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ABSTRACT

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

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

1. Introduction

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

Land use planners face a dilemma in balancing biodiversity conservation with the demands of human population growth and economic development. This is especially relevant in emerging economies, where the pressure on ecosystems and wildlife is extremely high and there may be limited legal and administrative protection of biodiversity. At the same time, many of these regions harbour the highest levels of biodiversity and endemism, which emphasises the importance of scientifically-based tools to guide land use planning to minimize impacts to biodiversity. Identifying and prioritizing areas for development, conservation, and restoration requires quantitative analysis that integrates ecological and urban planning theories (Xun et al., 2017). Conservation and land use planning have overlapping goals: conservationists are concerned with the sustainability of ecosystems and populations, while planners focus on sustainable delivery of goods and services for humans often provided by ecosystem services (Botequilha Leitão and Ahern, 2002). Balancing the preservation of biodiversity with economic development requires conservation actions that can maintain critical ecosystems functions while minimizing constraints on land development (DeFries et al., 2007). This can be achieved through efforts to optimize development and conservation strategies that maximize the conservation benefit with the least economic cost.

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

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

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

In this study we focus on Sabah, a Malaysian state in northern Borneo, which has been heavily impacted by deforestation and faces the challenge of rapid economic development and expanding urbanization, agriculture and infrastructure. Until recently, the island of Borneo was covered by one of the world's largest undisturbed blocks of tropical forest, supporting extremely high endemism and biodiversity (Woodruff, 2010). However, over the past several decades the island has had the world's highest deforestation rate. Forest cover on Borneo declined by 33.5% between 1973 and 2015 (Gaveau et al., 2016), due to deforestation for timber extraction and conversion to agriculture driven mainly by plantation industries (especially oil palm *Elaeis guineensis*, Cushman et al. 2017). The deforestation rate varies by region (Bryan et al., 2013), with the highest forest loss estimated in the Indonesian provinces of Kalimantan and the Malaysian states of Sabah and Sarawak (35.6%, 31.9% and 25.9% respectively; Gaveau et al. 2016).

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

Our goal in this study was to demonstrate the use of a GIS-based analytical framework that maps and quantifies the impact of future development and restoration scenarios on landscape connectivity, population distribution, density and genetic diversity of the Sunda clouded leopard across Sabah. We evaluated the impacts of 58 alternative development and ecological restoration scenarios described in the Structure Plan and the effects of spatially heterogenous mortality risk. Furthermore, we used spatial optimization to improve the scenarios we found had the largest negative impacts on clouded leopard population connectivity.

2. Methods

2.1.Study area

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

Nevertheless, the state of Sabah has committed to protecting its remaining forest, and increasing the sustainable utilization of forest products. The state contains extensive areas of highly disturbed, regenerating forests. Protected primary forest exists in relatively small patches (280–1399 km^2), including the Danum Valley, Maliau Basin and Imbak Canyon Conservation Areas, and the Crocker Range, Kinabalu and Tawau Hills Parks (Figure 1), but the vast majority of remaining forest has been previously logged (Reynolds et al., 2011). The majority of remaining forest belongs to the state-owned Permanent Forest Reserve, which includes State Parks, Wildlife Reserves as well as commercial Forest Reserves (Reynolds et al., 2011).

2.2. Development and restoration scenarios

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

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

Resistance surfaces

The base resistance surface for connectivity modelling was created by inverting and rescaling a clouded leopard path-selection function (e.g., Cushman and Lewis, 2010) model developed by Hearn et al. (2018) based on Sunda clouded leopard GPS telemetry data. The path-selection function was developed using conditional logistic regression to predict clouded leopard path selection in the Lower Kinabatangan landscape based on land cover, forest types, canopy cover, forest quality and river network (Table 1; Hearn et al., 2018) and showed that clouded leopard movement choices positively associated with high-canopy cover forest, and that plantation habitats with low canopy cover resist movement. This path-selection function model was extrapolated to the full extent of Sabah by Hearn et al., (2019). The final variables of the path-selection model are listed in Table 2.

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

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

Source points

Hearn et al. (2017) estimated a population of approximately 750 clouded leopards in the state of Sabah. Therefore, to represent the spatial pattern of clouded leopard resource use, we located 750 points in the study area, probabilistically with density and distribution reflecting the pattern of habitat suitability of our path-selection function (Hearn et al., 2018). For the17 forest restoration scenarios (potentially new suitable environments for clouded leopard), we generated additional occurrences inside the restoration areas. This was achieved by calculating the ratio of mean suitability within that restoration polygon in the base scenario and the restoration scenario, and dividing the number of source points in that polygon by that ratio. The result was an increase in source points proportional to the net increase in total suitability in that restoration polygon (Table 3).

Cumulative resistant kernels

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

Fragmentation analysis

The cumulative resistant kernels layers for the different scenarios were compared in several ways. First, we calculated the difference in the cumulative kernel surface between the base scenario and every other scenario, since differences between cumulative kernel surface summed across all pixels in the landscape reflect the total change in connectivity between the two connectivity maps. Additionally, we created a binary layer, by reclassifying the cumulative resistant kernel surfaces, giving all pixels lower or equal to 10 a value of 0, and pixels higher than 10, value 1. The choice of value 10 as a threshold to define the binary layer was based on the median value of the cumulative resistant kernels (Table S1). This creates a binary layer with areas of medium to high connectivity classified as 1. We calculated several FRAGSTATS metrics (McGarigal et al., 2012) to investigate the effect of the development and restoration scenarios on the extent, pattern and fragmentation of connectivity, including largest patch index (LPI), percent of landscape (PLAND) and correlation length (GYRATE_AM). LPI is the percentage of the landscape covered by the largest single patch of connected habitat, PLAND is the extent of the landscape covered by connected habitat, and GYRATE_AM is the expected distance from a random location in connected habitat to the edge of connected habitat moving in a straight line in a random direction. These landscape metrics were chosen since they have frequently been used in assessments of connectivity (e.g. Wasserman et al. 2012, Cushman et al. 2016) and have been shown to be highly related to genetic differentiation (Cushman et al., 2013b). For each scenario we calculated the difference in these metrics between that scenario and the base scenario. Based on the results of the difference in the sum of the cumulative kernel surface and landscape metrics we identified the most influential development and restoration scenarios – those which significantly decreased or increased connectivity in the study area.

