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1 **ABSTRACT**

2 Changes in land use/cover are the main drivers of global biodiversity loss, and thus tools to  
3 evaluate effects of landscape change on biodiversity are crucial. In this study we integrated  
4 several methods from landscape ecology and landscape genetics into a GIS-based analytical  
5 framework, and evaluated the impacts of development and forest restoration scenarios on  
6 landscape connectivity, population dynamics and genetic diversity of Sunda clouded leopard in  
7 the Malaysian state of Sabah. We also investigated the separate and interactive effects of  
8 changing mortality risk and connectivity. Our study suggested that the current clouded leopard  
9 population size is larger (+26%) than the current carrying capacity of the landscape due to time  
10 lag effects and extinction debt. Additionally, we predicted that proposed developments in Sabah  
11 may decrease landscape connectivity by 23% and, when including the increased mortality risk  
12 associated with these developments, result in a 40-63% decrease in population size and  
13 substantial reduction in genetic diversity. These negative impacts could be mitigated only to a  
14 very limited degree through extensive and targeted forest restoration. Our results suggest that  
15 realignment of roads and railways based on resistance to movement, without including mortality  
16 risk, might be misleading and may in some cases lead to decrease in population size. We  
17 therefore recommend that efforts to optimally plan road and railway locations base the  
18 optimization on effects of development on population size, density and distribution rather than  
19 solely on population connectivity.

20

21

22 **Keywords:** land use planning; landscape connectivity; population dynamics; cumulative  
23 resistant kernels; least-cost paths; mortality risk

24 **1. Introduction**

25 Anthropogenic changes in land cover and land use have been a major and direct driver of global  
26 terrestrial biodiversity loss (Gagné et al., 2015) and are predicted to increase substantially in the  
27 next decade (Hansen *et al.* 2013). Despite the recognition that effective and well informed  
28 landscape planning is crucial for mitigating the negative effects of landscape change on  
29 biodiversity, landscape ecological knowledge is not widely used by planning agencies, and  
30 science-based information and tools are not often incorporated in land use decision-making  
31 (Ahern, 2013; Gagné et al., 2015). This is in part because scientific papers do not often provide  
32 practical and feasible ways to quantitatively compare realistic alternative scenarios. Preserving  
33 biodiversity in rapidly developing landscapes requires a proactive approach where managers  
34 evaluate *a priori* effects of alternative development or conservation plans.

35 Land use planners face a dilemma in balancing biodiversity conservation with the demands of  
36 human population growth and economic development. This is especially relevant in emerging  
37 economies, where the pressure on ecosystems and wildlife is extremely high and there may be  
38 limited legal and administrative protection of biodiversity. At the same time, many of these  
39 regions harbour the highest levels of biodiversity and endemism, which emphasises the  
40 importance of scientifically-based tools to guide land use planning to minimize impacts to  
41 biodiversity. Identifying and prioritizing areas for development, conservation, and restoration  
42 requires quantitative analysis that integrates ecological and urban planning theories (Xun et al.,  
43 2017). Conservation and land use planning have overlapping goals: conservationists are  
44 concerned with the sustainability of ecosystems and populations, while planners focus on  
45 sustainable delivery of goods and services for humans often provided by ecosystem services  
46 (Botequilha Leitão and Ahern, 2002). Balancing the preservation of biodiversity with economic

47 development requires conservation actions that can maintain critical ecosystems functions while  
48 minimizing constraints on land development (DeFries et al., 2007). This can be achieved through  
49 efforts to optimize development and conservation strategies that maximize the conservation  
50 benefit with the least economic cost.

51 Critical components of evaluating the impacts of landscape change on wildlife include  
52 assessment of how it affects population size, genetic diversity and connectivity. Loss of habitat  
53 area and increases in mortality risk can lead to reductions of population size, often exhibiting  
54 threshold effects where populations decline abruptly after loss of a particular amount of habitat  
55 (e.g., Hearn et al. 2018). In addition, loss of connectivity can disrupt the ability of species to  
56 procure resources, seasonally migrate, shift home ranges, disperse to new home ranges, and  
57 exchange genes between local populations, which, in turn, can lead to decreased carrying  
58 capacity, loss of genetic variation, population declines and even extinction (Rudnick et al., 2012;  
59 Xun et al., 2017). Low genetic diversity can also inhibit the population's ability to respond to  
60 rapid environmental changes (Noël et al., 2007), and lead to inbreeding depression (Van  
61 Noordwijk, 1994), which can create an extinction vortex where populations decline (Frankham,  
62 2005).

63 To offset the impacts of fragmentation, degradation and loss of habitat on biodiversity,  
64 conservation efforts should focus on protecting and enhancing core population areas, reducing  
65 mortality risk and improving connectivity (Rudnick et al., 2012; Cushman et al. 2018). To  
66 achieve this, it is therefore crucial to quantitatively assess the pattern of mortality risk across the  
67 population as well as the strength and importance of core habitats and the corridors linking them,  
68 and integrate these in models that evaluate how alternative development scenarios affect  
69 population size, genetic diversity and connectivity (e.g., Cushman et al. 2016).

70 Measuring and predicting impacts of landscape change on population distribution, abundance,  
71 genetic diversity and functional connectivity has become more feasible thanks to new  
72 technologies, more powerful computers and freely available GIS data. Furthermore, the new  
73 methods in landscape ecology and landscape genetics, like cumulative resistant kernels  
74 (Compton et al. 20017), factorial least cost paths (Cushman et al., 2014) and spatially-explicit  
75 individual based population models (Landguth and Cushman 2010), enable rigorous and spatially  
76 synoptic assessment and prediction of population-level effects and make the analysis of  
77 connectivity more accurate and statistically powerful. Importantly, these new approaches, in  
78 contrast to traditional landscape assessment methods using structural metrics, are parameterized  
79 on the basis of the biology of particular species and the characteristics of the landscape that  
80 affect that species' distribution, abundance and movement providing a functional measure of  
81 connectivity (e.g. Cushman et al., 2018; Kaszta et al., 2018; Wasserman et al., 2013). There are  
82 however few published examples integrating landscape ecology and genetics tools such as  
83 empirically optimized resistance models, individual-based population and genetics models and  
84 synoptic connectivity modelling approaches for optimized land-use planning (e.g., Cushman et  
85 al., 2018a, 2016)

86 In this study we focus on Sabah, a Malaysian state in northern Borneo, which has been heavily  
87 impacted by deforestation and faces the challenge of rapid economic development and expanding  
88 urbanization, agriculture and infrastructure. Until recently, the island of Borneo was covered by  
89 one of the world's largest undisturbed blocks of tropical forest, supporting extremely high  
90 endemism and biodiversity (Woodruff, 2010). However, over the past several decades the island  
91 has had the world's highest deforestation rate. Forest cover on Borneo declined by 33.5%  
92 between 1973 and 2015 (Gaveau et al., 2016), due to deforestation for timber extraction and

93 conversion to agriculture driven mainly by plantation industries (especially oil palm *Elaeis*  
94 *guineensis*, Cushman et al. 2017). The deforestation rate varies by region (Bryan et al., 2013),  
95 with the highest forest loss estimated in the Indonesian provinces of Kalimantan and the  
96 Malaysian states of Sabah and Sarawak (35.6%, 31.9% and 25.9% respectively; Gaveau et al.  
97 2016).

98 To assess and map population core areas and landscape connectivity, landscape planners  
99 typically select a focal species or a set of focal species, which usually are area-sensitive species  
100 with habitat-restricted dispersal (Rudnick et al., 2012). Large carnivores are often chosen as focal  
101 species given they have these characteristics (Carroll et al., 2001; Noss et al., 1996) and they can  
102 also serve as ambassador species (Macdonald et al., 2017). The terrestrial apex predator in  
103 Borneo is the Sunda clouded leopard (*Neofelis diardi*). This medium-sized felid, endemic to  
104 Borneo and Sumatra, is genetically and morphologically distinct from the clouded leopard  
105 (*Neofelis nebulosa*) populations inhabiting mainland Southeast Asia (Buckley-Beason et al.,  
106 2006; Christiansen, 2009; Kitchener et al., 2006; Wilting et al., 2006). Due to its small and  
107 declining population (Sabah population ~750 individuals; Hearn et al., 2017), this species is  
108 listed as Vulnerable on the IUCN Red List (Hearn et al., 2015). Sunda clouded leopard is a likely  
109 wide-ranging, forest-dependent species (Hearn et al., 2018), and thus may act as an effective  
110 umbrella for other forest-dependent species. Therefore, changes in landscape connectivity and  
111 population dynamics of the Sunda clouded leopard might serve as a good indicator of health of  
112 the Sabah ecosystems, and a vehicle to evaluate the impacts of a range of alternative  
113 conservation and development scenarios on those ecosystems.

114 Our goal in this study was to demonstrate the use of a GIS-based analytical framework that maps  
115 and quantifies the impact of future development and restoration scenarios on landscape

116 connectivity, population distribution, density and genetic diversity of the Sunda clouded leopard  
117 across Sabah. We evaluated the impacts of 58 alternative development and ecological restoration  
118 scenarios described in the Structure Plan and the effects of spatially heterogenous mortality risk.  
119 Furthermore, we used spatial optimization to improve the scenarios we found had the largest  
120 negative impacts on clouded leopard population connectivity.

121

## 122 **2. Methods**

### 123 **2.1. Study area**

124 The Malaysian state of Sabah occupies an area of 73,631 km<sup>2</sup> in northern Borneo (Figure 1). The  
125 topography of Sabah is rugged, with extensive mountains, particularly in the central, northern  
126 and western parts of the state. Sabah has had the highest deforestation rate of all Borneo's  
127 political units (78.6% of forest cover in 1973 decreased to 47.5% in 2010; Gaveau et al. 2014),  
128 and one of the highest deforestation rates in the world (Cushman et al., 2017). Recent  
129 deforestation has been driven by conversion of forest to mono-culture plantations, mainly oil  
130 palm (21% of Sabah in 2015; McMorro and Talip 2001, Malaysian Palm Oil Board, 2016) but  
131 also timber plantations (3.3% of Sabah; Reynolds et al. 2011).

