

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

Short title: Assessing landscape change scenarios for Sunda clouded leopards

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

Abstract

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

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

1. Introduction

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

50

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

64

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

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

2. Material and methods

2.1 Study Area

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

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

2.2 Sunda clouded leopard telemetry data

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

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

2.3 Multiple Scale Path-level Modelling

We applied a multiscale path selection function to model Sunda clouded leopard movement as a function of landscape predictor variables. This approach employs conditional logistic regression to compare landscape characteristics around paths used by an animal with those from randomly generated available paths of identical length and topology, which are randomly shifted and rotated around the observed paths (e.g., Cushman and Lewis 2010; Elliot et al. 2014). We selected potential predictor variables for the path selection function based on existing knowledge of Sunda clouded leopard habitat associations (Hearn et al. 2015, 2016), including land cover, canopy cover, carbon density, and road and river distribution (for full details see Supplementary file S1). [All GIS layers were resampled to 15m pixel size for analysis.](#) To explicitly account for spatial scale in our analysis (e.g. Zeller et al. 2017), for each used path, we created 19 matched available paths, by shifting the x and y coordinates of the available path by a random value (up to the maximum distance specified at each scale of shift), and rotating its orientation by a random value between 0 and 360°. We used three spatial scales of shift: (1) no shift, and distances between (2) 0-5 km, and (3) 0-10 km. Optimizing the scale of the available neighbourhood in this way has been shown to be necessary to obtain correct

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

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

2.4 Resistance surface and connectivity modelling

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

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

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

2.5 Future Scenarios

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

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

3. Results

3.1 Visible inspection of movement paths

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

3.2 Multiple Scale Path-level Modelling

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

3.3 Resistance surface and connectivity modelling

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

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

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

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

3.4 Future Scenarios

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

4. Discussion

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

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

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

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

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

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

Scope and limitations

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

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

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

6. Conclusions

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

5. Acknowledgements

We are indebted to Drs Fernando Nájera, Senthilvel Nathan, Diana Ramírez Saldivar, Sergio Guerrero-Sánchez, Laura Benedict and the Sabah Wildlife Department's Wildlife Rescue Unit for providing veterinary support, and our numerous research assistants, especially Gilmoore Bolongon, Sajaril Utong and Paul Clenton. We thank Sabah Wildlife Department, Sabah Forestry Department and the Sabah Biodiversity Centre for granting us permission to conduct research.

6. Role of the funding source.

This research was funded by the Robertson Foundation, Sime Darby Foundation, Recanati-Kaplan Foundation, Clouded Leopard Project, Point Defiance Zoo and Aquarium, Houston Zoo, and Panthera. The funders did not have any role in the study design; in the collection, analysis, and interpretation of data; in the writing of the report; or in the decision to submit the paper for publication.

7. References

- Abrahms, B., Sawyer, S. C., Jordan, N. R., McNutt, J. W., Wilson, A. M., and Brashares, J. S. (2017). Does wildlife resource selection accurately inform corridor conservation? *Journal of Applied Ecology* 54, 412–422.
- Abram, N.K., Xofis, P., Tzanopoulos, J., MacMillan, D.C., Ancrenaz, M., Chung, R., Peter, L., Ong, R., Lackman, I., Goossens, B. and Ambu, L. (2014). Synergies for improving oil palm production and forest conservation in floodplain landscapes. *PLoS ONE*, 9(6), e95388.
- Ancrenaz, M., Goossens, B., Gimenez, O., Sawang, A., and Lackman-Ancrenaz, I. (2004). Determination of ape distribution and population size using ground and aerial surveys: a case study with orang-utans in lower Kinabatangan, Sabah, Malaysia. *Animal Conservation*, 7(4), 375–385.
- Baguette, M. and Van Dyck, H. (2007). Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape ecology*, 22(8), pp.1117–1129.
- Barton K (2016) Package “MuMIn”: Multi-Model Inference. R package, Version 1.15.6. Available at <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>. Accessed August 9, 2016.