Least cost path analyses

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

Alternative scenarios

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

Comparison of the development and restoration strategies

Each of the alternative road and railway segments was overlaid onto the base resistance surface and we recalculated cumulative resistant kernels for each of the alternative scenarios. Additionally, to compare the total change in connectivity we also calculated cumulative resistant kernels for four different development and restoration strategies: (1) ‘development with restoration’ - all proposed developments and restoration laid out in the Sabah Structure Plan are applied, including new roads and railways as well as the new forest connectivity areas, (2) ‘development strategy’, in which the development plan is applied by including only the planned new and upgraded highways and railroads , (3) ‘restoration strategy’ – plan accounting only for restoration of the 17 forest connectivity areas, (4) ‘alternative strategy’, which includes restoration of forest connectivity areas as well as development of all new railroads and highways, but the most disruptive segments are realigned to minimalize the total ecological cost defined as impact on the landscape connectivity and clouded leopard population dynamics. For each of the alternative scenarios and the four strategies we then calculated a sum of kernel values and the three previously mentioned landscape metrics (largest patch index, percentage of landscape and correlation length).

Simulated population dynamics

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

We used standard simulation parameters widely used in landscape genetics simulation modelling (e.g., Cushman and Landguth, 2010; Landguth et al., 2010b). We stipulated the population to have 30 loci, with 10 alleles per locus, which were randomly assigned among individuals. The mutation rate was parametrized to 0.0005. We used an inverse square mating and dispersal probability function, with the maximum cost-weighted dispersal distance of 125km reflecting the estimated maximum dispersal ability of clouded leopard *(*Hearn et al.*,* 2019; Macdonald et al., 2018). Reproduction was sexual with non-overlapping generations. The number of offspring was based on a Poisson probability draw of mean equal 2. We simulated 10 Monte Carlo replicates of each scenario. We simulated gene flow for 200 non-overlapping generations as previous studies have shown that this is sufficient time to ensure spatial genetic equilibrium (Landguth et al., 2010b, 2010a).

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

Mortality

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

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

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

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

Sensitivity analysis of road resistance

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

3. Results

Landscape connectivity of the base scenario

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

Comparison of development and restoration scenarios

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

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

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

Comparison of alternative segments and development strategies

Figure 2 shows a map of planned developments for Sabah along with proposed alternative scenarios for the 5 most disruptive highway and railroad segments (HN2, HN5, HN16, HU4, R6; based on Table 2). Based on sum of kernel values, realignment of the most disruptive segments of highways and railroads, with the exception of HU4, decreased the negative effect of these segments on connectivity (Table4). The negative effect of realigning HU4 arises because this segment already exists as a minor road, and construction of an additional segment of highway, even if possibly less disruptive in itself than upgrading the existing road, when combined with the existing road has a larger negative impact. The strongest improvement in the connectivity, based on sum of kernel values and landscape metrics, was recorded for realigned segment of highway HN5 (Table4). The realignment increased the sum of kernel values between 0.02 and 0.58 (the average increase of 0.33).

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

Population dynamics without mortality

The simulated mean population size of clouded leopard in Sabah after 200 generations dropped from the initial 750-760 to 575 for the restoration strategy without spatial mortality risk and about 550 for the development strategy without mortality risk (the number indicates a median of 10 Monte Carlo replicates, Figure 4). Results of ANOVA and Tukey HSD test indicated a positive (mean = +19.4) and significant ($p<0.05$) difference in clouded leopard population size between the restoration strategy and the base scenario (Table 6). Furthermore, the development strategy significantly reduced mean simulated population size compared to the restoration strategy, the full Sabah Structural Plan (combining restoration and development) or the alternative strategy (including our proposed realignments), with reductions of -23.6, -14.5 and -16.2 respectively (Table 6). Looking at the spatial variation in population density between the four scenarios and the base scenario, we found that the development strategy has a universally negative effect, with highest impacts in the eastern part of Lahad Datu District and Beluran District, as well as in the West Coast Division and Keningau District (Figure S10).

The differences between scenarios in allele richness, although resulting in lower numbers for the development scenarios and higher for the restoration scenarios, were not statistically significant (Table 6). Comparing heterozygosity across scenarios, the differences are more striking and most of them are statistically significant (Table 6). In particular, heterozygosity significantly increased with the restoration strategy compared to the development, development with restoration and alternative strategy (on average by 0.064, 0.047 and 0.047 respectively). Furthermore, both development with restoration and alternative scenarios significantly decreased heterozygosity compared to the base scenario (Table 6). Looking at the spatial differences in allelic richness and heterozygosity across scenarios, we can observe some important differences (Figure S10 and Figure S11). In general, if the future actions focus only on forest restoration, both allelic richness and heterozygosity will increase across Sabah. The alternative alignment scenario was the second-best strategy, and it increased heterozygosity in a large portion of the state. On the contrary, the scenario where development occurred without forest restoration decreased clouded leopard allelic richness and heterozygosity across Sabah.