132 Nevertheless, the state of Sabah has committed to protecting its remaining forest, and increasing  
133 the sustainable utilization of forest products. The state contains extensive areas of highly  
134 disturbed, regenerating forests. Protected primary forest exists in relatively small patches (280–  
135 1399 km<sup>2</sup>), including the Danum Valley, Maliau Basin and Imbak Canyon Conservation Areas,  
136 and the Crocker Range, Kinabalu and Tawau Hills Parks (Figure 1), but the vast majority of  
137 remaining forest has been previously logged (Reynolds et al., 2011). The majority of remaining

138 forest belongs to the state-owned Permanent Forest Reserve, which includes State Parks,  
139 Wildlife Reserves as well as commercial Forest Reserves (Reynolds et al., 2011).

## 140 **2.2. Development and restoration scenarios**

141 The Sabah Structure Plan for 2033 is a map of proposed future developments and forest  
142 restorations for the state of Sabah. The document was certified by the Director of Town and  
143 Regional Planning Department, adopted by the Central Town and Country Planning Board and  
144 was approved by the State Cabinet on the 20<sup>th</sup> July 2016. The plan includes, inter alia,  
145 transportation and connectivity infrastructure, special economic zones and environmentally  
146 sensitive areas.

147 In our analyses we considered 59 scenarios, which included a base scenario reflecting existing  
148 landscape conditions and 58 development and restoration scenarios proposed in the Sabah  
149 Structure Plan for 2033 (Figure 2, Table 2). Development and restoration scenarios based on the  
150 Sabah Structure Plan included: (1) 16 new segments of highways (4 lanes); (2) 15 segments of  
151 existing roads upgraded to highway (from 2 lanes to 4 lanes); (3) 10 new segments of railroads;  
152 (4) 17 new forest restoration (connected forest) areas (Figure 2).

### 153 *Resistance surfaces*

154 The base resistance surface for connectivity modelling was created by inverting and rescaling a  
155 clouded leopard path-selection function (e.g., Cushman and Lewis, 2010) model developed by  
156 Hearn et al. (2018) based on Sunda clouded leopard GPS telemetry data. The path-selection  
157 function was developed using conditional logistic regression to predict clouded leopard path  
158 selection in the Lower Kinabatangan landscape based on land cover, forest types, canopy cover,  
159 forest quality and river network (Table 1; Hearn et al., 2018) and showed that clouded leopard

160 movement choices positively associated with high-canopy cover forest, and that plantation  
161 habitats with low canopy cover resist movement. This path-selection function model was  
162 extrapolated to the full extent of Sabah by Hearn et al., (2019). The final variables of the path-  
163 selection model are listed in Table 2.

164 For each of the 58 scenarios (Figure 2) we built a resistance surface reflecting how the landscape  
165 change in that scenario would modify the resistance surface by reapplying the path selection  
166 function developed by Hearn et al. (2018) to GIS layers reflecting the proposed land use changes  
167 (Table 2). In scenarios involving creation of new forest restoration areas, these patches of  
168 restored forest were reclassified to forest. The resistance surfaces for each restoration scenario  
169 were generated by inverting and rescaling the predictions of the path selection function values  
170 between 1 (low resistance = high suitability) and 100 (high resistance = low suitability). As the  
171 empirical habitat suitability model did not account for impact of existing major sealed roads (2  
172 lanes), based on expert knowledge, we added them to the resistance surface as an additional  
173 resistance value of 10, and performed a set of sensitivity analyses to quantify the impact of  
174 different degrees of resistance assigned to roads (last sub-section of the Methods).

175 GIS layers for the development scenarios were created by ‘burning in’ each of the new segments  
176 of highways and railroads into the base resistance surface. Existing roads foreseen by the Sabah  
177 Structure Plan to be upgraded to highways were assigned an additional resistance value of 30, the  
178 new highways were given additional resistance of 40 and the new railroads value 20.

#### 179 *Source points*

180 Hearn et al. (2017) estimated a population of approximately 750 clouded leopards in the state of  
181 Sabah. Therefore, to represent the spatial pattern of clouded leopard resource use, we located 750  
182 points in the study area, probabilistically with density and distribution reflecting the pattern of

183 habitat suitability of our path-selection function (Hearn et al., 2018). For the 17 forest restoration  
184 scenarios (potentially new suitable environments for clouded leopard), we generated additional  
185 occurrences inside the restoration areas. This was achieved by calculating the ratio of mean  
186 suitability within that restoration polygon in the base scenario and the restoration scenario, and  
187 dividing the number of source points in that polygon by that ratio. The result was an increase in  
188 source points proportional to the net increase in total suitability in that restoration polygon (Table  
189 3).

#### 190 *Cumulative resistant kernels*

191 We implemented cumulative resistant kernel connectivity modelling (Compton et al., 2007) with  
192 the UNICOR software (Landguth et al., 2012). The resistant kernel approach to landscape  
193 connectivity maps the most cost-effective movement routes from a source cell to every other cell  
194 in the landscape within a maximum dispersal cost-distance. The cumulative resistant kernel  
195 surface, which reflects the incidence function of rate of movement through each cell in the  
196 landscape (Kaszta et al. 2018), is calculated by summing all individual least-cost kernels from all  
197 population source points (Compton et al., 2007). The kernels for each source point were  
198 calculated with a cost distance threshold of 125,000 reflecting maximum distance of 125 km a  
199 clouded leopard can travel in a uniform landscape of optimal low resistance (i.e., resistance = 1;  
200 Hearn et al., 2019; Macdonald et al., 2018).

#### 201 *Fragmentation analysis*

202 The cumulative resistant kernels layers for the different scenarios were compared in several  
203 ways. First, we calculated the difference in the cumulative kernel surface between the base  
204 scenario and every other scenario, since differences between cumulative kernel surface summed  
205 across all pixels in the landscape reflect the total change in connectivity between the two

206 connectivity maps. Additionally, we created a binary layer, by reclassifying the cumulative  
207 resistant kernel surfaces, giving all pixels lower or equal to 10 a value of 0, and pixels higher  
208 than 10, value 1. The choice of value 10 as a threshold to define the binary layer was based on  
209 the median value of the cumulative resistant kernels (Table S1). This creates a binary layer with  
210 areas of medium to high connectivity classified as 1. We calculated several FRAGSTATS  
211 metrics (McGarigal et al., 2012) to investigate the effect of the development and restoration  
212 scenarios on the extent, pattern and fragmentation of connectivity, including largest patch index  
213 (LPI), percent of landscape (PLAND) and correlation length (GYRATE\_AM). LPI is the  
214 percentage of the landscape covered by the largest single patch of connected habitat, PLAND is  
215 the extent of the landscape covered by connected habitat, and GYRATE\_AM is the expected  
216 distance from a random location in connected habitat to the edge of connected habitat moving in  
217 a straight line in a random direction. These landscape metrics were chosen since they have  
218 frequently been used in assessments of connectivity (e.g. Wasserman et al. 2012, Cushman et al.  
219 2016) and have been shown to be highly related to genetic differentiation (Cushman et al.,  
220 2013b). For each scenario we calculated the difference in these metrics between that scenario  
221 and the base scenario. Based on the results of the difference in the sum of the cumulative kernel  
222 surface and landscape metrics we identified the most influential development and restoration  
223 scenarios – those which significantly decreased or increased connectivity in the study area.

#### 224 *Least cost path analyses*

225 To investigate how dispersal corridors for Sunda clouded leopards might be affected by the  
226 Sabah Structure Plan, we calculated factorial least cost paths (Cushman et al. 2009) in UNICOR  
227 for the selected most influential scenarios. As an input we used the same source points layers and  
228 resistant surfaces which were used to calculate cumulative resistance kernels. We then analysed

229 the difference in the strength and locations of least cost paths between each of the selected  
230 development and restoration scenarios and the current situation.

### 231 *Alternative scenarios*

232 We used our analytical approaches to suggest less impactful alternative routing of road and  
233 railway segments. Specifically we rerouted the planned segments of highways and railroads with  
234 the most negative impact on the landscape connectivity by calculating the least cost path  
235 connecting two source points representing ends of a highway or railroad segment. The cost layer  
236 for these new routes was developed by combining the path selection function suitability layer  
237 and a function of topographical slope. The input cost surface was generated by additively  
238 combining the clouded leopard habitat suitability layer and topographical slope. The latter was  
239 created by first calculating slope in ArcGIS 10.x (ESRI, 2012) from a digital elevation model  
240 (DEM; Jarvis et al. 2008) and then by fitting an exponential function to the resulting slope layer  
241 ( $\exp(\text{slope}/10)$ ) to represent the cost. This resulted in realignment of road and railway segments  
242 to new routes that minimize impact on clouded leopard habitat suitability at the pixel scale while  
243 avoiding steep slopes that are topographically unsuitable for road or railway development.

### 244 *Comparison of the development and restoration strategies*

245 Each of the alternative road and railway segments was overlaid onto the base resistance surface  
246 and we recalculated cumulative resistant kernels for each of the alternative scenarios.  
247 Additionally, to compare the total change in connectivity we also calculated cumulative resistant  
248 kernels for four different development and restoration strategies: (1) ‘development with  
249 restoration’ - all proposed developments and restoration laid out in the Sabah Structure Plan are  
250 applied, including new roads and railways as well as the new forest connectivity areas, (2)  
251 ‘development strategy’, in which the development plan is applied by including only the planned

252 new and upgraded highways and railroads , (3) ‘restoration strategy’ – plan accounting only for  
253 restoration of the 17 forest connectivity areas, (4) ‘alternative strategy’, which includes  
254 restoration of forest connectivity areas as well as development of all new railroads and highways,  
255 but the most disruptive segments are realigned to minimize the total ecological cost defined as  
256 impact on the landscape connectivity and clouded leopard population dynamics. For each of the  
257 alternative scenarios and the four strategies we then calculated a sum of kernel values and the  
258 three previously mentioned landscape metrics (largest patch index, percentage of landscape and  
259 correlation length).

#### 260 *Simulated population dynamics*

261 We evaluated the influence of the proposed and alternative development and restoration  
262 strategies on Sunda clouded leopard population dynamics and genetic diversity by simulating  
263 changes in clouded leopard population size, allelic richness and heterozygosity. We used CDPOP  
264 (Landguth and Cushman, 2010), an individual-based, spatially explicit cost-distance population  
265 genetics program, to simulate spatial patterns of mating and dispersal as a function of suitable  
266 habitat and dispersal cost.

