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

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

Keywords: Borneo; connectivity; scenarios; path selection function; resistant kernel; factorialleast 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 disturbance, and developing ways in which to mitigate such changes, is thus critical to the 14 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

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

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#### 34 **1. Introduction**

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The island of Borneo is an evolutionary hotspot and centre of biodiversity and endemism 36 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 and deforestation (e.g., Meijaard et al., 2005; Wilcove et al., 2013), coupled with increased 39 40 pressures from hunting and poaching (e.g., Brodie et al., 2015a). In recent years, Borneo has experienced some of the world's highest rates of deforestation, principally as a result of the 41 42 conversion to oil palm (Elaeis guineensis) plantations (Cushman et al., 2017). In 1973, an estimated 76% (558,060 km<sup>2</sup>) of Borneo's land area (737,188 km<sup>2</sup>) remained under old-growth 43 44 forest cover (Gaveau et al., 2014). By 2010, Borneo's 1973 forest cover had declined by an 45 estimated 139,333 km<sup>2</sup> (25%), and by 2015 a further 47,174 km<sup>2</sup> (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 the prevalence and impacts of this rapid transition from a largely pristine landscape to a human 48 49 dominated one, is thus critical to the conservation of Borneo's wildlife.

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 Vulnerable on the IUCN Red List of Threatened Species as a result of a presumed small and 53 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).

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.

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#### 89 2. Material and methods

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91 2.1 Study Area
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The study area consists of approximately 4,000 km<sup>2</sup> of the Lower Kinabatangan floodplain in eastern Sabah, Malaysian Borneo (Figure 1). Much of the region's forests have been cleared for oil palm and the remaining forests have been repeatedly logged over the past century, resulting in a fragmented chain of forest patches along both banks of the Kinabatangan River (Ancrenaz et al. 2004; Abram et al. 2014). These forests are characterised primarily by seasonal freshwater swamp forest, freshwater swamp forest and severely degraded remnants of mixed

dipterocarp forest. Approximately 27,900 ha of the region's forests were gazetted as the Lower 99 100 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 2010/11 the study area included around 30,000 ha of unprotected, privately owned forest, 102 103 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, which are all part of the largest contiguous area of forest in Sabah, and to the east lies an 105 106 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, and another runs east/west to the north of the forested areas. 108

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#### 110 2.2 Sunda clouded leopard telemetry data

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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 deployed locally constructed, double ended, steel mesh box traps (1 x 1 x 3 m) in Lots 5 and 6 114 115 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 concurrent camera trapping efforts, suggest the collared animals were all adult, and likely 122

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

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#### 130 2.3 Multiple Scale Path-level Modelling

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132 We applied a multiscale path selection function to model Sunda clouded leopard movement as a function of landscape predictor variables. This approach employs conditional logistic 133 134 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; McGarigal148 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 (wi).

168

169 2.4 Resistance surface and connectivity modelling

We produced a resistance surface for Sunda clouded leopard movement using ArcInfo 171 172 workstation (v10.2, ESRI 2010). This was done in two steps. First, we calculated the Z variable 173 for the path selection function:  $z = \beta 1v1 + \beta 2v2 + ... + \beta nvn$ , where,  $\beta i$  is the regression 174 coefficient for variable vi. 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

We used cumulative resistant kernel (Compton et al. 2007; Cushman et al. 2010) and factorial 180 181 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).

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 cost units for the factorial least cost path. We chose 25,000 cost units since it reflects the 198 199 potential radius of a Sunda clouded leopard home range (22.6 km<sup>2</sup>, 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).

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#### 206 2.5 Future Scenarios

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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).

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

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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 mangrove system, but no direct connectivity between the LKWS and Ulu Segama Forest 261 262 Reserve or Tabin Wildlife Reserve.

263

The factorial least cost path network map (Figure 3b) identifies the same two core areas of high connectivity as the resistant kernel map. However, the least cost path model indicates strong concentration of movement paths funnelled into the narrow bottleneck between these two core patches, and also in the area of predicted low connectivity identified in the resistant kernel in the far eastern part of the study area. The factorial least cost path analysis does, however, match the resistant kernel analysis in identifying the reduced connectivity along the river in the far western part of the study area, indicating that this area may be particularly limiting.

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273 3.4 Future Scenarios

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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, with predicted breakage in connectivity in three places in the western part of the study 287 288 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** 

In this study, we present the first high-resolution data regarding the movements of an 293 294 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.