Population dynamics with mortality

The clouded leopard population size and genetic diversity measured by the level of heterozygosity and allelic richness after 200 generations greatly varied when different thresholds of mortality were applied (Figure 4). Overall, including spatially varying mortality risk caused dramatic declines in population size and genetic diversity for all scenarios (Figure S13), with large decreases in effect at higher levels of mortality risk. A statistically significant drop in population size was observed across all scenarios, except the base scenario, even with the lowest mortality threshold (Figure 4, Table S3). At the lowest level of mortality risk the simulation predicted the base scenario (current landscape condition) to result in declines in clouded leopard population size from current 750 to 500, allelic richness from 170 (base scenario after 200 generations) to 145 and heterozygosity from 0.53 (base scenario after 200 generations) to 0.48 (Figure 4, Table S3).

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

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

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

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

Sensitivity analysis of roads' resistance

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

4. Discussion

In this paper we integrated individual-based, spatially explicit population, genetic and connectivity modelling to evaluate habitat extent, population size, population connectivity and genetic diversity of Sunda clouded leopard under a range of realistic development and conservation scenarios and attempted to optimize alternative development plans to minimize impacts on Sunda clouded leopards across the Malaysian state of Sabah in Borneo. This study is the first to combine these methods from landscape ecology and landscape genetics to evaluate effects of alternative development and conservation scenarios and to test the impact of mortality imposed by landscape features, such as road kill and risk of poaching. In the past, this kind of integration was difficult due to the challenges of characterizing the ecology and behaviour of the target species (Fu et al., 2010) and limited development of spatial modelling tools to quantitatively compare scenarios.

Comparison with previous studies

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

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

Gagné et al. (2015) concluded that ecological guidelines are usually not considered in land use planning due to limitations in their practicality and feasibility. Most guidelines require species-specific information which is often scarce at the scales required for planning. Collection of such data is costly and time-consuming, and in most planning offices the resources allocated to the acquisition of biodiversity data are insufficient (Botequilha Leitão and Ahern, 2002; Gagné et al., 2015; Miller et al., 2009). As a result, lack of information is often a decisive argument for not attending to biodiversity impact analysis (Botequilha Leitão and Ahern, 2002). Furthermore, according to review of Gagné et al. (2015), it is difficult for planners, who often lack the ecological expertise, to translate biological knowledge into specific planning actions. Finally, guidelines are often presented in an unintegrated manner, lacking clear protocols which limits their usability. This study represents an elaboration and extension of this line of work in that for the first time we have produced a comprehensive model-based framework to quantitatively compare scenarios of alternative landscape change in terms of their potential impacts on habitat connectivity, population size and genetic diversity of a focal species.

Significance for clouded leopard conservation

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

Most importantly, however, our findings strongly indicate that development of infrastructure, like highways and railroads, is likely to have large negative impacts on clouded leopard populations (23% drop in connectivity), including large population declines across Sabah and extinction of some subpopulations. For example, our simulations suggest that construction of new highways and railways in Sabah (even accompanied by habitat restoration) may cause future loss of local clouded leopard population in Tawau Hills National Park. One of our most important results is that this detrimental effect of development is immensely stronger when clouded leopard mortality is considered. Including mortality effects led to population declines from 40% to 63% (for the low mortality and high mortality effects, respectively, compared to the scenario without mortality effects. Similarly, Kramer-Schadt et al. (2004) found that mortality significantly impedes dispersal probability of lynx when including road mortality and Frair et al. (2008) demonstrated that even relatively low road density significanltly increase mortality of elk. Roads and railways have a diffusive effect on an animal survival, generating not only a direct risk of a road kill (Kramer-Schadt et al., 2004), but they also provide an access for humans elevating the risk of an animal being poached (Frair et al., 2008; Haines et al., 2012). This diffusive effect of human infrastructure is broader for mobile carnivores with large home ranges (Kramer-Schadt et al., 2004). As a consequence, road-related mortality can create localized population sinks (Nielsen et al., 2006) and alter the demographic structure of populations (Steen and Gibbs, 2004). Our results dramatically demonstrate this, with large decreases in population size and genetic diversity predicted across Sabah under all mortality scenarios. This emphasizes the critical importance of mitigating mortality risk in addition to preserving core habitats and connectivity between them.

Not all the development scenarios are predicted to have equally negative effects on the clouded leopard population. Some of the planned segments of highways and railroad were predicted to have negligible effect on the population connectivity. In contrast, certain segments of proposed new roads or railways would have disproportionately large negative influences on landscape connectivity of clouded leopard populations across almost entire Sabah state. Developing the new segment of railroad R6, especially when combined with upgrading existing road to highway HU4, significantly decreases the connectivity in southern part of Sabah, which might begin a disintegration of the large southern core area into two separate parts (Figure S1-E). Developments in one place affects strength of corridors in a much wider extent, weakening or straightening some of the connections (Figure S2-S9). This shows how important it is to evaluate potential impacts of new infrastructure in the landscape and to alter development plans to minimize ecological costs while achieving the development goals.

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

However, results of our scenarios that included mortality risk demonstrated that habitat restoration could be ineffective if mortality risks associated with development are not accounted for and reduced. Clouded leopard population size and generic diversity dropped dramatically when we simulated spatially heterogeneous mortality risk associated with developments, even when development was accompanied by forest restoration. While the difference in population size and heterozygosity was significant for the development and restoration scenario as compared to the development strategy without restoration, it was a relatively small benefit compared to the massive effects of development on the population when development produces elevated mortality risk in addition to impacting connectivity alone.

