



Using simulation modelling to evaluate the relative efficacy of core area and corridor-based conservation designs for biodiversity conservation

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Abstract

Context The efficient and effective design of protected areas is a fundamental challenge in landscape ecology, focusing on how spatial patterns of habitat influence conservation outcomes. This has sparked debate about the relative importance of habitat area versus connectivity in maintaining populations across fragmented landscapes.

Objectives We evaluate the relative importance of habitat area and connectivity by comparing counterfactual scenarios for landscape configuration on Borneo. We examine how habitat area and connectivity influence Sunda clouded leopard population size and genetic diversity across scenarios and dispersal abilities.

Methods We compared 28 landscape scenarios on Borneo, incorporating combinations of core areas and movement corridors. We modelled population size

and genetic diversity across five dispersal thresholds, using spatially explicit genetic simulations, to assess how area and connectivity influence conservation outcomes.

Results Our analysis reveals a strong, disproportionate relationship between habitat area and population size and genetic diversity. Even when controlling for overall extent, landscapes that protect larger areas consistently provide superior conservation outcomes. Corridors showed minimal impact, becoming effective only at the highest dispersal thresholds. Habitat area emerged as the primary driver of conservation success, challenging assumptions about the importance of connectivity and highlighting the complex interactions between landscape configuration and species mobility.

Conclusions Our findings reinforce the fundamental importance of habitat area for biodiversity conservation, while suggesting that conservation initiatives based on connectivity may have limitations, particularly when corridors are relatively long and narrow, or exceed species' dispersal abilities. While connectivity remains a valuable conservation tool in fragmented landscapes, our results indicate that expanding core habitat areas should be the primary focus, with corridor investments strategically targeted to specific cases.

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Introduction

In the face of the biodiversity and extinction crisis (Ceballos et al. 2017; Dirzo et al. 2022), it is more urgent than ever to develop and apply the most effective and efficient conservation strategies (Laycock et al. 2011; Walls 2018; Camaclang et al. 2022). Without diminishing the importance of conservation beyond protected areas (e.g. Tyrrell et al. 2020), protected area networks remain an essential foundation for biodiversity conservation (Müller et al. 2020; Zhang et al. 2020). In many parts of the world, remnant biodiversity is highly concentrated in protected areas, highlighting the importance of these protected lands for preserving biodiversity (Thomas and Gillingham 2015; Cuesta et al. 2017). However, considerable uncertainty and debate persist regarding how best to design protected area networks to most effectively and efficiently meet conservation objectives (Sink 2016; Bicknell et al. 2017; WWF et al. 2023; Macdonald et al. 2024).

A central question of this debate is the relative importance of habitat area versus habitat configuration, including habitat connectivity, for supporting biodiversity and species populations. The distinction between habitat loss and the separate, though linked, concept of habitat fragmentation was first observed by Curtis (1956) and Moore (1962). This distinction is important. While habitat loss is undoubtedly a primary driver of species declines, the pattern of habitat loss can occur in ways that result in greater or lesser degrees of fragmentation, independent of the area of remaining habitat. Early approaches to solving this conundrum did so through the lens of the theory of island biogeography (MacArthur and Wilson 1967); however, this led to a misguided focus on patch-based measures over landscape-based measures (McGarigal and Cushman 2002), and the implicit conflation of area and fragmentation (Fahrig 2019). Despite the large literature on habitat fragmentation, only a small proportion of studies examine ecological effects across landscapes while controlling for habitat amount (Fahrig 2003). One recent review of such studies finds mixed results with most showing weak or non-significant effects of fragmentation (Fahrig 2017). Of the studies that did show an effect, 76% exhibited a positive response, while 24% exhibited a negative response (Fahrig 2017). However, these

findings remain contested (Fletcher et al. 2018; Gonçalves-Souza et al. 2025).