- Blazquez-Cabrera, S., Gastón, A., Beier, P., Garrote, G., Simón, M. Á., and Saura, S. (2016). Influence of separating home range and dispersal movements on characterizing corridors and effective distances. *Landscape Ecology*, 31, 2355–2366.
- Brodie, J.F., Giordano, A.J., Zipkin, E.F., Bernard, H., Mohd-Azlan, J. and Ambu, L. (2015a). Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. *Conservation Biology*, 29(1), 110–121.
- Brodie, J.F., Giordano, A.J., Dickson, B., Hebblewhite, M., Bernard, H., Mohd-Azlan, J., Anderson, J. and Ambu, L. (2015b). Evaluating multispecies landscape connectivity in a threatened tropical mammal community. *Conservation Biology*, 29(1), 122–132.
- Chetkiewicz, C.-L. B., C. C. St. Clair, and M. S. Boyce. 2006. Corridors for Conservation: Integrating Pattern and Process. *Annual Review of Ecology, Evolution, and Systematics* 37, 317–342.
- Compton, B.W., McGarigal, K., Cushman, S.A., and Gamble, L.R. (2007). A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conservation Biology*, 21(3), 788–799.
- Cushman, S. A. (2010). Animal movement data: GPS telemetry, autocorrelation and the need for path-level analysis. In Cushman, S.A. and Huettmann, F. (eds). *Spatial complexity, informatics, and wildlife conservation*. Springer, Tokyo, 131–149.
- Cushman, S.A., and Lewis, J.S. (2010). Movement behavior explains genetic differentiation in American black bears. *Landscape ecology*, 25(10), 1613–1625.
- Cushman, S.A., McKelvey, K.S., Hayden, J., and Schwartz, M.K. (2006). Gene flow in complex landscapes: testing multiple hypotheses with causal modelling. *The American Naturalist*, 168(4), 486-499.
- Cushman, S.A., Landguth, E.L. and Flather, C.H., (2013). Evaluating population connectivity for species of conservation concern in the American Great Plains. *Biodiversity and conservation*, 22(11), pp.2583-2605.
- Cushman, S. A., E. A. Macdonald, E. L. Landguth, Y. Malhi and D. W. Macdonald (2017). "Multiple-scale prediction of forest loss risk across Borneo." *Landscape Ecology*: 1–18.
- Elliot, N.B., Cushman, S.A., Macdonald, D.W., and Loveridge, A.J. (2014). The devil is in the dispersers: predictions of landscape connectivity change with demography. *Journal of Applied Ecology*, 51(5), 1169–1178.

- Fahrig, L. (1997) Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management*, 61, 603–610.
- Fattebert, J., Robinson, H. S., Balme, G., Slotow, R., and Hunter, L. (2015). Structural habitat predicts functional dispersal habitat of a large carnivore: How leopards change spots. *Ecological Applications* 25:1911–1921.
- Frair, J.L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N.J., and Pedrotti, L. (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365(1550), 2187–2200.
- Gaveau, D.L., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., Ancrenaz, M., Nasi, R., Quinones, M., Wielaard, N. and Meijaard, E. (2014). Four decades of forest persistence, clearance and logging on Borneo. *PLoS ONE*, 9(7), e101654.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R. and Kommareddy, A. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160), 850–853.
- Hearn, A.J., Ross, J., Pamin, D., Bernard, H., Hunter, L., and Macdonald, D.W. (2013). Insights into the spatial and temporal ecology of the Sunda clouded leopard *Neofelis diardi*. *Raffles Bulletin of Zoology*, 61(2): 871–875.
- Hearn, A., Ross, J., Brodie, J., Cheyne, S., Haidir, I.A., Loken, B., Mathai, J., Wilting, A. and McCarthy, J. (2015). *Neofelis diardi*. The IUCN Red List of Threatened Species 2015.
- Hearn, A.J., Ross, J., Macdonald, D.W., Bolongon, G., Cheyne, S.M., Mohamed, A., Samejima, H., Brodie, J.F., Giordano, A., Alfred, R., Boonratana, R., Bernard, H., Loken, B., Augeri, D.M., Heydon, M., Hon, J., Mathai, J., Marshall, A.J., Pilgrim, J.D., Hall, J., Breitenmoser-Würsten, C., Kramer-Schadt, S., and Wilting, A. (2016). Predicted distribution of the Sunda Clouded leopard *Neofelis diardi* (Mammalia: Carnivora: Felidae) on Borneo. *Raffles Bulletin of Zoology*, Supplement No. 33: 165–172.
- Hearn, A.J., Ross, J., Bernard, H., Bakar, S.A., Goossens, B., Hunter, L.T.B. and Macdonald, D.W. (2017). Responses of Sunda clouded leopard *Neofelis diardi* population density to anthropogenic disturbance: refining estimates of its conservation status in Sabah. *Oryx*.