267 We used standard simulation parameters widely used in landscape genetics simulation modelling  
268 (e.g., Cushman and Landguth, 2010; Landguth et al., 2010b). We stipulated the population to  
269 have 30 loci, with 10 alleles per locus, which were randomly assigned among individuals. The  
270 mutation rate was parametrized to 0.0005. We used an inverse square mating and dispersal  
271 probability function, with the maximum cost-weighted dispersal distance of 125km reflecting the  
272 estimated maximum dispersal ability of clouded leopard (Hearn et al., 2019; Macdonald et al.,  
273 2018). Reproduction was sexual with non-overlapping generations. The number of offspring was  
274 based on a Poisson probability draw of mean equal 2. We simulated 10 Monte Carlo replicates of

275 each scenario. We simulated gene flow for 200 non-overlapping generations as previous studies  
276 have shown that this is sufficient time to ensure spatial genetic equilibrium (Landguth et al.,  
277 2010b, 2010a).

278 We tested for significant differences in clouded leopard population size, allelic richness and  
279 heterozygosity across the scenarios with ANOVA and Tukey HSD using R (R Development  
280 Core Team, 2012). Furthermore, we used the kernel point density function in ArcGIS 10.x  
281 (ESRI, 2012) to map spatial patterns in population density, and used kriging to map allelic  
282 richness and heterozygosity (all as an average of 10 Monte Carlo replicates) of Sunda clouded  
283 leopard populations across Sabah and computed differences between the base and alternative  
284 scenarios.

#### 285 *Mortality*

286 Many recent papers on effects of landscape structure on biodiversity conservation have focused  
287 on connectivity without explicitly evaluating effects of spatially heterogenous mortality risk  
288 (e.g., Cushman et al., 2018b, 2016; Thatte et al., 2018). We investigated the effect of mortality  
289 risk, in addition to landscape connectivity, on population dynamics and genetic diversity of  
290 clouded leopard. However, the relationship between landscape elements, such as land cover  
291 types, roads and railroads, and risk of mortality for clouded leopard is unknown, but likely is  
292 associated with habitat quality and landscape resistance (e.g., Mateo-Sanchez et al. 2016, 2017;  
293 Zeller et al. 2018). Therefore, we simulated spatial mortality risk as proportional to landscape  
294 resistance at several levels: base mortality (mortality risk is equal to landscape resistance), 1.25 x  
295 base mortality (125% threshold), 1.5 x base mortality (150% threshold) and 2 x base mortality  
296 (200% threshold).

297 Roads and railways have an additional mortality effect on clouded leopards through road kill and  
298 poaching associated with road access to the region surrounding the road, which are not included  
299 in the resistance surfaces. Therefore, we simulated an additional effect of linearly decreasing  
300 mortality risk up to 10km from roads and railways. The 10km range of this effect accounts for  
301 large home ranges of clouded leopard and the probability of an animal being exposed to the road  
302 and off-road poaching.

303 We then multiplied each of the mortality layers by 1.25, 1.5 and 2 to investigate the sensitivity of  
304 the mortality values on the CDPOP results. As the values of the input CDPOP mortality layer  
305 need to be between 1 to 100, we saturated all mortality values above 100 to 100.

306 The CDPOP results for each scenario were then compared (including comparison of all  
307 scenarios with and without spatially heterogeneous mortality risk) and tested for significant  
308 differences using ANOVA and Tukey HSD test. Furthermore, to compare the spatial patterns of  
309 population size and genetic diversity across scenarios we produced a point density maps for  
310 population size and interpolation maps for allelic richness and heterozygosity using kriging in  
311 ArcGIS 10x.

### 312 *Sensitivity analysis of road resistance*

313 The resistance value assigned to roads was based on expert opinion and not on empirical data.  
314 Therefore, we performed a set of sensitivity analysis using the base resistance scenario reflecting  
315 current landscape. We built three sets of resistance layers to each assigning different resistance  
316 values for roads: 5, 10 and 15. These resistance layers were then used to calculate cumulative  
317 resistance surfaces, least cost paths layers, as well as population density, alleles richness and  
318 heterozygosity surfaces. To evaluate how sensitive the results are to the parameterization of road

319 resistance we calculated correlation and averaged absolute difference across the three road  
320 resistance scenarios in the base landscape.

### 321 **3. Results**

#### 322 *Landscape connectivity of the base scenario*

323 There are two main core clouded leopard populations in Sabah (Figure 3-B): the larger is located  
324 in central Sabah and encompasses the Yayasan Sabah Forest Management Area, and the smaller  
325 core area is located in the north-western mountainous region, and includes Crocker Range,  
326 Kinabalu Park and Trus Madi Forest Reserve. These core areas are associated with the largest  
327 contiguous forested areas in Sabah. The core areas are connected by three strong linkages located  
328 in central Sabah and one weaker western corridor (Figure 3-A)

#### 329 *Comparison of development and restoration scenarios*

330 Among the 17 investigated forest restoration scenarios two substantially improved connectivity  
331 in Sabah (CF 2 and CF10); these increased the sum of kernel values across Sabah by 2.43% and  
332 3.45% respectively (Table ). Both of these restoration areas also significantly increased the  
333 percentage of landscape, largest patch index and correlation length of connected habitat. Three of  
334 the 17 planned forest restoration areas did not improve connectivity in Sabah (CF4, CF5 and  
335 CF16), and two areas had weak positive influence (CF1 and CF14). Only four planned forest  
336 connectivity areas increased all the investigated landscape metrics (CF1, CF2, CF3 and CF10),  
337 with scenarios CF2 and CF10 having by far the largest positive impact on Sabah-wide  
338 connectivity (Table 2, Figure S1-G, H). Furthermore, forest restoration area CF2 shifts the  
339 corridor linking northern and southern core areas to the east (Figure S8), contrary to the CF10

340 (Figure S9), which had an opposite effect – strengthening the western corridor and weakening  
341 the eastern connection between the two core areas.

342 Most new segments of roadway (12 segments out of 16) decreased landscape connectivity in  
343 Sabah, with 3 segments (HN2, HN5 and HN16) predicted to have large negative impacts  
344 (difference in kernel sum with the base scenario of -3.68%, -2.31% and -2.44% respectively;  
345 Table 2 and Figure S1-B, C,D). Incorporating these three new highway segments into the  
346 landscape also significantly decreased the landscape metrics LPI, PLAND, and GYRATE\_AM.  
347 One of the road segments slated to be upgraded from a minor road to a highway (HU4) had even  
348 greater effects on connectivity, decreasing the sum of kernel values by 3.87% (Table 2, Figure  
349 S1-E), the largest impact amongst all road development scenarios (Table 2). However, the  
350 highest negative influence on connectivity was recorded for the railroad R6 segment (Figure S1-  
351 F), which decreased the sum of kernel values by 4.58% (Table 2). Furthermore, construction of  
352 new segments of highways and railroads shifts the strength of some linkages and has mainly  
353 negative effect on connectivity (Figure S2-S7).

#### 354 *Comparison of alternative segments and development strategies*

355 Figure 2 shows a map of planned developments for Sabah along with proposed alternative  
356 scenarios for the 5 most disruptive highway and railroad segments (HN2, HN5, HN16, HU4, R6;  
357 based on Table 2). Based on sum of kernel values, realignment of the most disruptive segments  
358 of highways and railroads, with the exception of HU4, decreased the negative effect of these  
359 segments on connectivity (Table4). The negative effect of realigning HU4 arises because this  
360 segment already exists as a minor road, and construction of an additional segment of highway,  
361 even if possibly less disruptive in itself than upgrading the existing road, when combined with  
362 the existing road has a larger negative impact. The strongest improvement in the connectivity,

363 based on sum of kernel values and landscape metrics, was recorded for realigned segment of  
364 highway HN5 (Table4). The realignment increased the sum of kernel values between 0.02 and  
365 0.58 (the average increase of 0.33).

366 When looking at the combined effect of scenarios, the strategy including restoration of the 17  
367 forest connectivity areas without any development improved the total Sabah connectivity by  
368 9.38% based on sum of kernel values, and it also increased all the three landscape metrics  
369 (Table5). Not surprisingly the development of highways and railroads without forest restoration  
370 had a large negative effect on connectivity (~ 23% decrease in the sum of kernel values; Table  
371 5). Combining development of new highways and railroads with forest restoration increased the  
372 sum of kernel values by 6.4% compared to the development-only strategy. Furthermore,  
373 realignment of the 5 most disruptive segments of highways and railroads additionally improved  
374 connectivity by almost 3% (Table 5).

#### 375 *Population dynamics without mortality*

376 The simulated mean population size of clouded leopard in Sabah after 200 generations dropped  
377 from the initial 750-760 to 575 for the restoration strategy without spatial mortality risk and  
378 about 550 for the development strategy without mortality risk (the number indicates a median of  
379 10 Monte Carlo replicates, Figure 4). Results of ANOVA and Tukey HSD test indicated a  
380 positive (mean = +19.4) and significant ( $p < 0.05$ ) difference in clouded leopard population size  
381 between the restoration strategy and the base scenario (Table 6). Furthermore, the development  
382 strategy significantly reduced mean simulated population size compared to the restoration  
383 strategy, the full Sabah Structural Plan (combining restoration and development) or the  
384 alternative strategy (including our proposed realignments), with reductions of -23.6, -14.5 and -  
385 16.2 respectively (Table 6). Looking at the spatial variation in population density between the

386 four scenarios and the base scenario, we found that the development strategy has a universally  
387 negative effect, with highest impacts in the eastern part of Lahad Datu District and Beluran  
388 District, as well as in the West Coast Division and Keningau District (Figure S10).  
389 The differences between scenarios in allele richness, although resulting in lower numbers for the  
390 development scenarios and higher for the restoration scenarios, were not statistically significant  
391 (Table 6). Comparing heterozygosity across scenarios, the differences are more striking and most  
392 of them are statistically significant (Table 6). In particular, heterozygosity significantly increased  
393 with the restoration strategy compared to the development, development with restoration and  
394 alternative strategy (on average by 0.064, 0.047 and 0.047 respectively). Furthermore, both  
395 development with restoration and alternative scenarios significantly decreased heterozygosity  
396 compared to the base scenario (Table 6). Looking at the spatial differences in allelic richness and  
397 heterozygosity across scenarios, we can observe some important differences (Figure S10 and  
398 Figure S11). In general, if the future actions focus only on forest restoration, both allelic richness  
399 and heterozygosity will increase across Sabah. The alternative alignment scenario was the  
400 second-best strategy, and it increased heterozygosity in a large portion of the state. On the  
401 contrary, the scenario where development occurred without forest restoration decreased clouded  
402 leopard allelic richness and heterozygosity across Sabah.