Alongside the question of fragmentation per se is the role of connectivity between patches, and whether maintaining or restoring dispersal corridors is effective. Connectivity is a central pillar of the Kunming-Montreal Global Biodiversity Framework's ambition to protect 30% of Earth's area by 2030 (CBD 2022), yet only 10% of current protected areas are connected (Ward et al. 2020). Many papers emphasise the importance of connectivity (e.g. Correa Ayram et al. 2016; Keeley et al. 2021). There is also a substantial focus on ways to measure and assess it (Bleyhl et al. 2017; Petsas et al. 2020), under the assumption that preserving connectivity is beneficial and often essential to population vigour and viability. However, few studies have rigorously demonstrated the effects and importance of connectivity on conservation outcomes (Cushman 2006; Gilbert-Norton et al. 2010; Fontoura et al. 2022). As with the debate about habitat fragmentation, it is important to understand whether corridors improve or maintain ecological functioning, and in particular whether any changes are independent of the overall amount of area protected (Brodie et al. 2025).

The drivers of the relationships between habitat area, fragmentation per se, and connectivity remain poorly understood. Thus, the purpose of this paper is to rigorously evaluate these interacting effects on conservation outcomes for a single species at a landscape scale. To do this, a simulation framework is needed (Cushman 2014, 2015; Shirk et al. 2014; Landguth et al. 2017; Kaszta et al. 2019). Empirical data are an essential foundation for ecological science, but their analysis involves inductive reasoning, in which the patterns in the data are associated with alternative hypotheses of processes that generate them, usually through correlation or regression (e.g. Cushman et al. 2010; Cushman 2015). While this provides a critical way to quantify patterns of biodiversity and their associations with landscape structure and composition, it does not offer a means to identify and evaluate the drivers and their relative effects. The processes are inferred statistically and not known ontologically. Simulation solves this inferential problem by controlling the process (e.g. Landguth and Cushman 2010) that drives the relationship. This, in turn, enables researchers to conduct modelling experiments (e.g. Shirk et al. 2014;

Balkenhol et al. 2015; Kaszta et al. 2019) which can systematically vary parameters or scenario elements, thereby allowing researchers to control the patterns and the processes together and therefore rigorously predict the relative effects of different scenarios (Wiersma 2022).

Amongst models available to assess landscape effects on biodiversity, a particularly important class comprises individual-based, spatially-explicit population and genetics models. These stipulate processes related to habitat suitability for occurrence, dispersal in relation to landscape structure and composition, and differential fitness or mortality risk across landscapes (e.g. Landguth and Cushman 2010; Landguth et al. 2017, 2020, 2012). While much interest in conservation biology sensibly focuses on multi-species strategies (Brodie et al. 2015; DeMatteo et al. 2023), we believe it would be wise to begin the assessment of the relative impacts of core area versus corridor conservation strategies using individual-based, spatially-explicit population modelling. Multi-species biodiversity is the emergent pattern of the individual species' population dynamics and distribution processes (Macdonald et al. 2020). Therefore, focusing on a single focal species using a rigorous population and genetic model is a prudent first step towards addressing the debate surrounding area, configuration, and connectivity in conservation strategy development.

As an example, we have chosen the Sunda clouded leopard (*Neofelis diardi*) in Borneo for several reasons. *N. diardi* is the apex carnivore throughout the island of Borneo and in much of Sumatra, and is listed as Vulnerable in the latest IUCN Red List species assessment (Hearn et al. 2015, 2016) with the Bornean subspecies *N. diardi ssp. borneensis* listed as Endangered (Hearn et al. 2008). It is certainly an emerging conservation priority (e.g. Sabah Wildlife Department 2019), and clearly impacted by the very high and accelerating rates of deforestation (Cushman et al. 2017) which is driving loss, fragmentation, and degradation of their habitat (Hearn et al. 2018; Macdonald et al. 2018a, 2018b). In addition, apex predators contribute important ecosystem services (Estes et al. 2004, 2011; Ripple et al. 2014); clouded leopards are keystone species for much of forest biodiversity in the region (Chiaverini et al. 2022) and are compelling ambassadors for conservation (Macdonald et al. 2017).