- Hinton, J. W., C. Proctor, C., Kelly, M. J., van Manen, F. T., Vaughan, M. R., and Chamberlain, M. J. (2016). Space Use and Habitat Selection by Resident and Transient Red Wolves (*Canis rufus*). PLOS ONE 11:e0167603.
- Killeen, J., Thurfjell, H., Ciuti, S., Paton, D., Musiani, M., and Boyce, M. S. (2014). Habitat selection during ungulate dispersal and exploratory movement at broad and fine scale with implications for conservation management. *Movement Ecology* 2:13.
- Krishnamurthy, R., Cushman, S.A., Sarkar, M.S., Malviya, M., Naveen, M., Johnson, J.A. and Sen, S. (2016). Multi-scale prediction of landscape resistance for tiger dispersal in central India. *Landscape Ecology*, 31(6): 1355–1368.
- Landguth, E.L., Hand, B.K., Glassy, J., Cushman, S.A. and Sawaya, M.A. (2012). UNICOR: a species connectivity and corridor network simulator. *Ecography*, 35, 9–14.
- Masenga, E. H., Jackson, C. R., Mjingo, E.E., Jacobson, A., Riggio, J., Lyamuya, R.D., Fyumagwa, R.D., Borner, M., and Røskaft, E. (2015). Insights into long-distance dispersal by African wild dogs in East Africa. *African Journal of Ecology*, 103–106.
- Mateo-Sánchez, M.C., Balkenhol, N., Cushman, S.A., Pérez, T., Domínguez, A., and Saura, S. (2015). A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow? *Landscape Ecology*, 30(8), 1405–1420.
- McGarigal, K., Cushman, S.A., Ene, E. (2012). FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology* 31:1161–1175.
- Meijaard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T., Lammertink, M., Rachmatika, I., Wong, A. and Soehartono, T., Stanley, S. and O'Brien, T. (2005). Life after logging: Reconciling Wildlife Conservation and Production Forestry in Indonesian Borneo. Center for International Forestry Research, Bogor, Indonesia.
- Miettinen, J., Shi, C., Tan, W.J. and Liew, S.C. (2012). 2010 land cover map of insular Southeast Asia in 250-m spatial resolution. *Remote Sensing Letters*, 3(1), 11–20.

- Morrison, C. D., Boyce, M. S., and Nielsen, S. E. (2015). Space-use, movement and dispersal of sub-adult cougars in a geographically isolated population. *PeerJ* 3:e1118.
- Nájera, F., Hearn, A.J., Ross, J., Ramírez Saldivar, D.A., Evans, M.N., Guerrero-Sánchez, S., Nathan, S.K.S.S., de Gaspar Simón, I., Macdonald, D.W., Goossens, B. and Revuelta Rueda, L. (2017). Chemical immobilization of free-ranging and captive Sunda clouded leopards (*Neofelis diardi*) with two anesthetic protocols: Medetomidine-Ketamin and Tiletamine-Zolazepam. *Journal of Veterinary Medical Science* 79(11): 1892–1898.
- R Development Team. (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Rabinowitz, A., Andau, P. and Chai, P.P. (1987). The clouded leopard in Malaysian Borneo. *Oryx*, 21(02), 107–111.
- Ross, J., Hearn, A.J., Bernard, H., Secoy, K. and Macdonald, D.W. (2010) A Framework for a Wild Cat Action Plan for Sabah. Global Canopy Programme, Oxford.
- Santiapillai, C. and Ashby, K.R. (1988). The clouded leopard in Sumatra. *Oryx*, 22(01), 44–45.
- Shirk, A.J., Wallin, D.O., Cushman, S.A., Rice, C.G. and Warheit, K.I. (2010). Inferring landscape effects on gene flow: a new model selection framework. *Molecular Ecology*, 19, 3603–3619.
- Shirk, A.J., Schroeder, M.A., Robb, L.A. and Cushman, S.A. (2015). Empirical validation of landscape resistance models: insights from the greater sage-grouse (*Centrocercus urophasianus*). *Landscape Ecology*, 30(10), 1837–1850.
- Spear, S.F., Balkenhol, N., Fortin, M.J., McRae, B.H. and Scribner, K.I.M. (2010). Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology*, 19(17), 3576–3591.
- Taylor, P.D., Fahrig, L., Henein, K. and Merriam, G., 1993. Connectivity is a vital element of landscape structure. *Oikos*, 571–573.
- Wasserman, T.N., Cushman, S.A., Schwartz, M.K. and Wallin, D.O. (2010). Spatial scaling and multi-model inference in landscape genetics: *Martes americana* in northern Idaho. *Landscape Ecology*, 25(10), 1601–1612.