#### 403 *Population dynamics with mortality*

404 The clouded leopard population size and genetic diversity measured by the level of  
405 heterozygosity and allelic richness after 200 generations greatly varied when different thresholds  
406 of mortality were applied (Figure 4). Overall, including spatially varying mortality risk caused  
407 dramatic declines in population size and genetic diversity for all scenarios (Figure S13), with  
408 large decreases in effect at higher levels of mortality risk. A statistically significant drop in

409 population size was observed across all scenarios, except the base scenario, even with the lowest  
410 mortality threshold (Figure 4, Table S3). At the lowest level of mortality risk the simulation  
411 predicted the base scenario (current landscape condition) to result in declines in clouded leopard  
412 population size from current 750 to 500, allelic richness from 170 (base scenario after 200  
413 generations) to 145 and heterozygosity from 0.53 (base scenario after 200 generations) to 0.48  
414 (Figure 4, Table S3).

415 The most dramatic decline in population size (from 750 to 275-450 individuals depending on the  
416 mortality threshold), number of alleles (from 165 to 125-145 depending on the mortality  
417 threshold) and heterozygosity (from 0.49 to 0.1-0.32 depending on the mortality threshold) was  
418 found for development strategy (Figure 4). For population size we observed a statistically  
419 significant, steep linear decline with increasing mortality threshold. Number of alleles and  
420 heterozygosity exhibited a decreasing but non-linear trend with increasing mortality threshold  
421 (Figure 4, Table S3). The negative effect of development on population size and genetic diversity  
422 comparing to the base scenario was observed across almost entire Sabah state (Figure S13B,  
423 Figure S14B and Figure S15B).

424 Even when development was accompanied by restoration, the population size, allelic richness  
425 and heterozygosity decreased significantly and systematically with growing mortality threshold  
426 (Figure 4). However, for almost all mortality thresholds, with exception of the base mortality,  
427 restoration applied with development statistically significantly increased population size as  
428 compared to development without restoration (by 20-21 individuals) and heterozygosity (by  
429 0.03-0.09) (Table S4). This positive difference in population size between development strategy  
430 with and without restoration was particularly pronounced in Papar, Tambunan, Ranau and  
431 Nabawan districts (Figure 5A), and in case of heterozygosity across the entire Sabah (Figure 5B).

432 Overall, including mortality at different thresholds in the development and restoration strategies  
433 caused statistically significant decreases in population size (from -111 to -269 individuals),  
434 allelic richness (from -31 to -50 alleles) and heterozygosity (from -0.15 to -0.3) when comparing  
435 to the base scenario without mortality (Table S4). This decrease was observed across entire state  
436 of Sabah (Figure 6).

437 Realignment of the segments of roads and railways (the alternative strategy) did not increase  
438 population size or genetic diversity compared to the original development and restoration  
439 strategy (Figure 4, Table S3). Furthermore, with mortality at the 150% threshold, the alternative  
440 strategy produced a statistically significant decrease in population size (-25 individuals in  
441 comparison with the original development and restoration strategy).

#### 442 *Sensitivity analysis of roads' resistance*

443 The sensitivity analysis of road resistance showed that all three base scenarios with different  
444 resistance values for roads are highly correlated (Pearson's correlation  $\geq 0.97$ ; Table S2).  
445 Furthermore, the absolute averaged difference between the three roads scenarios were very small  
446 (Table S2).

#### 447 **4. Discussion**

448 In this paper we integrated individual-based, spatially explicit population, genetic and  
449 connectivity modelling to evaluate habitat extent, population size, population connectivity and  
450 genetic diversity of Sunda clouded leopard under a range of realistic development and  
451 conservation scenarios and attempted to optimize alternative development plans to minimize  
452 impacts on Sunda clouded leopards across the Malaysian state of Sabah in Borneo. This study is  
453 the first to combine these methods from landscape ecology and landscape genetics to evaluate  
454 effects of alternative development and conservation scenarios and to test the impact of mortality

455 imposed by landscape features, such as road kill and risk of poaching. In the past, this kind of  
456 integration was difficult due to the challenges of characterizing the ecology and behaviour of the  
457 target species (Fu et al., 2010) and limited development of spatial modelling tools to  
458 quantitatively compare scenarios.

459  
460 *Comparison with previous studies*

461  
462 Several authors have attempted to quantify the effects of existing or future landscape structures  
463 on connectivity. Such attempts, however, typically were not based on biological data about the  
464 species of interest (Xun et al., 2017), did not consider alternative landscape change scenarios (Fu  
465 et al., 2010), and few analysed the effects of the scenarios on landscape connectivity, population  
466 dynamics or genetic diversity, and none of the previous studies incorporated the potential effects  
467 of landscape change mortality risk. The study of Wasserman et al. (2010, 2012a, b) to date is the  
468 only paper that combined resistant kernels and individual-based population dynamics models to  
469 predict effects of climate change on population connectivity, population size and genetic  
470 diversity of American marten (*Martes americana*). The design of the Wasserman et al. (2010)  
471 study was, however, not focused on providing guidelines for land use planning agencies.  
472 Recently, Thatte et al. (2018) used CDPOP to compare alternative development and conservation  
473 scenarios in their impacts on tiger population size and genetic diversity in Central India, and is  
474 an excellent example of using individual-based simulation modelling to compare scenarios, but  
475 did not implement spatially heterogeneous mortality risk as part of their scenarios. Our analysis  
476 extends this by including spatially heterogeneous mortality risk as a function of landscape  
477 features, and optimal realignment of proposed developments and additional evaluation of  
478 connectivity and landscape patterns (kernels, least-cost paths and landscape pattern analysis).

479 The negative impact of land use change and road expansion on wildlife populations is not only  
480 due to its disruptive effect on habitat connectivity but also through increasing direct mortality via  
481 vehicle collisions and likely increased poaching as roads provide improved access across the  
482 landscape. For example, Kramer-Schadt et al. (2004) found that most suitable patches could be  
483 interconnected by movements of dispersing lynx but become isolated due to the high mortality of  
484 dispersing lynx. Our results showed that including mortality in individual-based population  
485 dynamics models can have immense effects on the results and should not be ignored when  
486 investigating effects of developments on survival and genetic stability of a population. Similarly  
487 to the study of Kramer-Schadt et al. (2004), our analysis showed that the true effect of the  
488 proposed developments on population size and genetic diversity of Sunda clouded leopards is  
489 greater than simulated only by connectivity modelling itself, which accounts only for decreased  
490 connectivity and not increased mortality.

491 Gagné et al. (2015) concluded that ecological guidelines are usually not considered in land use  
492 planning due to limitations in their practicality and feasibility. Most guidelines require species-  
493 specific information which is often scarce at the scales required for planning. Collection of such  
494 data is costly and time-consuming, and in most planning offices the resources allocated to the  
495 acquisition of biodiversity data are insufficient (Botequilha Leitão and Ahern, 2002; Gagné et al.,  
496 2015; Miller et al., 2009). As a result, lack of information is often a decisive argument for not  
497 attending to biodiversity impact analysis (Botequilha Leitão and Ahern, 2002). Furthermore,  
498 according to review of Gagné et al. (2015), it is difficult for planners, who often lack the  
499 ecological expertise, to translate biological knowledge into specific planning actions. Finally,  
500 guidelines are often presented in an unintegrated manner, lacking clear protocols which limits  
501 their usability. This study represents an elaboration and extension of this line of work in that for

502 the first time we have produced a comprehensive model-based framework to quantitatively  
503 compare scenarios of alternative landscape change in terms of their potential impacts on habitat  
504 connectivity, population size and genetic diversity of a focal species.

505 *Significance for clouded leopard conservation*

506 Our analysis suggests that the current clouded leopard population size in Sabah may dramatically  
507 decline (~ -26%), even without additional development, likely reflecting the time lag effect and  
508 extinction debt of recent massive and rapid habitat loss. Our results imply that without creating  
509 new suitable habitats for clouded leopard, the current carrying capacity of the available habitat is  
510 not sufficient to sustain the current population size. For example, similarly to the findings of  
511 Hearn et al. (2019), our models predicted loss of the clouded leopard local population in the  
512 lower Kinabatangan floodplain due to current isolation and past loss of habitat.

513 Most importantly, however, our findings strongly indicate that development of infrastructure,  
514 like highways and railroads, is likely to have large negative impacts on clouded leopard  
515 populations (23% drop in connectivity), including large population declines across Sabah and  
516 extinction of some subpopulations. For example, our simulations suggest that construction of  
517 new highways and railways in Sabah (even accompanied by habitat restoration) may cause future  
518 loss of local clouded leopard population in Tawau Hills National Park. One of our most  
519 important results is that this detrimental effect of development is immensely stronger when  
520 clouded leopard mortality is considered. Including mortality effects led to population declines  
521 from 40% to 63% (for the low mortality and high mortality effects, respectively, compared to  
522 the scenario without mortality effects. Similarly, Kramer-Schadt et al. (2004) found that  
523 mortality significantly impedes dispersal probability of lynx when including road mortality and  
524 Frair et al. (2008) demonstrated that even relatively low road density significantly increase

525 mortality of elk. Roads and railways have a diffusive effect on an animal survival, generating not  
526 only a direct risk of a road kill (Kramer-Schadt et al., 2004), but they also provide an access for  
527 humans elevating the risk of an animal being poached (Frair et al., 2008; Haines et al., 2012).  
528 This diffusive effect of human infrastructure is broader for mobile carnivores with large home  
529 ranges (Kramer-Schadt et al., 2004). As a consequence, road-related mortality can create  
530 localized population sinks (Nielsen et al., 2006) and alter the demographic structure of  
531 populations (Steen and Gibbs, 2004). Our results dramatically demonstrate this, with large  
532 decreases in population size and genetic diversity predicted across Sabah under all mortality  
533 scenarios. This emphasizes the critical importance of mitigating mortality risk in addition to  
534 preserving core habitats and connectivity between them.

535 Not all the development scenarios are predicted to have equally negative effects on the clouded  
536 leopard population. Some of the planned segments of highways and railroad were predicted to  
537 have negligible effect on the population connectivity. In contrast, certain segments of proposed  
538 new roads or railways would have disproportionately large negative influences on landscape  
539 connectivity of clouded leopard populations across almost entire Sabah state. Developing the  
540 new segment of railroad R6, especially when combined with upgrading existing road to highway  
541 HU4, significantly decreases the connectivity in southern part of Sabah, which might begin a  
542 disintegration of the large southern core area into two separate parts (Figure S1-E).

