Freshwater Swamp Forest	2.35	0.39	1.00	6.07	< 2e-16
SFD ³	Lowland Mixed Dipterocarp Forest	2.29	0.32	1.00	7.16	< 2e-16
Gaveau ²	Logged forests	2.19	0.88	1.00	2.49	0.013
Abram ³	Freshwater swamp forest	1.35	0.37	1.00	3.67	0.000
Miettinen ⁴	Lowland forest	0.38	0.45	0.63	0.85	0.394
Miettinen ⁴	Plantation/regrowth	0.30	0.40	0.46	0.75	0.453
Abram ³	Carbon	-0.14	0.18	0.55	0.79	0.430
Abram ³	Dry lowland forest	0.09	0.27	0.30	0.33	0.744
Hansen ⁵	Tree cover	0.06	0.02	1.00	3.76	0.000

687

688 **Table 3.** Percentage of the landscape predicted to be connected by movement (non-zero cumulative
 689 resistant kernel values) and correlation length (non-zero factorial least cost values) for each scenario, and
 690 % change from the present condition of the landscape.

691

Scenario	Cumulative resistant kernel				Factorial least cost path		
	Change in forest cover (km ²)	% landscape connected	% change from current	% change per km ² of reforestation	Correlation length	% change from current	% change per km ² of reforestation
Present condition	-	35.82	-	-	18452	-	-
S1: 50m riparian buffer	3.60	36.01	0.53	0.15	18890	2.42	0.67
S2: non-productive oil palm to forest	140.92	46.12	28.75	0.20	20304	10.04	0.07
S3: S1 & S2	144.50	46.1	28.67	0.20	20290	9.96	0.07
S4: Private forest to oil palm	-132.70	23.8	-33.59	-	11844	-35.81	-

692