- 601 Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B. and Koh, L.P. (2013). Navjot's nightmare
602 revisited: logging, agriculture and biodiversity in Southeast Asia. *Trends in Ecology and*
603 *Evolution*, 28, 531–540.
- 604
- 605 Wilting, A., Mohamed, A., Ambu, L.N., Lagan, P., Mannan, S., Hofer, H. and Sollmann, R. (2012).
606 Density of the vulnerable Sunda clouded leopard *Neofelis diardi* in two commercial
607 forest reserves in Sabah, Malaysian Borneo. *Oryx*, 46(03), 423–426.
- 608
- 609 Woodruff, D.S. (2010). Biogeography and conservation in Southeast Asia: how 2.7 million years
610 of repeated environmental fluctuations affect today's patterns and the future of the
611 remaining refugial-phase biodiversity. *Biodiversity and Conservation*, 19(4), 919–941.
- 612
- 613 Yue, S., Brodie, J. F., Zipkin, E. F. and Bernard, H. (2015). Oil palm plantations fail to support
614 mammal diversity. *Ecological Applications*, 25(8), 2285–2292.
- 615
- 616 Zeller, K.A., McGarigal, K. and Whiteley, A.R. (2012). Estimating landscape resistance to
617 movement: a review. *Landscape Ecology*, 27(6), 777–797.
- 618
- 619 Zeller, K.A., Rabinowitz, A., Salom-Perez, R. and Quigley, H. (2013). The Jaguar Corridor
620 Initiative: A range-wide conservation strategy. In Ruiz-Garcia, M. and Shostell, J.M.
621 (eds). *Molecular Population Genetics, Evolutionary Biology and Biological Conservation*
622 *of Neotropical Carnivores*. Nova Science Publishers, New York, 629–658.
- 623
- 624 Zeller, K.A., McGarigal, K., Beier, P., Cushman, S.A., Vickers, T.W. and Boyce, W.M. (2014).
625 Sensitivity of landscape resistance estimates based on point selection functions to scale
626 and behavioral state: pumas as a case study. *Landscape Ecology*, 29(3), 541–557.
- 627
- 628 Zeller, K.A., McGarigal, K., Cushman, S.A., Beier, P., Vickers, T.W. and Boyce, W.M. (2015). Using
629 step and path selection functions for estimating resistance to movement: pumas as a
630 case study. *Landscape Ecology*, 31 (6), 1319–1335.
- 631
- 632 Zeller, K. A., Vickers, T. W., Ernest, H. B., Boyce, W. M. Pollinger, J. and Ernest, H. (2017). Multi-
633 level, multi-scale resource selection functions and resistance surfaces for conservation
634 planning: Pumas as a case study. *Plos One* 12:e0179570.