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

Scope and limitations

Our analysis is based on the only existing dataset on Sunda clouded leopard movement and the only existing empirically based model of landscape resistance for the species (Hearn et al., 2018). This data set, however, being derived from a relatively small number of individuals in a single landscape in lowland Sabah, may not represent the full scope of clouded leopard movement behaviour in relation to environmental features. For example, the movement data were collected in an area with no major roads which made it impossible to empirically estimate the resistance of roads to clouded leopard movement; hence we had to assess it based on expert knowledge. Future research, therefore, should focus on gathering more extensive clouded leopard movement data from a wider geographical extent.

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

Our methodological framework provided an example of optimizing placement of roads connecting given locations. For this purpose we used least cost path analysis to minimize ecological cost (e.g., intersection with cumulative habitat suitability) and engineering feasibility (e.g., topographical slope). Topographical slope is a critical factor considered by engineers in designing and routing roads and is an obvious factor to consider in such realignment analysis. However, one should remember that decision of developing a road network is often grounded in complex economic and socio-political factors. We did not have knowledge and necessary data to incorporate these factors in our road optimization model. The example provided in this paper is relatively simple and not tied to socio-economic factors affecting decision-making in Sabah. Nevertheless, the analysis provides useful suggestions for how road impacts could be minimized and illustrates a methodology that can be extended to incorporate any relevant spatial layer into road resistant surface, (e.g., political considerations, economic factors, social attitudes, geology, real costs of road construction, etc.).

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

Wider implications

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

The most important point to keep in mind when interpreting our results is that it is not a projection of what we expect the actual clouded leopard population response will be if any of the investigated development scenarios were actually implemented. Rather, it is a quantitative assessment of the differences in expected impact between scenarios, assuming all other factors stay the same, and omitting factors not included in the model. The future of Sabah, as everywhere in the developing world, includes a complex of interacting factors affecting land use change and human exploitation of wildlife. Our modeling approach provides a framework that is highly flexible and powerful to include multiple and interacting factors. However, to do this realistically requires knowledge of how landscapes will change in the future, how those changes will affect human behaviours and attitudes, and how these in conjunction will affect wildlife habitat and wildlife populations. In this paper we implemented analysis of 58 landscape change scenarios that are officially described in the Sabah Structural Plan 2033, which gives our analysis a foundation in plausible reality. However, the actual development that Sabah will follow will most probably dramatically differ from that aspirational and general plan. As presented here, our results show the effectiveness of the tools and their utility for comparing the impacts of alternative scenarios on connectivity, population size and genetic diversity. The specific findings are useful in identifying the locations of development and restoration that would be most impactful among those analysed. However, for this approach to be directly relevant to conservation in Sabah in the future it should be integrated formally in the official planning process, where actual and realistic development plans are evaluated, both in terms of their incremental impact on connectivity but also on poaching risk and in affecting likely future patterns of landscape change (e.g. Cushman et. al 2017).

5. Conclusions

The approach we presented here could be usefully applied to a wide range of systems and species. This study focused on balancing Sunda clouded leopard conservation with development goals in Sabah. We developed an integrated modelling framework to evaluate the relative impacts of 58 different development and forest restoration scenarios, with and without mortality risk, on population connectivity, population size and genetic diversity, and illustrated a method to adjust development plans to minimize negative ecological impacts. We hope that these results will be useful in guiding the Sabah government in deciding the best way to jointly conserve their precious natural heritage and achieve their economic development goals. We also hope that this example will be a step forward to achieve the broader, and critical, goal of integrating scenario optimization in conservation and development planning around the world.

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TABLES

Table 1. GIS layers used to build the resistance surface

Name	Resolution	Source
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

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

Input layer	**Turned into**
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

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^2]**	**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

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
	CF2	**2.43**	**0.78**	**0.81**	**0.13**
	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
	CF10	**3.45**	**0.72**	**0.74**	**0.02**
	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
	HN2	**-3.68**	**-0.65**	**-0.67**	**0.00**
	HN3	-1.88	0.00	0.00	0.00
	HN4	0.00	0.00	0.00	0.00
	HN5	**-2.31**	**-0.47**	**-0.49**	**-0.27**
	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

	HN16	**-2.44**	**-0.52**	**-0.54**	**0.46**
Roads upgraded to highway	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
	HU4	**-3.87**	**-0.17**	**-0.17**	**-0.02**
	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
Railroads	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
	R6	**-4.58**	**-0.20**	**-0.21**	**0.02**
	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

Table 5. Difference in kernel sum, percentage of landscape, largest patch index and correlation length between each of the development strategies or alternative segments of roads and railroads, and the base scenario (HN – highway new, HU – highway upgraded, R – railroad; in bold are the values from before the realignment of the roads and 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/**-3.68**	-0.82/**-0.65**	-0.85/**-0.67**	0.01/**0**
HN5 alternative	-1.73/**-2.31**	-0.44/**-0.47**	-0.46/**-0.49**	-0.23/**-0.27**
HN16 alternative	-2.42/**-2.44**	-0.55/**-0.52**	-0.57/**-0.54**	0.49/**0.46**
HU4 alternative	-5.22/**-3.87**	-0.16/**-0.17**	-0.16/**-0.17**	-0.01/**-0.02**
R6 alternative	-4.25/**-4.58**	-0.28/**-0.20**	-0.29/**-0.21**	0.19/**0.02**