For practical reasons, the Sunda clouded leopard is also an apt model with which to explore the relative effects of habitat loss and fragmentation on conservation strategy development since the species has been the subject of extensive occurrence detection surveys, as well as expert based habitat suitability (e.g. Macdonald et al. 2018b) and movement resistance (e.g. Hearn et al. 2016) modelling studies. This provides an opportunity to base a simulation study of this issue of broad theoretical importance on unusually abundant knowledge of species biology, habitat associations, and movement patterns. Similarly, the island of Borneo is an apt example given it is an isolated closed system of sufficient size to contain a large population of the focal species, and, importantly, because its spatial extent and the configuration of remaining habitat patches and connectivity networks (e.g. Macdonald et al. 2018b) can be used to develop a large number of alternative conservation scenarios, each representing different strategies to protect, various combinations of core habitat areas and corridors. Using individual-based, spatially explicit simulation modelling (Landguth and Cushman 2010) on these scenarios enables us to evaluate the relative effects and importance of focusing conservation strategies on habitat core areas vs corridors.

Our main hypotheses are:

1. Conserving the full network is best: Scenarios including the full network of core areas and corridors outperform all other configurations. This tests the foundational assumption of landscape-scale conservation planning: that preserving the full connectivity and spatial extent of ecologically important areas maximises conservation outcomes.
2. Small patches have limited benefits: In unconnected landscapes, removing either or both smaller patches of core habitat does not substantially worsen outcomes across metrics. This hypothesis examines whether smaller, isolated habitat patches contribute meaningfully to conservation outcomes in the absence of connectivity. It is important because it helps determine whether conserving such patches is an efficient use of resources when connectivity cannot be maintained or restored.

3. The largest patch of core area in a network dominates: Scenarios excluding the largest core area perform worse than all scenarios that retain it. This hypothesis tests the disproportionate value of the largest habitat patch within a network. This is important because it informs prioritisation decisions, highlighting the critical role of large, contiguous habitat areas in sustaining population size and genetic diversity.
4. Corridors do not mitigate for the loss of core areas: A full network of core areas without corridors, outperforms any scenario in which core habitat is lost, regardless of corridor presence. This hypothesis tests the assumption that corridors can compensate for habitat loss by maintaining connectivity. It is important because it clarifies the limits of corridor effectiveness, testing whether connectivity can substitute for the loss of core areas of habitat.
5. Overall area of the network dominates: When retaining either two or a single core area, scenarios with greater total habitat area perform better. This hypothesis tests whether total habitat area is a stronger determinant of conservation outcomes than specific spatial configurations. It is important because it supports area-based conservation targets and helps evaluate trade-offs between conserving fewer large areas versus more fragmented ones.
6. Corridors enhance measures of population and genetic diversity: Scenarios that include corridors perform better across all metrics compared to those with the same core area configuration, but without corridors. This hypothesis evaluates the role of corridors in facilitating movement and gene flow between habitat patches. It is important because it provides evidence for the added value of connectivity infrastructure in fragmented landscapes, even when the extent of core area remains constant.

Each of these hypotheses comprises a set of predictions ($n=39$ in total) detailed in Table 1. Because we are interested in the role of landscape configuration, independent of the area of habitat, we test the above hypotheses using both raw, and area-weighted measures of population size and genetic diversity.

Methods

The 39 predictions reference scenarios that are depicted in Fig. 1. We designed 28 landscape conservation scenarios that illustrate different combinations of core areas and connectivity corridors for clouded leopards based on the work of Macdonald et al. (2018b). Specifically, Macdonald et al. (2018b) used multi-scale optimization modelling (e.g. McGarigal et al. 2016) to optimize prediction of clouded leopard core areas and corridors across Borneo drawing on recommendations from a panel of species experts. The results of this expert-derived model were subsequently validated by comparing the expert model to the results of a similar, empirically derived model produced for the Sabah region (Hearn et al. 2019). This comparison showed that while the empirical model estimated slightly higher population sizes, both models exhibited broadly similar spatial patterns of connectivity – an outcome critical for the present study.