Figures

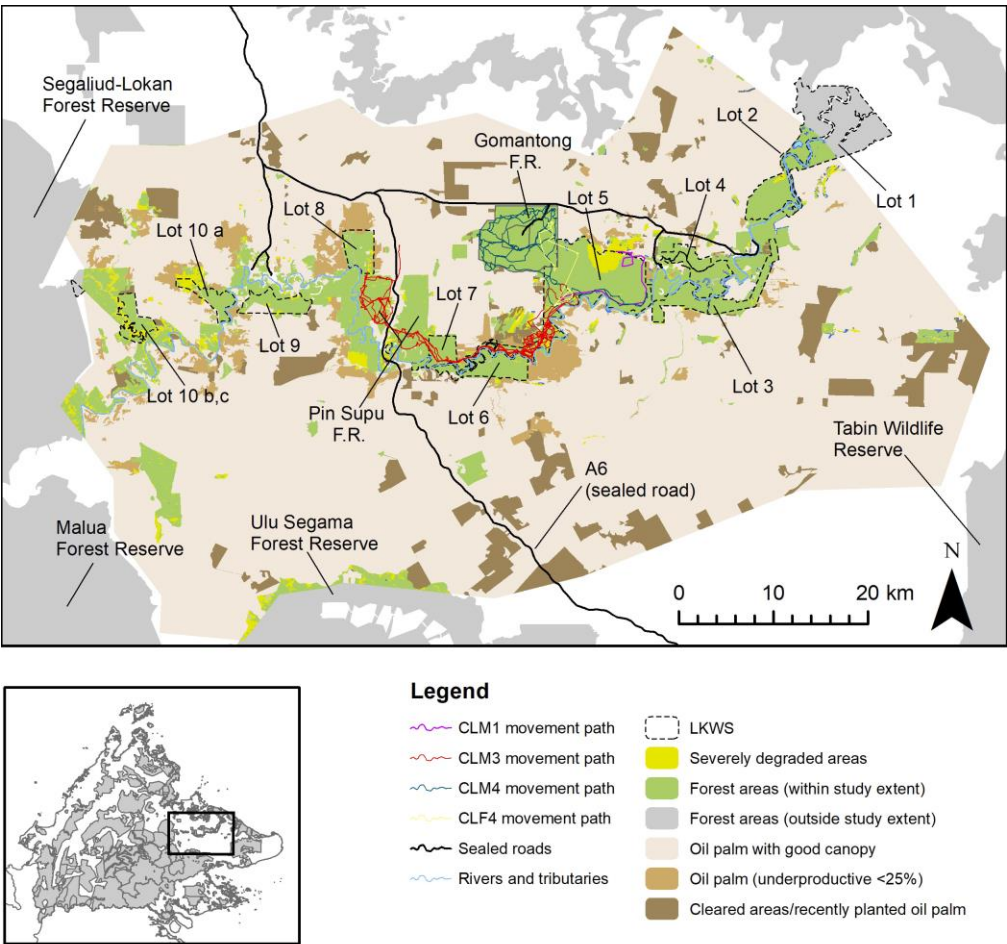
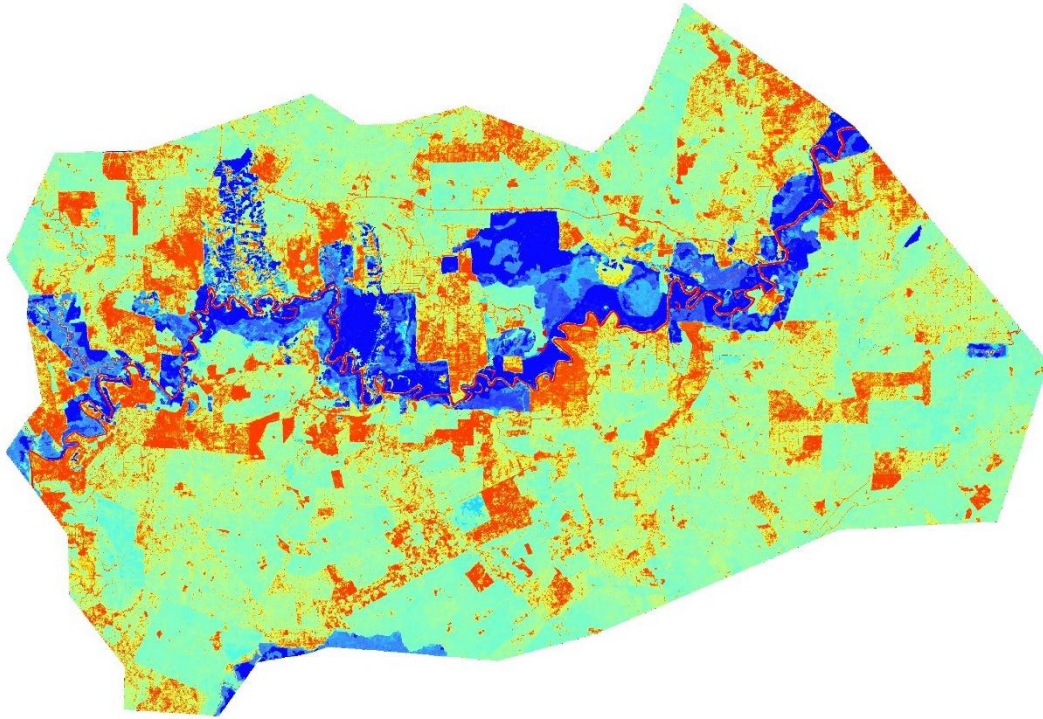


Figure 1. Map of the Lower Kinabatangan floodplain, showing the study extent and land use. Inset map shows the Malaysian state of Sabah, and bounding box shows location of the Kinabatangan floodplain. Land cover data modified from Abram et al. (2014).