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

318

Our connectivity modelling and land use change scenarios provide a useful basis on which to 319 320 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 protection and or restoration. 332

333

Given the Kinabatangan's limited forest cover and the Sunda clouded leopard's low local population density (1.5 individuals per 100 km<sup>2</sup>; Hearn et al., 2017) it is essential to maintain and/or enhance this broad-scale connectivity through the retention and expansion of forest cover. However, around 30,000 ha, or 40% of the Kinabatangan's forests lie outside of the protected areas, and at least 64% of these unprotected forests have been allocated for future oil palm cultivation (Abram et al., 2014). We predicted that conversion of these forests to oil

palm plantations would not only significantly reduce the amount of available Sunda clouded 340 341 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. We predicted that the reforestation of riparian forest close to the river resulted in the highest 348 349 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

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An animal's behavioural state (e.g., resident individuals within home ranges vs. exploring or dispersing individuals outside their home ranges) can be a significant determinant of resource selection patterns, and thus failure to recognize this distinction may lead to misidentification of animal movement corridors and ineffective use of limited conservation resources (e.g., Abrahms et al. 2017). Habitat selection during the dispersal phase differed greatly to that within the home-range in studies of elk (*Cervus elaphus*, Killeen et al. 2014), lions (*Panthera*  *leo*, Elliot et al. 2014), cougars (*Puma concolor*, Morrison et al. 2015), Iberian lynx (*Lynx pardinus*, Blazquez-Cabrera et al. 2016), red wolves (*Canis rufus*, Hinton et al. 2016), and African wild dogs (*Lycaon pictus*, Abrahms et al. 2017). This pattern may not be universal, however. Fattebert et al. (2015) showed that juvenile African leopards (*Panthera pardus*) use resident adult suitable habitats during dispersal, regardless of their behavioural state, and Masenga et al. (2015) found that African wild dogs disperse through suitable habitat with 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 as many demographic classes as possible, and ideally from dispersing animals (presumably 382 383 young males).

384

385 6. Conclusions

Path selection functions enabled us to produce the first empirical movement based resistance 387 388 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 vegetation, particularly recently cleared/planted and underproductive (flooded) plantation 390 391 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 across their full life-cycle. 401

402

## 403 **5. Acknowledgements**

404

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419	
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## 635 Figures



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



**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).



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.



**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

678 <b>Ta</b>	able 1.	Telemetry	data f	from	Sunda	clouded	leopards	captured	and	tagged	within	the	Lower	Kinabatangai
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679 Wildlife Sanctuary, Sabah, Malaysian Borneo.

Animal ID	Sex	Estimated	Duration of collar da	No. fixes DOP <8	No. used		
Animal ID		age	Dates	No. days	(% success rate)	paths	
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	

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

	Variable	0	сг 0	AICc	7.00050	
Source	Name	— р	SE p	importance	z-score	p-value
$NA^1$	River	-12.11	4.85	1.00	2.50	0.013
Gaveau <sup>2</sup>	Agroforest/forest regrowth	3.60	0.86	1.00	4.21	0.000
SFD <sup>3</sup>	Lowland Freshwater Swamp Forest	2.35	0.39	1.00	6.07	< 2e-16
SFD <sup>3</sup>	Lowland Mixed Dipterocarp Forest	2.29	0.32	1.00	7.16	< 2e-16
Gaveau <sup>2</sup>	Logged forests	2.19	0.88	1.00	2.49	0.013
Abram <sup>3</sup>	Freshwater swamp forest	1.35	0.37	1.00	3.67	0.000
Miettinen <sup>4</sup>	Lowland forest	0.38	0.45	0.63	0.85	0.394
Miettinen4	Plantation/regrowth	0.30	0.40	0.46	0.75	0.453
Abram <sup>3</sup>	Carbon	-0.14	0.18	0.55	0.79	0.430
Abram <sup>3</sup>	Dry lowland forest	0.09	0.27	0.30	0.33	0.744
Hansen⁵	Tree cover	0.06	0.02	1.00	3.76	0.000

688 Table 3. Percentage of the landscape predicted to be connected by movement (non-zero cumulative

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.

		Cumul	ative resist	tant kernel	Factorial least cost path			
Scenario	Change in forest cover (km²)	% landscape connected	% change from current	% change per km <sup>2</sup> of reforestation	Correlation length	% change from current	% change per km <sup>2</sup> 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		23.8	-33.59	-	11844	-35.81	-	