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
NO MORTALITY						
Base – Alternative	-12	0.093	-8.9	0.414	**0.037**	**0.010**
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	**0.047**	**0.000**
Develop – Alternative	**-16.2**	**0.010**	-10.9	0.220	-0.017	0.506
Develop & restore – Base	10.3	0.196	6.4	0.717	**-0.033**	**0.026**
Restoration – Base	**19.4**	**0.001**	4.4	0.908	0.009	0.884
Develop – Base	-4.2	0.895	-2	0.995	**-0.054**	**0.000**
Restoration – Develop & restore	9.1	0.306	-2	0.995	**0.043**	**0.002**
Develop – Develop & restore	-14.5	**0.026**	-8.4	0.473	-0.020	0.309
Develop-Restoration	-23.6	**0.000**	-6.4	0.717	-0.064	**0.000**
MORTALITY WITH THRESHOLD 150%						
Base – Alternative	**190.3**	**0.000**	**25.2**	**0.000**	**0.268**	**0.000**
Develop & restore – Alternative	**25.5**	**0.001**	3.8	0.797	0.015	0.531
Develop - Alternative	5.5	0.877	7.5	0.197	**-0.075**	**0.000**
Restoration – Alternative	**201.6**	**0.000**	**27.2**	**0.000**	**0.285**	**0.000**
Develop & restore – Base	**-164.8**	**0.000**	**-21.4**	**0.000**	**-0.253**	**0.000**
Develop– Base	**-184.8**	**0.000**	**-17.7**	**0.000**	**-0.342**	**0.000**
Restoration – Base	11.3	0.309	2	0.976	0.017	0.365
Develop – Develop & restore	**-20**	**0.010**	3.7	0.812	-0.089	0.000
Restoration – Develop & restore	**176.1**	**0.000**	**23.4**	**0.000**	**0.270**	**0.000**

Restoration - Develop	**196.1**	**0.000**	**19.7**	**0.000**	**0.360**	**0.000**

FIGURES

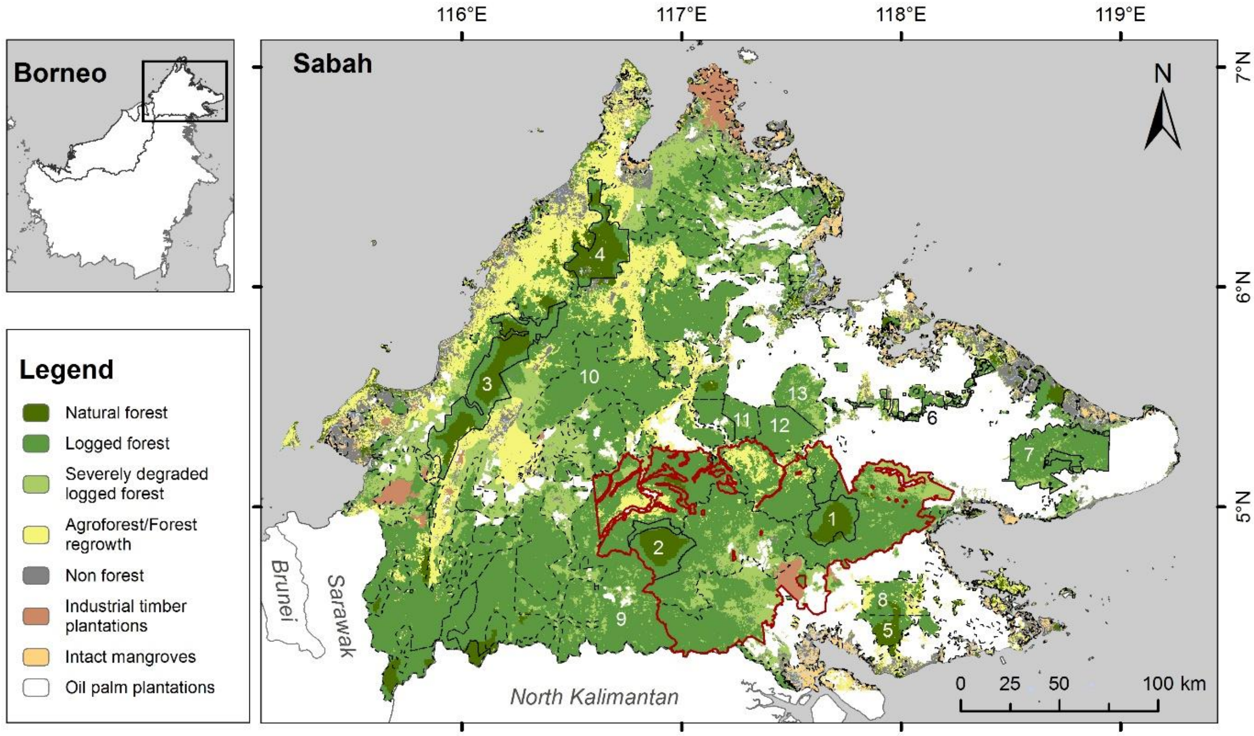

Figure 1. Map of the Malaysian state of Sabah, northern Borneo, showing land use in 2010 (Gaveau et al., 2014). Fully protected forest areas (National Parks, Wildlife Reserves and Conservation Areas) are outlined in solid black lines and include: (1) Danum Valley and (2) Maliau Basin Conservation Areas,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