647

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

651

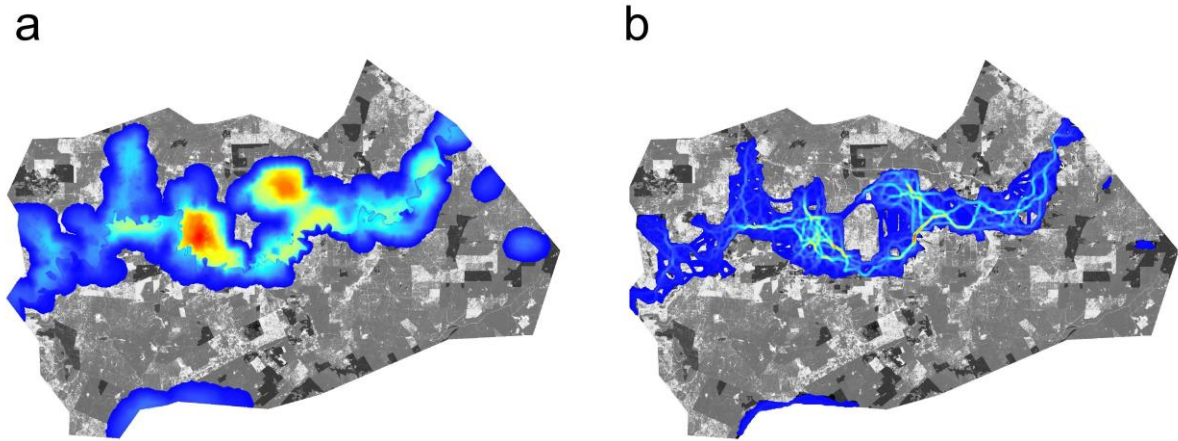


Figure 3. Cumulative resistant kernel surface (a) and Factorial least cost path density (b) networks for the Kinabatangan study area. The maps show predictions of Sunda clouded leopard connectivity for the present condition of the landscape. The colour ramps are scaled linearly from min to max (dark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