543 Developments in one place affects strength of corridors in a much wider extent, weakening or  
544 straightening some of the connections (Figure S2-S9). This shows how important it is to  
545 evaluate potential impacts of new infrastructure in the landscape and to alter development plans  
546 to minimize ecological costs while achieving the development goals.

547 Furthermore, findings of our study demonstrate that the negative effect of roads and railways can  
548 be mitigated by targeted forest restoration efforts, however, only to very limited extents. We  
549 found very large differences in the effectiveness of forest restorations depending on where they  
550 are in the landscape. Specifically, some proposed forest restoration areas were not predicted to  
551 have any positive (or negative) effect, suggesting that conservation investment may be more  
552 efficiently deployed elsewhere. However, some of the proposed restoration areas, like CF2 and  
553 CF10 (Table 2, Figure 2 and Figure S1), substantially improved landscape connectivity, with  
554 large impacts on simulated genetic diversity. Our results show that effective forest restoration is  
555 not only a function of the size of restored areas, but their location also has a disproportionately  
556 large influence. Four out of the five restoration areas that had the highest impact on connectivity  
557 had substantially higher influence than predicted by their size alone and CF2 had more than 2.5  
558 times higher influence than expected based on its size alone (Figure S16). The large impact  
559 resulting from the restoration of the forest connectivity area CF2 is because it links two large  
560 core areas around Trus Madi and Tankulap-Piningah Forest Reserves, enabling connectivity in  
561 regions which previously were fragmented. This shows that evaluating and optimizing  
562 alternative restoration scenarios is critical to maximize the effectiveness of conservation action.  
563 The finding that forest restoration could effectively increase population connectivity of clouded  
564 leopards are consistent with Hearn et al., (2018) who concluded that riparian corridors were cost  
565 effective measures to increase connectivity, and reforestation of inundated/flooded plantation  
566 areas greatly increased connectivity whilst minimising the financial impact to the plantation  
567 industry.

568 However, results of our scenarios that included mortality risk demonstrated that habitat  
569 restoration could be ineffective if mortality risks associated with development are not accounted

570 for and reduced. Clouded leopard population size and generic diversity dropped dramatically  
571 when we simulated spatially heterogeneous mortality risk associated with developments, even  
572 when development was accompanied by forest restoration. While the difference in population  
573 size and heterozygosity was significant for the development and restoration scenario as  
574 compared to the development strategy without restoration, it was a relatively small benefit  
575 compared to the massive effects of development on the population when development produces  
576 elevated mortality risk in addition to impacting connectivity alone.

577 We would like to stress the importance of considering mortality effects in decision making  
578 regarding spatial planning of landscape development and siting highways and railways. We  
579 found that realignment of the most impactful segments of highways and railroads based on  
580 resistance to movement, without accounting for mortality risk, might be misleading. For  
581 example, our road and railway realignment without including mortality showed significant  
582 improvement in population connectivity, population size and genetic diversity. However, when  
583 we simulated elevated mortality risk associated with the realignment it appeared that not only did  
584 the proposed realignment not prove to be better, but at one mortality threshold it significantly  
585 decreased population size compared to the original development and restoration plan.

#### 586 *Scope and limitations*

587 Our analysis is based on the only existing dataset on Sunda clouded leopard movement and the  
588 only existing empirically based model of landscape resistance for the species (Hearn et al.,  
589 2018). This data set, however, being derived from a relatively small number of individuals in a  
590 single landscape in lowland Sabah, may not represent the full scope of clouded leopard  
591 movement behaviour in relation to environmental features. For example, the movement data  
592 were collected in an area with no major roads which made it impossible to empirically estimate

593 the resistance of roads to clouded leopard movement; hence we had to assess it based on expert  
594 knowledge. Future research, therefore, should focus on gathering more extensive clouded  
595 leopard movement data from a wider geographical extent.

596 In addition, our development scenarios only included the specific planned actions in the Sabah  
597 Structure Plan 2033. However, construction of one road usually leads to a fishbone effect, with  
598 additional roads built off of the main road. These roads will also facilitate human disturbance,  
599 poaching and land conversion (e.g., Cushman et al., 2017) These are not incorporated into the  
600 model, which was intended to provide a focused evaluation of the specific foreseen actions in the  
601 official Sabah Structure Plan. Thus, our predictions should be seen as a highly conservative  
602 bottom end of negative impacts and future research should strive to integrate all these factors to  
603 provide a fuller accounting of ecological impacts of alternative development scenarios.

604 Our methodological framework provided an example of optimizing placement of roads  
605 connecting given locations. For this purpose we used least cost path analysis to minimize  
606 ecological cost (e.g., intersection with cumulative habitat suitability) and engineering feasibility  
607 (e.g., topographical slope). Topographical slope is a critical factor considered by engineers in  
608 designing and routing roads and is an obvious factor to consider in such realignment analysis.

609 However, one should remember that decision of developing a road network is often grounded in  
610 complex economic and socio-political factors. We did not have knowledge and necessary data to  
611 incorporate these factors in our road optimization model. The example provided in this paper is  
612 relatively simple and not tied to socio-economic factors affecting decision-making in Sabah.

613 Nevertheless, the analysis provides useful suggestions for how road impacts could be minimized  
614 and illustrates a methodology that can be extended to incorporate any relevant spatial layer into

615 road resistant surface, (e.g., political considerations, economic factors, social attitudes, geology,  
616 real costs of road construction, etc.).

617 There is little information about road resistance and effects of landscape structure and change on  
618 mortality risk for clouded leopard. As a result we used sensitivity analysis to evaluate the effects  
619 of this uncertainty. We found that across a realistic range of road resistance levels the results did  
620 not markedly change, indicating relatively high certainty in the implications of our road  
621 connectivity analysis. In contrast, however, there were immense differences in the effects of  
622 different levels of spatial mortality risk. Given that mortality risk had huge impacts on predicted  
623 population size and genetic diversity, improving understanding of how landscape features and  
624 landscape change affect risk of mortality is critical.

#### 625 *Wider implications*

626 The GIS-based analytical framework we described in this paper was built to integrate  
627 connectivity modelling and landscape genetics tools to provide decision makers in Sabah  
628 information to optimize the trade-off between economic development and biodiversity  
629 conservation. Although our analyses were based on the Sabah Structural Development Plan and  
630 its impact on Sunda clouded leopard, the presented methodological workflow and tools can be  
631 applied to almost any area and species.

632 The most important point to keep in mind when interpreting our results is that it is not a  
633 projection of what we expect the actual clouded leopard population response will be if any of the  
634 investigated development scenarios were actually implemented. Rather, it is a quantitative  
635 assessment of the differences in expected impact between scenarios, assuming all other factors  
636 stay the same, and omitting factors not included in the model. The future of Sabah, as

637 everywhere in the developing world, includes a complex of interacting factors affecting land use  
638 change and human exploitation of wildlife. Our modeling approach provides a framework that is  
639 highly flexible and powerful to include multiple and interacting factors. However, to do this  
640 realistically requires knowledge of how landscapes will change in the future, how those changes  
641 will affect human behaviours and attitudes, and how these in conjunction will affect wildlife  
642 habitat and wildlife populations. In this paper we implemented analysis of 58 landscape change  
643 scenarios that are officially described in the Sabah Structural Plan 2033, which gives our analysis  
644 a foundation in plausible reality. However, the actual development that Sabah will follow will  
645 most probably dramatically differ from that aspirational and general plan. As presented here, our  
646 results show the effectiveness of the tools and their utility for comparing the impacts of  
647 alternative scenarios on connectivity, population size and genetic diversity. The specific findings  
648 are useful in identifying the locations of development and restoration that would be most  
649 impactful among those analysed. However, for this approach to be directly relevant to  
650 conservation in Sabah in the future it should be integrated formally in the official planning  
651 process, where actual and realistic development plans are evaluated, both in terms of their  
652 incremental impact on connectivity but also on poaching risk and in affecting likely future  
653 patterns of landscape change (e.g. Cushman et. al 2017).

## 654 **5. Conclusions**

655 The approach we presented here could be usefully applied to a wide range of systems and  
656 species. This study focused on balancing Sunda clouded leopard conservation with development  
657 goals in Sabah. We developed an integrated modelling framework to evaluate the relative  
658 impacts of 58 different development and forest restoration scenarios, with and without mortality  
659 risk, on population connectivity, population size and genetic diversity, and illustrated a method

660 to adjust development plans to minimize negative ecological impacts. We hope that these results  
661 will be useful in guiding the Sabah government in deciding the best way to jointly conserve their  
662 precious natural heritage and achieve their economic development goals. We also hope that this  
663 example will be a step forward to achieve the broader, and critical, goal of integrating scenario  
664 optimization in conservation and development planning around the world.

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673

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859 **TABLES**

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Table 1. GIS layers used to build the resistance surface

<b>Name</b>	<b>Resolution</b>	<b>Source</b>
Forest quality and land cover 2010	50m	Gaveau et al. (2014)
Forest types	50m	Sabah Forestry Department
Land cover 2010	250m	Miettinen et al. (2012)
Canopy cover	30m	Hansen (2013)
Rivers	Vector	Sabah Forestry Department

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Table 2. Change in the variables of clouded leopard habitat suitability model for the scenarios considering new forest connectivity areas.

<b>Input layer</b>	<b>Turned into</b>
Agroforest/forest regrowth (Gaveau et al., 2014)	Logged forest (Gaveau et al., 2014)
Oilpalm plantation (Gaveau et al., 2014)	Logged forest (Gaveau et al., 2014)
Logged forest (Gaveau et al., 2014)	Remained the same
Plantation regrowth (Miettinen et al., 2012)	0
Lowland mosaic (Miettinen et al., 2012)	0
Lowland open (Miettinen et al., 2012)	0
Lowland freshwater swamp forest (Miettinen et al., 2012)	Remained the same
Lowland mixed dipt (Miettinen et al., 2012)	Remained the same
Lowland mixed dipt limestone (Miettinen et al., 2012)	Remained the same
Forest cover (Hansen, 2013) < 0.75	0.75
Rivers	Remained the same

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Table 3. Number of clouded leopard source locations in each forest restoration area (CF – connected forest) in the base scenario (current state) and the restoration scenario.