For this study, we used the 2010 maps from Macdonald et al. (2018b) to identify distinct core population areas, and the strongest linkages, or corridors, between them. Core areas were defined as those with a kernel density value exceeding a threshold value of 75.7. This threshold was selected to yield three core areas, each containing no fewer than 100 source points. Since the number of source points used in Macdonald et al. (2018b) represents a realistic upper estimate of the clouded leopard density on Borneo, the smallest core area could plausibly support a population of 100 individuals. Corridors were defined by applying a threshold path value of 1000. This threshold was selected iteratively to produce a viable number of corridors ($n=4$) that connected pairs of core areas, while minimising the inclusion of corridors terminating at only one core area. Any remaining partial corridors were excluded. Our simulation experiment is based on these three core areas and these four corridors (Fig. 1).

In the simulation experiment, each scenario represents a counterfactual land use configuration, illustrating a different plausible combination of core areas and corridors (see Fig. 1 for maps of each scenario). For instance, Scenario 1 includes all three core areas and all four corridors, while Scenario 28 includes none. The remaining scenarios depict all other feasible combinations. For example, scenarios 8, 9, 10,

Table 1 List of hypotheses and predictions tested. Each prediction was evaluated by comparing the outputs of a CDPOP population and genetics simulation for all dispersal thresholds (65, 125, 250, 375 and 500 kcu; see methods for more details). The scenarios listed in the right-hand column correspond to the land use configurations described in Fig. 1

Hypothesis	Specific prediction	Prediction number	Comparison between scenarios
1. Conserving the full network is best	Scenarios that include the full network of core areas and corridors perform better than all other scenarios	1.01	1 > all others
2. Small patches have limited benefits	When considering unconnected landscapes, the removal of either, or both smaller patches of core habitat does not result in substantially worse outcomes across all metrics	2.01	22 ∇ 25
		2.02	22 ∇ 26
		2.03	22 ∇ 5
3. The largest patch of core area in a network dominates	Scenarios that do not include the largest core area will perform worse than all scenarios that do contain the largest core area	3.01	4 < all others (excluding 6, 7, 27)
		3.02	6 < all others (excluding 4, 7, 27)
		3.03	7 < all others (excluding 4, 6, 27)
		3.04	27 < all others (excluding 4, 6, 7)
4. Corridors do not mitigate for the loss of core areas	The full network of core areas with no corridors, performs better than any scenario that loses core habitat, regardless of the presence of corridors	4.01	22 > 2
		4.02	22 > 3
		4.03	22 > 4
		4.04	22 > 23
		4.05	22 > 24
5. Overall area of the network dominates	When keeping two core areas of core habitat, or, when keeping a single core area of habitat, scenarios with larger area perform better	5.01	25 > 26
		5.02	26 > 27
		5.03	25 > 27
		5.04	5 > 6
		5.05	5 > 7
		5.06	6 > 7
6. Corridors enhance measures of population and genetic diversity	Scenarios that have corridors perform better across all metrics when compared with scenarios that contain the same pattern of core areas, but without corridors	6.01	1 > 22
		6.02	8 > 22
		6.03	9 > 22
		6.04	10 > 22
		6.05	11 > 22
		6.06	12 > 22
		6.07	13 > 22
		6.08	14 > 22
		6.09	15 > 22
		6.10	16 > 22
		6.11	17 > 22
		6.12	18 > 22
		6.13	19 > 22
		6.14	20 > 22
		6.15	21 > 22
		6.16	4 > 27
6.17	2 > 25		
6.18	23 > 25		
6.19	24 > 25		
6.20	3 > 26		