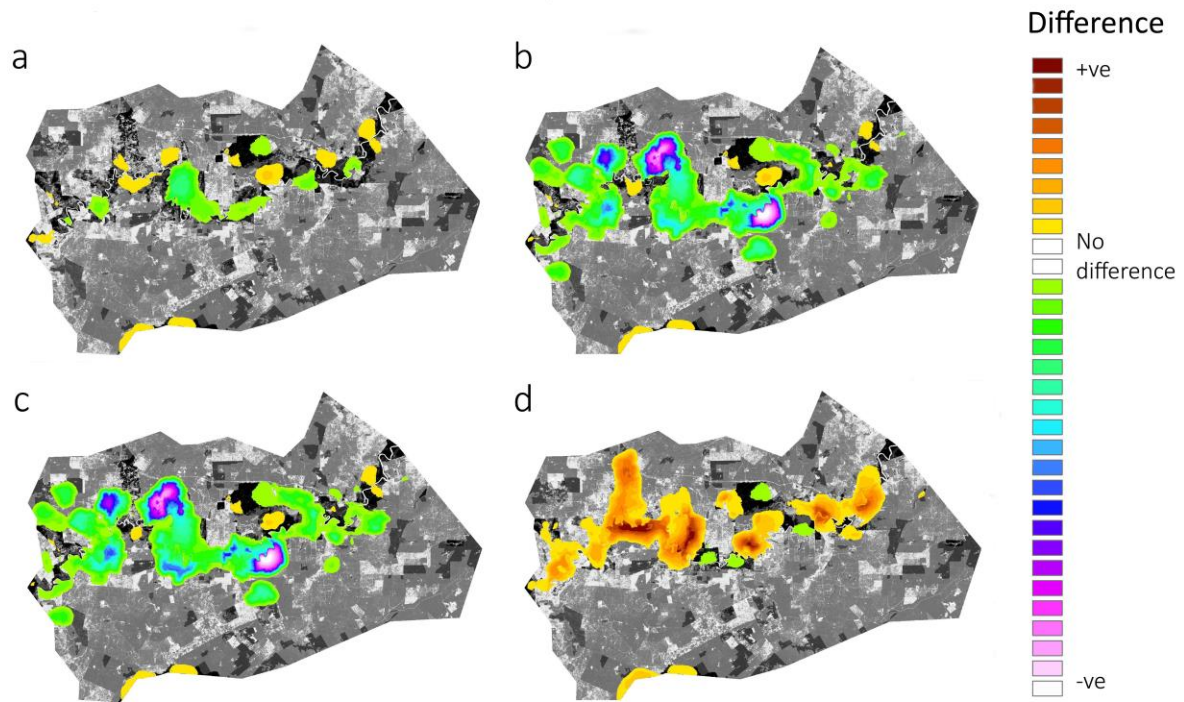


Figure 4. Maps showing the differences between the cumulative kernel surface for the present condition of the landscape and four scenarios of future landscape change. The difference is present surface - scenario surface and positive values indicate areas where the present landscape has higher kernel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

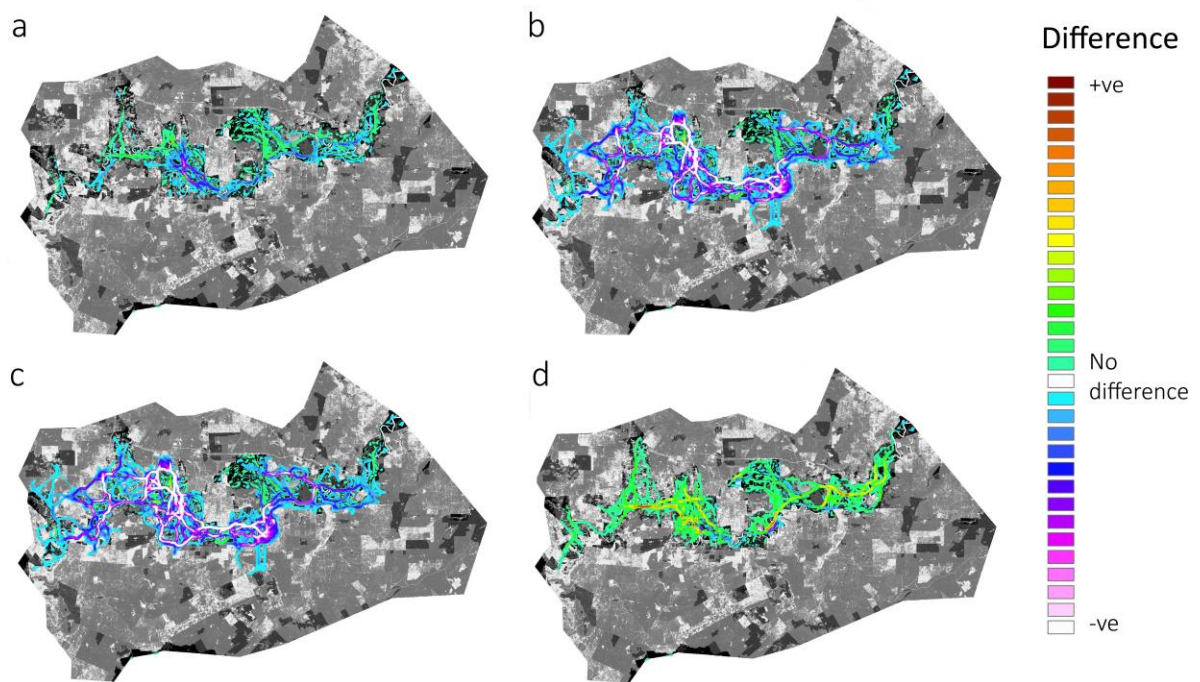


Figure 5. Maps showing the differences between the factorial least cost path surface for the present condition of the landscape and four scenarios of future landscape change. The difference is present surface - scenario surface and positive values indicate areas where the present landscape has higher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

676 Tables

677

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

680

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

681

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

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

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

691

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

692