Restoration area	Size [km <sup>2</sup> ]	Number of source locations	
		Base scenario	Restoration scenario
CF1	440	5	5
CF2	362	7	8
CF3	1270	8	10
CF4	20	0	0
CF5	83	0	1
CF6	136	0	1
CF7	59	0	1
CF8	230	1	3
CF9	38	0	1
CF10	1413	22	23
CF11	60	1	1
CF12	71	1	1
CF13	281	3	3
CF14	41	1	1
CF15	177	3	4
CF16	41	1	2
CF17	65	1	1

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Table 4. Difference in kernel sum, percentage of landscape, largest patch index and correlation length between each development scenario and the base scenario (CF – connected forest, HN – highway new, HU – highway upgraded, R – railroad; the most influential scenarios are in bold).

Scenario	Kernel sum [%]	Percentage of landscape [%]	Largest Patch Index [%]	Correlation length [%]	
New forest connectivity areas	CF1	0.40	0.35	0.37	0.23
	<b>CF2</b>	<b>2.43</b>	<b>0.78</b>	<b>0.81</b>	<b>0.13</b>
	CF3	0.80	0.22	0.22	0.04
	CF4	0.00	0.00	0.00	0.00
	CF5	0.00	0.00	0.00	0.00
	CF6	0.03	0.00	0.00	0.00
	CF7	0.01	0.00	0.00	0.00
	CF8	0.03	0.06	0.00	-0.05
	CF9	0.24	0.03	0.03	-0.02
	<b>CF10</b>	<b>3.45</b>	<b>0.72</b>	<b>0.74</b>	<b>0.02</b>
	CF11	0.02	0.00	0.00	0.00
	CF12	0.81	0.03	0.04	-0.02
	CF13	0.96	0.00	0.00	0.00
	CF14	0.02	0.00	0.00	0.00
	CF15	0.12	0.05	0.05	0.01
	CF16	0.00	0.00	0.00	0.00
	CF17	0.03	0.02	0.00	-0.02
New Highways	HN1	0.00	0.00	0.00	0.00
	<b>HN2</b>	<b>-3.68</b>	<b>-0.65</b>	<b>-0.67</b>	<b>0.00</b>
	HN3	-1.88	0.00	0.00	0.00
	HN4	0.00	0.00	0.00	0.00
	<b>HN5</b>	<b>-2.31</b>	<b>-0.47</b>	<b>-0.49</b>	<b>-0.27</b>
	HN6	-0.12	0.00	0.00	0.00
	HN7	0.00	0.00	0.00	0.00
	HN8	0.00	0.00	0.00	0.00
	HN9	-0.01	0.00	0.00	0.00
	HN10	-0.11	-0.13	-0.14	-0.05
	HN11	-0.01	-0.02	-0.02	0.00
	HN12	-0.05	-0.01	-0.02	-0.01
	HN13	-1.21	-0.24	-0.25	-0.09
	HN14	-0.77	-0.34	-0.35	0.10
	HN15	-1.80	-0.28	-0.29	0.15

	<b>HN16</b>	<b>-2.44</b>	<b>-0.52</b>	<b>-0.54</b>	<b>0.46</b>
<b>Roads upgraded to highway</b>	HU1	0.00	0.00	0.00	0.00
	HU2	0.00	0.00	0.00	0.00
	HU3	-0.01	-0.02	-0.02	-0.02
	<b>HU4</b>	<b>-3.87</b>	<b>-0.17</b>	<b>-0.17</b>	<b>-0.02</b>
	HU5	0.00	0.00	0.00	0.00
	HU6	0.00	0.00	0.00	0.00
	HU7	0.00	0.00	0.00	0.00
	HU	0.00	0.00	0.00	0.00
	HU9	-0.40	-0.51	-0.53	-0.05
	HU10	-1.32	-0.06	-0.06	0.03
	HU11	-0.02	0.00	0.00	0.00
	HU12	0.00	0.00	0.00	0.00
	HU13	-0.81	-0.29	-0.30	-0.13
	HU14	-0.90	-0.25	-0.26	0.02
	HU15	-0.19	-0.08	-0.08	0.02
<b>Railroads</b>	R1	0.00	0.00	0.00	0.00
	R2	-0.07	-0.06	-0.06	-0.05
	R3	0.00	0.00	0.00	0.00
	R4	-0.02	-0.01	-0.01	0.00
	R5	-0.44	-0.28	-0.29	0.20
	<b>R6</b>	<b>-4.58</b>	<b>-0.20</b>	<b>-0.21</b>	<b>0.02</b>
	R7	-0.05	-0.05	-0.05	-0.05
	R8	0.00	0.00	0.00	0.00
	R9	-0.20	-0.09	-0.09	0.02
	R10	0.00	0.00	0.00	0.00

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876 Table 5. Difference in kernel sum, percentage of landscape, largest patch index and correlation length between each  
 877 of the development strategies or alternative segments of roads and railroads, and the base scenario (HN – highway  
 878 new, HU – highway upgraded, R – railroad; in bold are the values from before the realignment of the roads and  
 879 railroads).

Strategy/scenario	Kernel sum [%]	Percentage of landscape [%]	Largest Patch Index [%]	Correlation length [%]
Development + restoration	-16.55	-2.91	-3.11	-0.68
Restoration	9.38	2.27	2.26	0.06
Development	-22.92	-5.53	-5.73	-0.64
Alternative	-13.63	-3.06	-3.25	-0.99
HN2 alternative	-3.29/ <b>-3.68</b>	-0.82/ <b>-0.65</b>	-0.85/ <b>-0.67</b>	0.01/ <b>0</b>
HN5 alternative	-1.73/ <b>-2.31</b>	-0.44/ <b>-0.47</b>	-0.46/ <b>-0.49</b>	-0.23/ <b>-0.27</b>
HN16 alternative	-2.42/ <b>-2.44</b>	-0.55/ <b>-0.52</b>	-0.57/ <b>-0.54</b>	0.49/ <b>0.46</b>
HU4 alternative	-5.22/ <b>-3.87</b>	-0.16/ <b>-0.17</b>	-0.16/ <b>-0.17</b>	-0.01/ <b>-0.02</b>
R6 alternative	-4.25/ <b>-4.58</b>	-0.28/ <b>-0.20</b>	-0.29/ <b>-0.21</b>	0.19/ <b>0.02</b>

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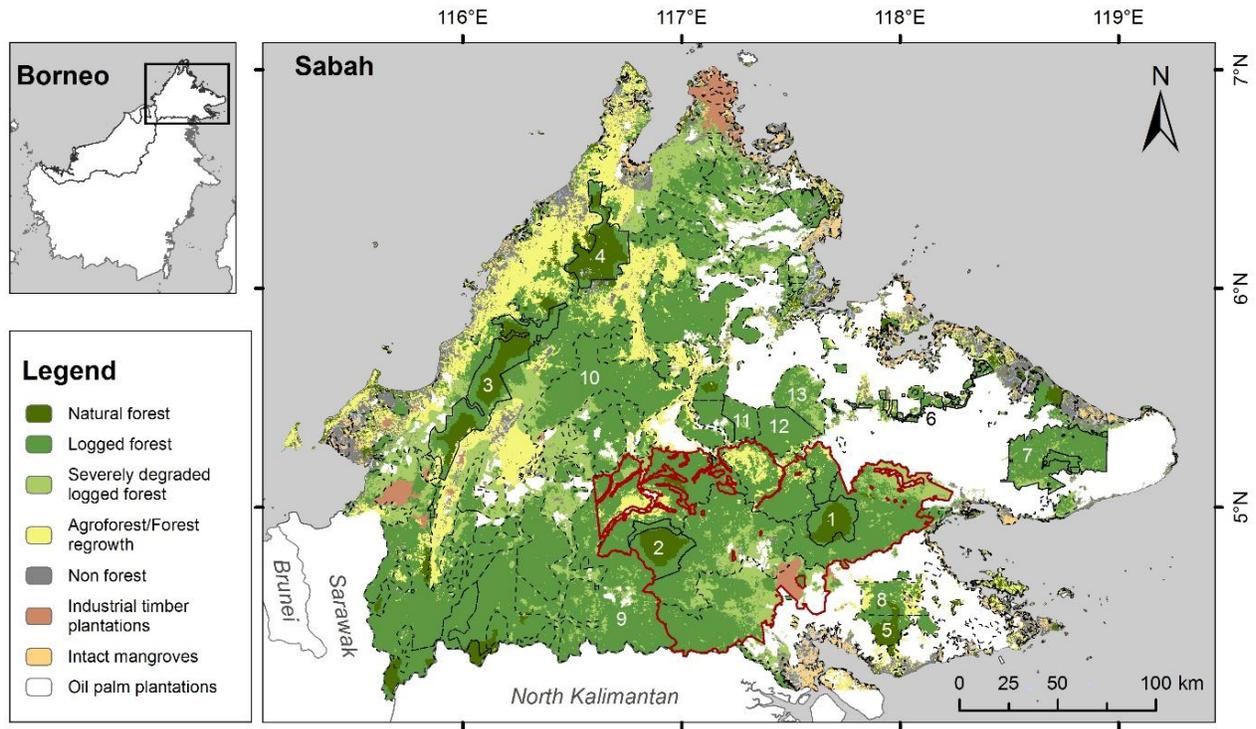
Table 6. Results of Tukey HSD test comparing differences in clouded leopard population size after 200 generations between development strategies without mortality and with mortality at 150% threshold.