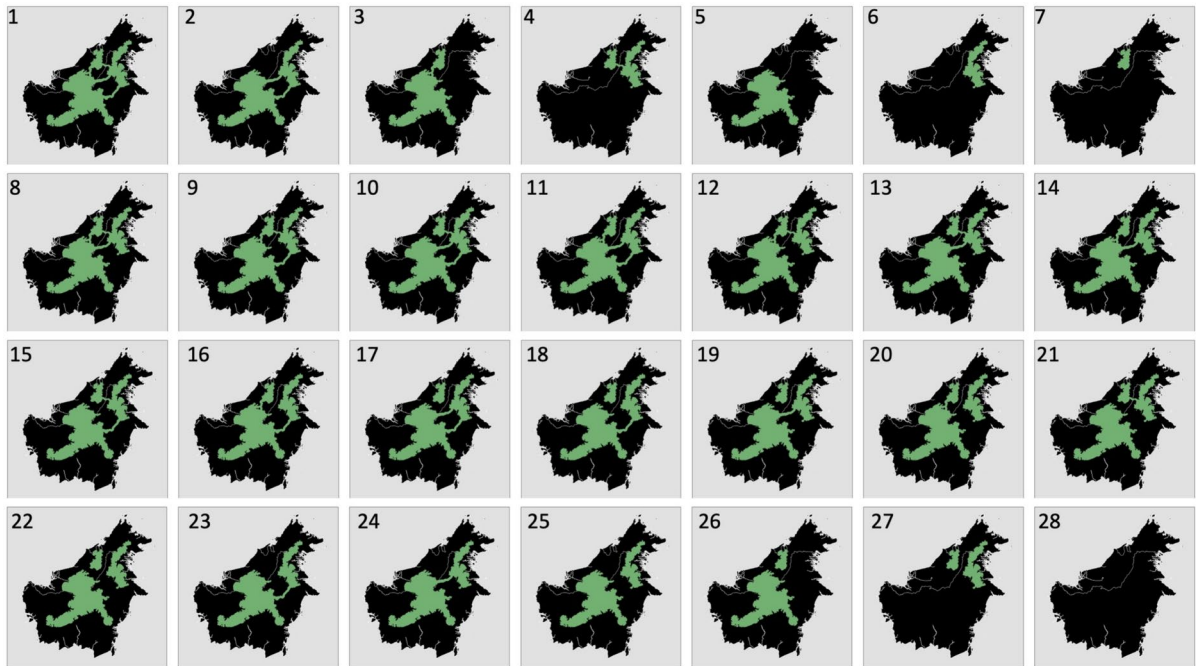


Fig. 1 Land use configuration scenarios used in the CDPOP population and genetics simulations. These scenarios represent all plausible combinations of core areas and connectivity corridors for clouded leopards. The three core areas represent the areas with highest kernel density value from Macdonald et al.

and 11 include all three core areas but each excludes a different single corridor. Similarly, scenarios 2, 3, 4, and 23–27 represent combinations of two core areas, both with and without corridors. As this is a theoretical exploration of the effectiveness of core area, corridor, and combined conservation strategies, all areas outside each scenario's protected network were assigned a resistance value of 100. This creates a simplified context in which areas beyond the protected network are considered highly resistant to movement—analogue to full conversion to human-dominated land uses.

For each of the 28 scenarios, we used CDPOP 1.0 (Landguth and Cushman 2010) to simulate population size, total number of alleles, and observed heterozygosity after 100 generations under the given landscape condition. CDPOP is an individually based, spatially explicit population and genetics model that simulates changes in population size, distribution, genetic diversity, and genetic differentiation as a function of habitat suitability for occurrence, dispersal ability, landscape resistance, and differential

(2018b), and the four corridors represent the least cost paths between these core areas also from Macdonald et al. (2018b) (see methods for more details). Comparison of the CDPOP population and genetic simulations under each scenario allow us to test the specific hypotheses described in Table 1

mortality risk. The model identifies destination points or mating pairs through a probabilistic draw from a cost distance matrix. Locations separated by a long, but low-cost corridor can have a lower relative cost distance than points that are geographically closer yet divided by high-resistance landscape features. Since CDPOP selects destinations for dispersing individuals or mating pairs based on these cost distances, corridors are maximally effective, providing the most favourable possible assessment of corridors. CDPOP is particularly powerful for evaluating the effects of landscape change (Macdonald et al. 2018b) or climate change (Wasserman et al. 2013, 2012) on species' population size, distribution and genetic differentiation. It has also been used to assess the relative benefits and efficiencies of alternative conservation and development scenarios (e.g. Kaszta et al. 2019; Macdonald et al. 2024).