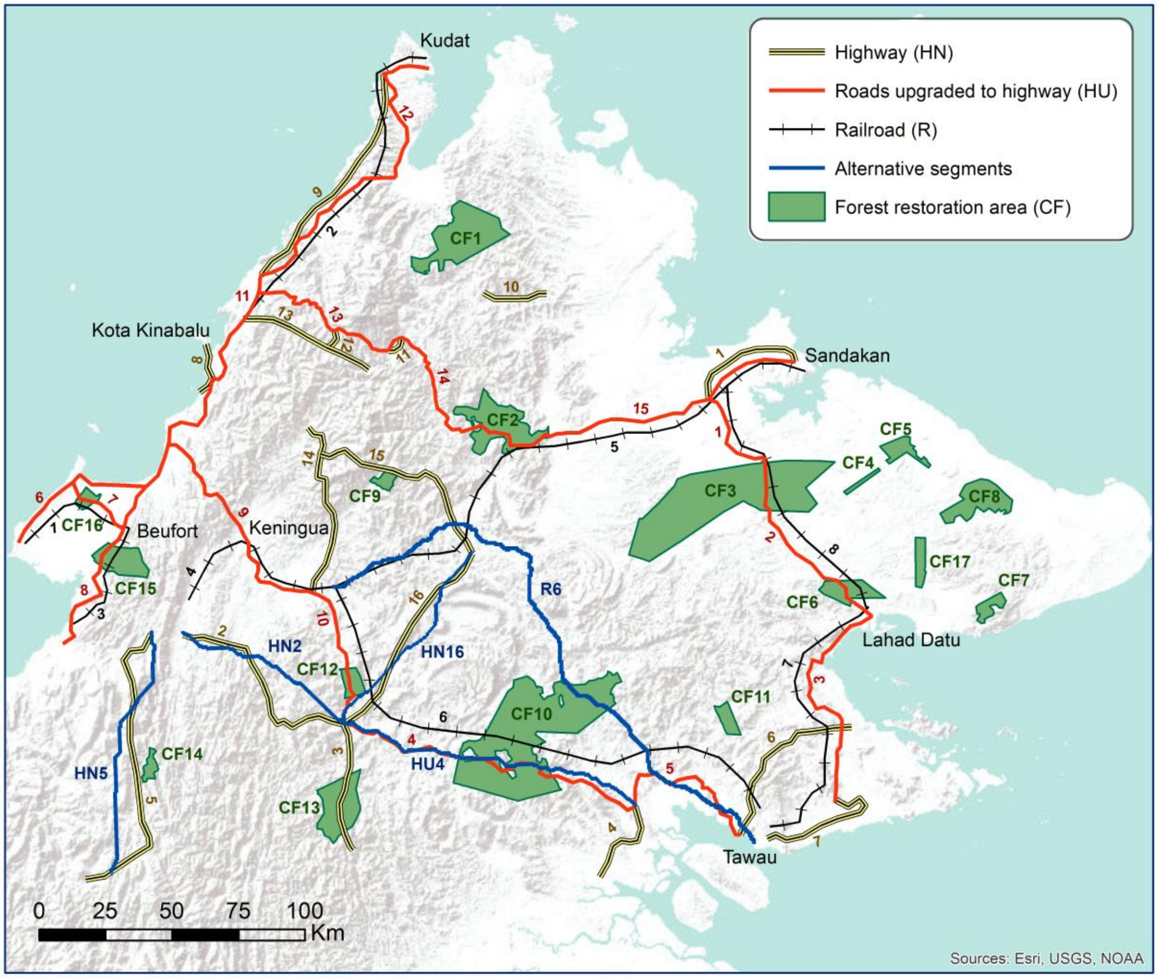

Figure 2. Development and restoration scenarios (with a reference number given to each segment) foreseen in the Sabah Structure Plan for 2033 and the alternative realignment of the most disruptive segments of proposed new highways and railroad (blue lines). Number assigned to a road/railway segment and 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.