STRATEGY	POPULATION SIZE		ALLELS		HETEROZIGOSITY	
	Difference	p	Difference	p	Difference	p
<b>NO MORTALITY</b>						
Base – Alternative	-12	0.093	-8.9	0.414	<b>0.037</b>	<b>0.010</b>
Develop & restore – Alternative	-1.7	0.996	-2.5	0.988	0.004	0.997
Restoration – Alternative	7.4	0.514	-4.5	0.901	<b>0.047</b>	<b>0.000</b>
Develop – Alternative	<b>-16.2</b>	<b>0.010</b>	-10.9	0.220	-0.017	0.506
Develop & restore – Base	10.3	0.196	6.4	0.717	<b>-0.033</b>	<b>0.026</b>
Restoration – Base	<b>19.4</b>	<b>0.001</b>	4.4	0.908	0.009	0.884
Develop – Base	-4.2	0.895	-2	0.995	<b>-0.054</b>	<b>0.000</b>
Restoration – Develop & restore	9.1	0.306	-2	0.995	<b>0.043</b>	<b>0.002</b>
Develop – Develop & restore	-14.5	<b>0.026</b>	-8.4	0.473	-0.020	0.309
Develop-Restoration	-23.6	<b>0.000</b>	-6.4	0.717	-0.064	<b>0.000</b>
<b>MORTALITY WITH THRESHOLD 150%</b>						
Base – Alternative	<b>190.3</b>	<b>0.000</b>	<b>25.2</b>	<b>0.000</b>	<b>0.268</b>	<b>0.000</b>
Develop & restore – Alternative	<b>25.5</b>	<b>0.001</b>	3.8	0.797	0.015	0.531
Develop - Alternative	5.5	0.877	7.5	0.197	<b>-0.075</b>	<b>0.000</b>
Restoration – Alternative	<b>201.6</b>	<b>0.000</b>	<b>27.2</b>	<b>0.000</b>	<b>0.285</b>	<b>0.000</b>
Develop & restore – Base	<b>-164.8</b>	<b>0.000</b>	<b>-21.4</b>	<b>0.000</b>	<b>-0.253</b>	<b>0.000</b>
Develop– Base	<b>-184.8</b>	<b>0.000</b>	<b>-17.7</b>	<b>0.000</b>	<b>-0.342</b>	<b>0.000</b>
Restoration – Base	11.3	0.309	2	0.976	0.017	0.365
Develop – Develop & restore	<b>-20</b>	<b>0.010</b>	3.7	0.812	-0.089	0.000
Restoration – Develop & restore	<b>176.1</b>	<b>0.000</b>	<b>23.4</b>	<b>0.000</b>	<b>0.270</b>	<b>0.000</b>

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Restoration - Develop	<b>196.1</b>	<b>0.000</b>	<b>19.7</b>	<b>0.000</b>	<b>0.360</b>	<b>0.000</b>
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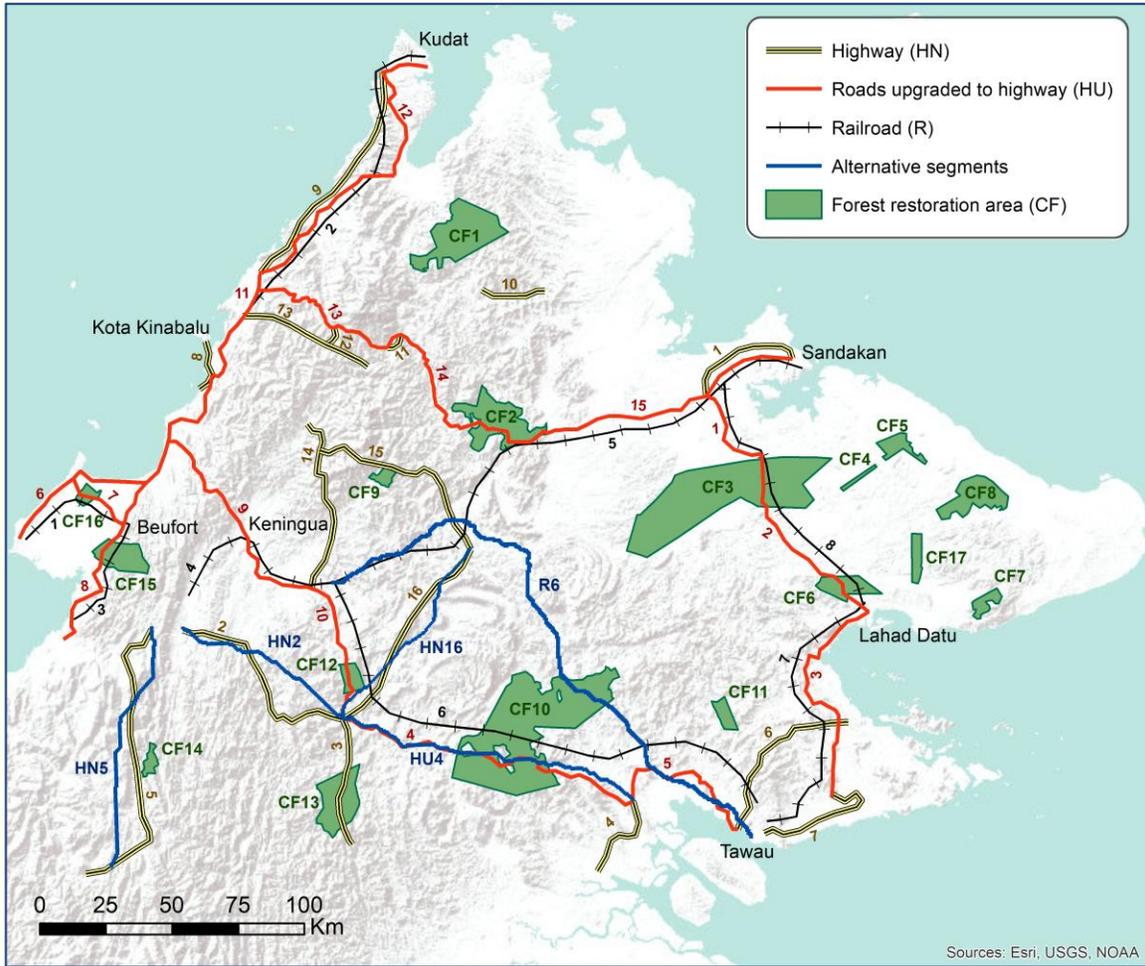
885 **FIGURES**  
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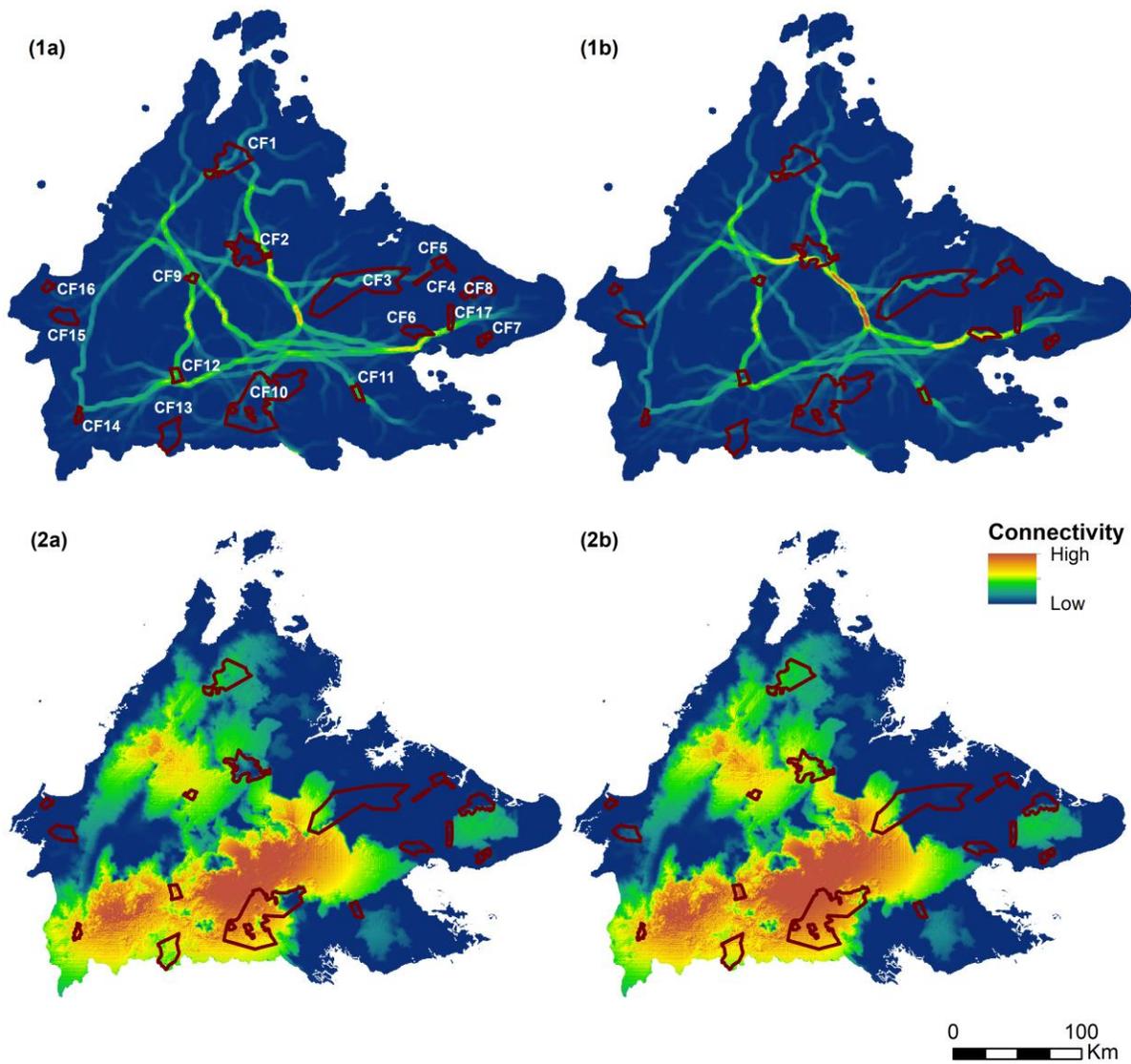
888 Figure 1. Map of the Malaysian state of Sabah, northern Borneo, showing land use in 2010 (Gaveau et al., 2014).  
889 Fully protected forest areas (National Parks, Wildlife Reserves and Conservation Areas) are outlined in solid black  
890 lines and include: (1) Danum Valley and (2) Maliau Basin Conservation Areas, (3) Crocker Range, (4) Kinabalu and  
891 (5) Tawau Hills Parks, and (6) Lower Kinabatangan and (7) Tabin Wildlife Reserves. Commercial Forest Reserves  
892 are outlined in dashed black lines; key areas include (8) Ulu Kalumpang, (9) Sapulut, (10) Trus Madi, (11)  
893 Tankulap-Piningah, (12) Deramakot and (13) Segaliud Lokan Forest Reserves. The Yayasan Sabah Forest  
894 Management Area is outlined in dark red. Polygons represent the state owned, Permanent Forest Reserve system.

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Figure 2. Development and restoration scenarios (with a reference number given to each segment) foreseen in the Sabah Structure Plan for 2033 and the alternative realignment of the most disruptive segments of proposed new highways and railroad (blue lines). Number assigned to a road/railway segment and a restoration area together with the abbreviation included in the legend (HN, HU, R, CF) relates directly to the Table 4 listing all the scenarios.