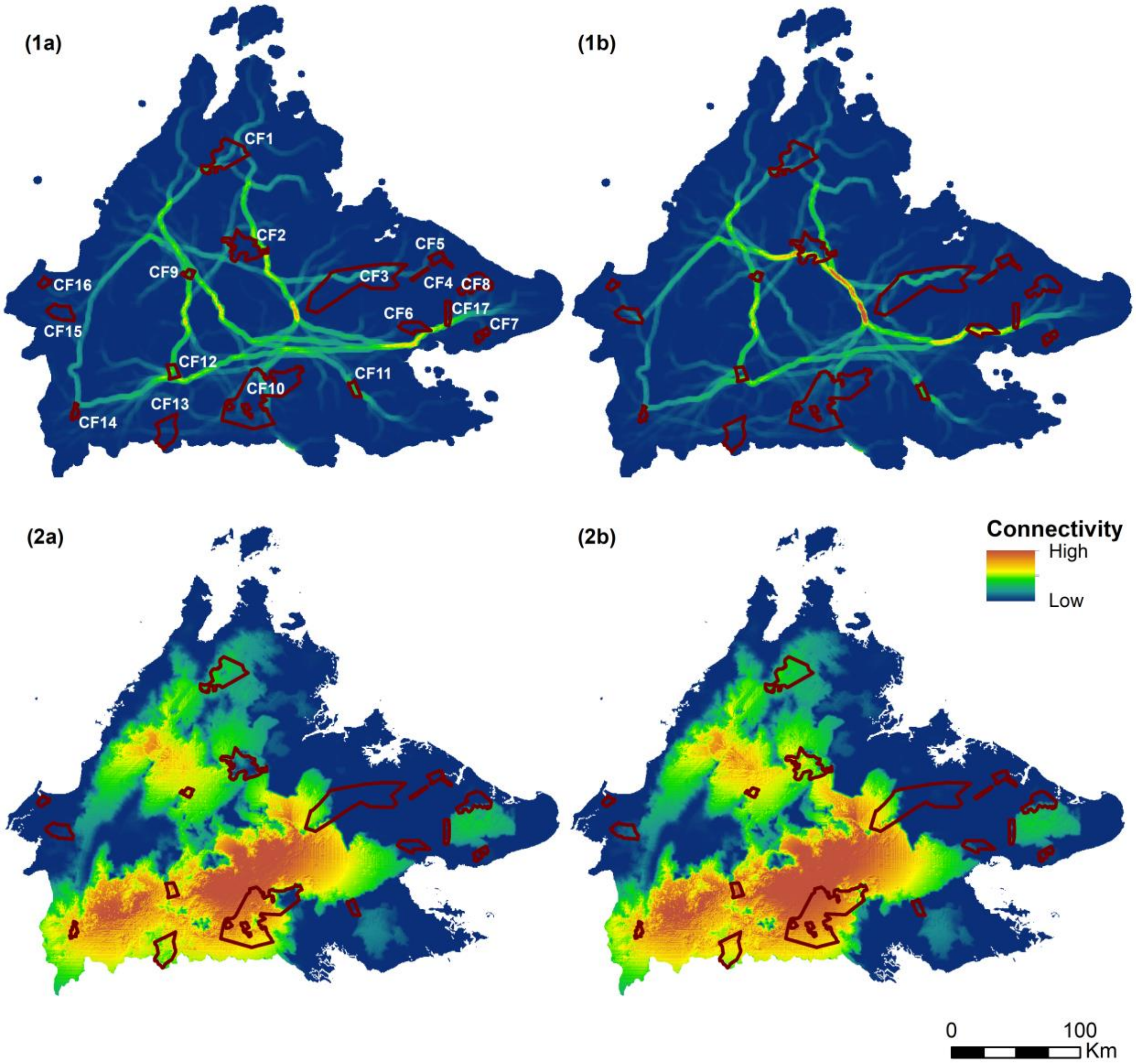

Figure 3. Factorial least cost paths (1) and resistant kernels (2) for the base scenario (a) and scenario incorporating all forest restoration areas (b). Each forest restoration area is marked in red and its ID is given on map (1a).

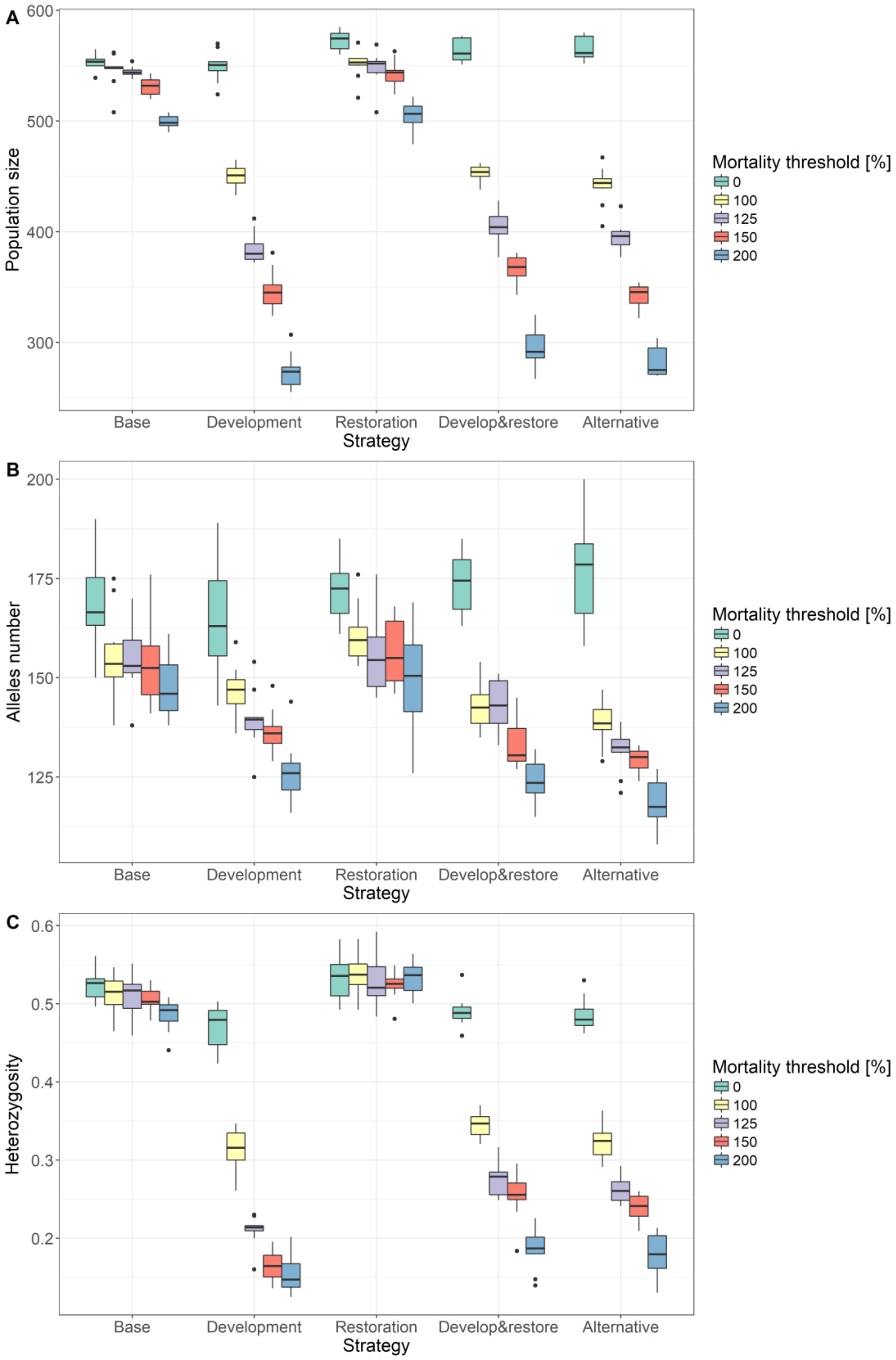
A
Population size
600
500
400
300
B
Alleles number
200
175
150
125
C
Heterozygosity
0.6
0.5
0.4
0.3
0.2
Base
Development
Restoration
Develop&restore
Alternative
Strategy
Mortality threshold [%]
0
100
125
150
200

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)

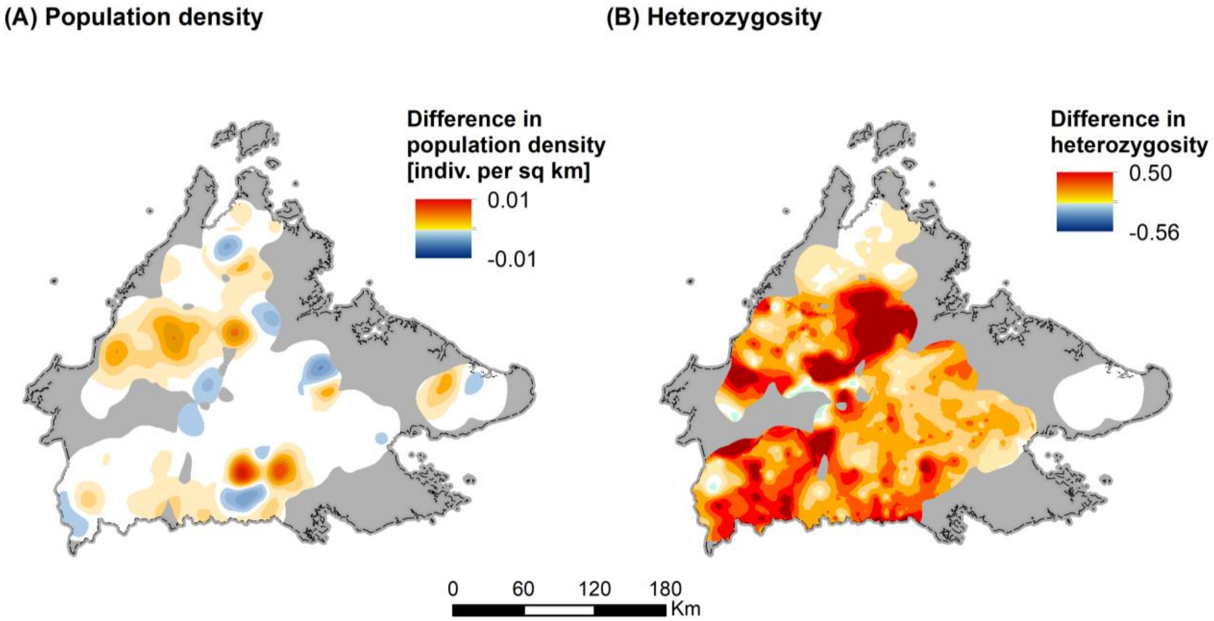

Figure 5. Difference in clouded leopard population density and heterozygosity in 200 generations between the development & restoration and the development strategies with mortality at 150% threshold.

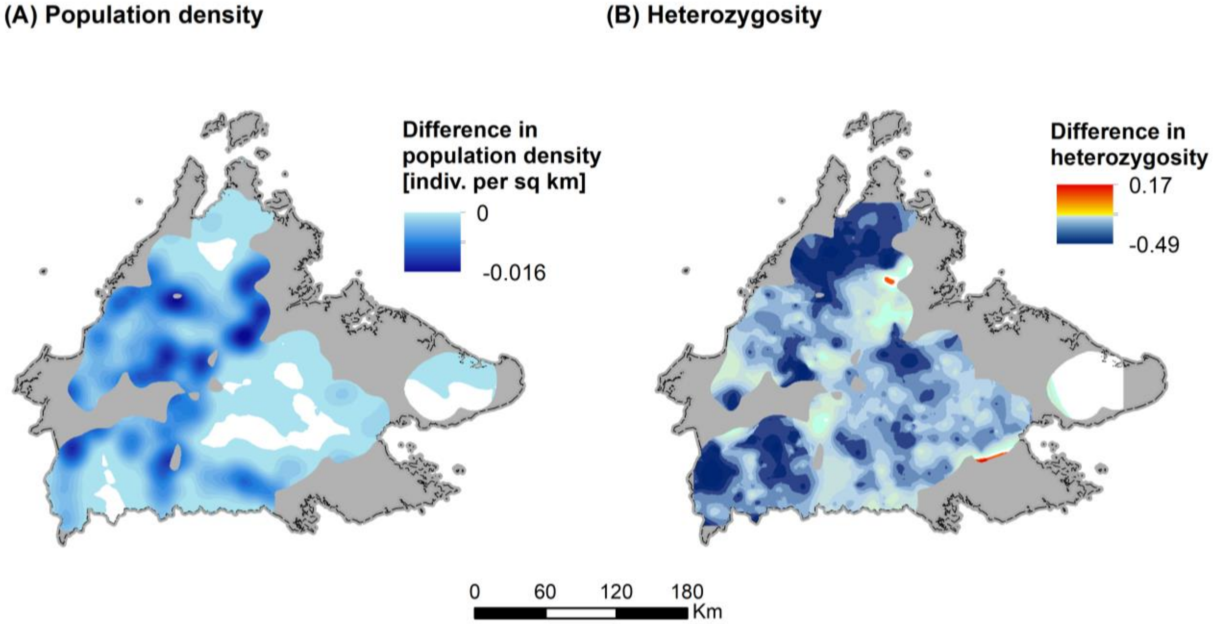

Figure 6. Difference in clouded leopard population density and heterozygosity in 200 generations between the development & restoration strategy with mortality at 150% threshold and without mortality.