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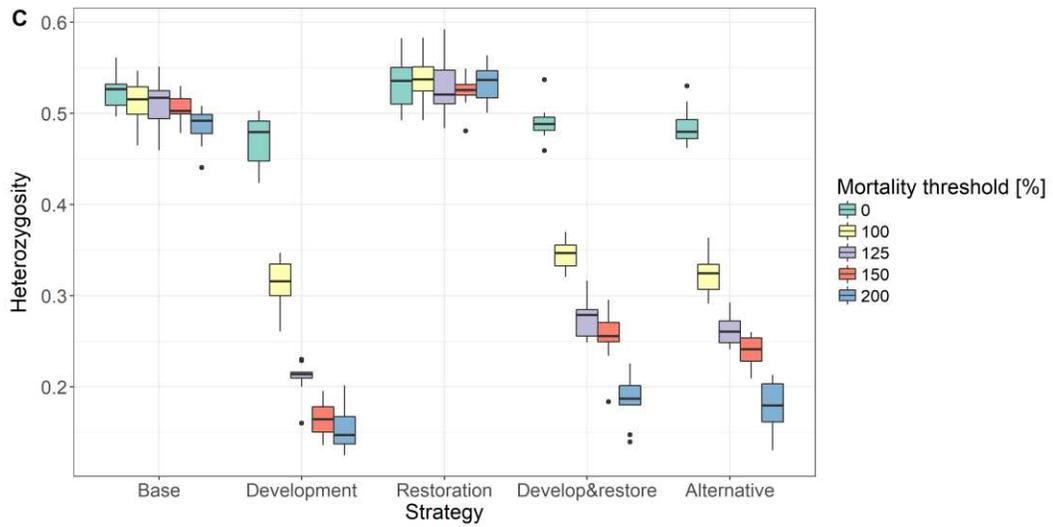
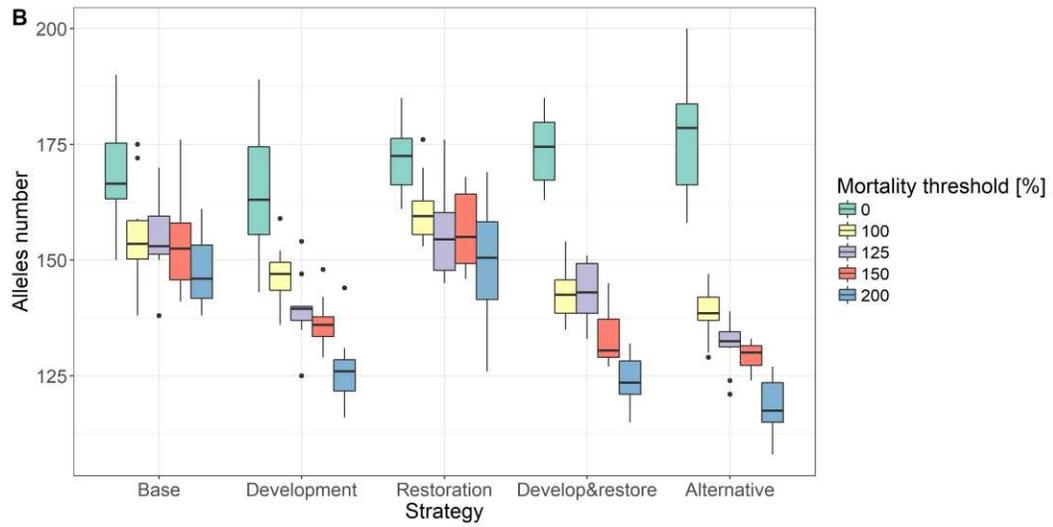
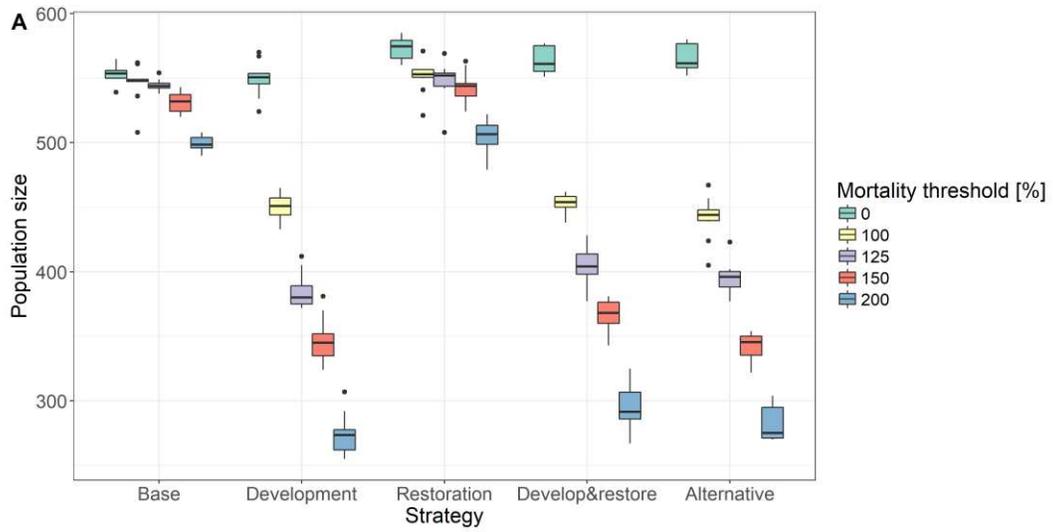
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Figure 3. Factorial least cost paths (1) and resistant kernels (2) for the base scenario (a) and scenario incorporating all forest restoration areas (b). Each forest restoration area is marked in red and its ID is given on map (1a).

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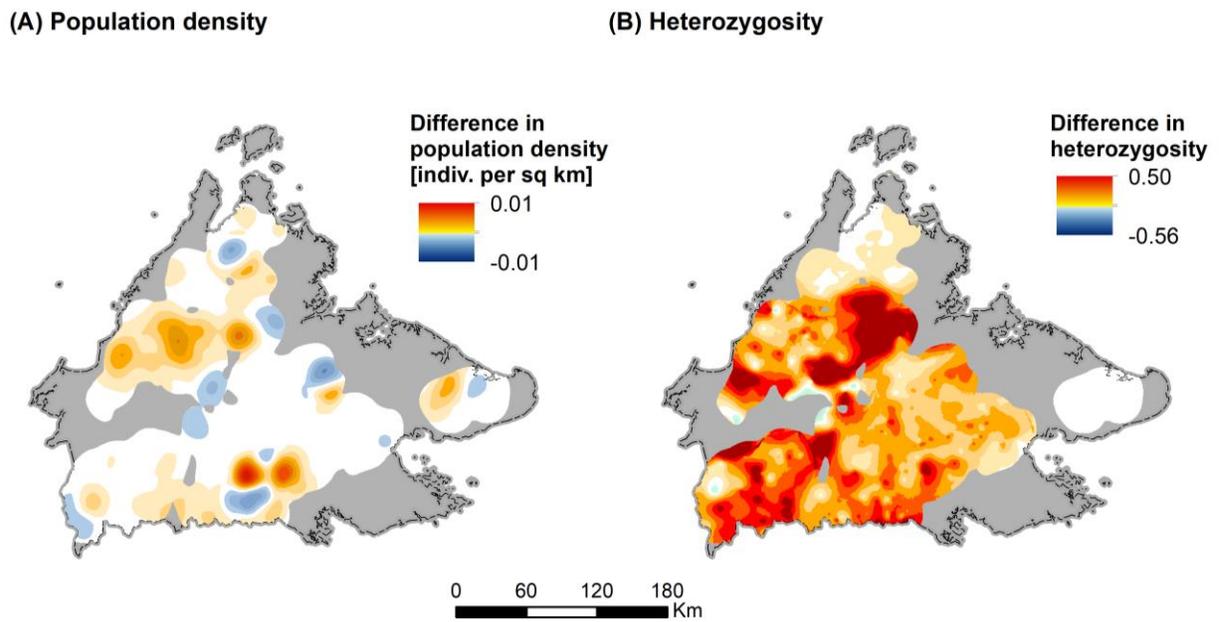
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Figure 4. Populations size, allelic richness and heterozygosity of clouded leopard population after 200 generations under different development strategies without mortality (mortality threshold = 0) and with mortality of various thresholds (100 = base mortality, 125 = base mortality x1.25, 150 = base mortality x1.5, 200 = base mortality x2)



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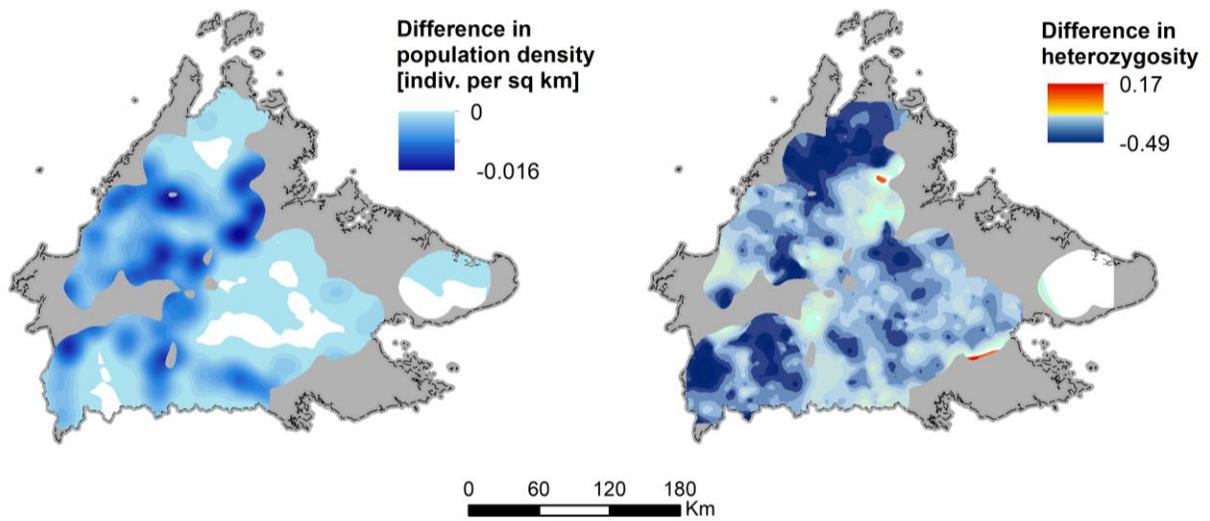
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Figure 5. Difference in clouded leopard population density and heterozygosity in 200 generations between the development & restoration and the development strategies with mortality at 150% threshold.

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(A) Population density

(B) Heterozygosity



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Figure 6. Difference in clouded leopard population density and heterozygosity in 200 generations between the development & restoration strategy with mortality at 150% threshold and without mortality.

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