In each of the 28 scenarios above, we used the same source points as Macdonald et al. (2018b) to simulate the locations of individual clouded leopards. This was done by generating a grid of random

values (0–1) matching the dimensions and cell size of the resistance surface, and then multiplying this grid by the inverse of the landscape resistance values. Macdonald et al. (2018b) used a threshold that yielded 2595 source points, representing a conservative estimate of the population size of clouded leopards on Borneo. We used a similar parameterization of CDPOP to Macdonald et al. (2018b) to ensure maximum comparability with previous studies (see the Supplementary Information (SI) for a full list of parameters).

For each scenario, we ran 50 Monte Carlo simulations in CDPOP to account for stochastic variability, and simulated gene flow for 100 non-overlapping generations. We extracted global measures of population genetic structure: population size, observed heterozygosity and the total number of alleles. To account for the varying spatial extent of each scenario, we also calculated area-weighted versions of these measures.

We acknowledge that the landscape is unlikely to remain static over 100 generations – or indeed a single generation. The aim of the simulation is not to forecast the future status of the clouded leopard population, but rather to enable a rigorous comparative evaluation of alternative conservation strategies, using a consistent modelling framework and parameter set.

We evaluated five dispersal thresholds. Two of these – 125,000 and 250,000 cost units—were drawn from Macdonald et al. (2018b), corresponding to 125 km and 250 km, respectively under idealised conditions. In this context, cost units provide a functional measure of distance, incorporating both Euclidean distance and cumulative resistance encountered when moving across heterogeneous landscape features. The dispersal threshold represents the maximum total cost an individual can incur during dispersal.

In addition to the thresholds used by Macdonald et al. (2018b), we included a lower threshold of 65,000 cost units (65 kcu), representing the conservative lower bound of plausible dispersal ability. We also tested thresholds of 375,000, 500,000 cost units to explore the sensitivity of simulation outcomes to a wider range of dispersal capacities. Dispersal distances of this magnitude are consistent with those observed in other large felids (e.g. Elliot et al. 2014). Although empirical data on clouded leopard dispersal are limited, it is likely that their maximum dispersal distance lies between 65 and 500 km.

Dispersal was modelled as a linear function of cost distance up to the specified thresholds for each of the 28 landscape scenarios, resulting in a total of 140 simulation scenarios (28 landscape configurations and 5 dispersal thresholds).

To explore the relationship between response variables (population size, total number of alleles, and observed heterozygosity) and habitat fragmentation, we used FRAGSTATS (McGarigal et al. 2012) to calculate a suite of habitat fragmentation metrics for each scenario. Specifically, the metrics calculated were area-weighted mean patch size, area-weighted mean radius of gyration (correlation length), area-weighted circumscribing circle, area-weighted mean patch contiguity index, landscape division index, effective mesh size, and splitting index (see SI for details).

Statistical analyses

We employed analysis of variance (ANOVA) and general contrasts to test each of the 36 predictions across the six response variables. These response variables were (1) total population size, (2) total number of alleles, (3) observed heterozygosity, (4) area-weighted population size, (5) area-weighted number of alleles, and (6) area-weighted observed heterozygosity.

Results

We calculated the total number of alleles, observed heterozygosity, and population size at generation 100 for each of scenario (Fig. 2). As anticipated, there was considerable variation in conservation outcomes across scenarios; however, scenarios 4, 6, 7, 27 and 28 consistently performed worst across all three measures. While the landscape configurations for each scenario are depicted in Fig. 1, the most salient feature shared by these lower-performing scenarios is the absence of the largest core habitat patch, resulting in a reduced overall spatial extent. This observation is supported by linear regression analysis which revealed that total number of alleles, observed heterozygosity, and population size are all significantly and positively correlated with landscape area across all dispersal distances (SI). These findings align with

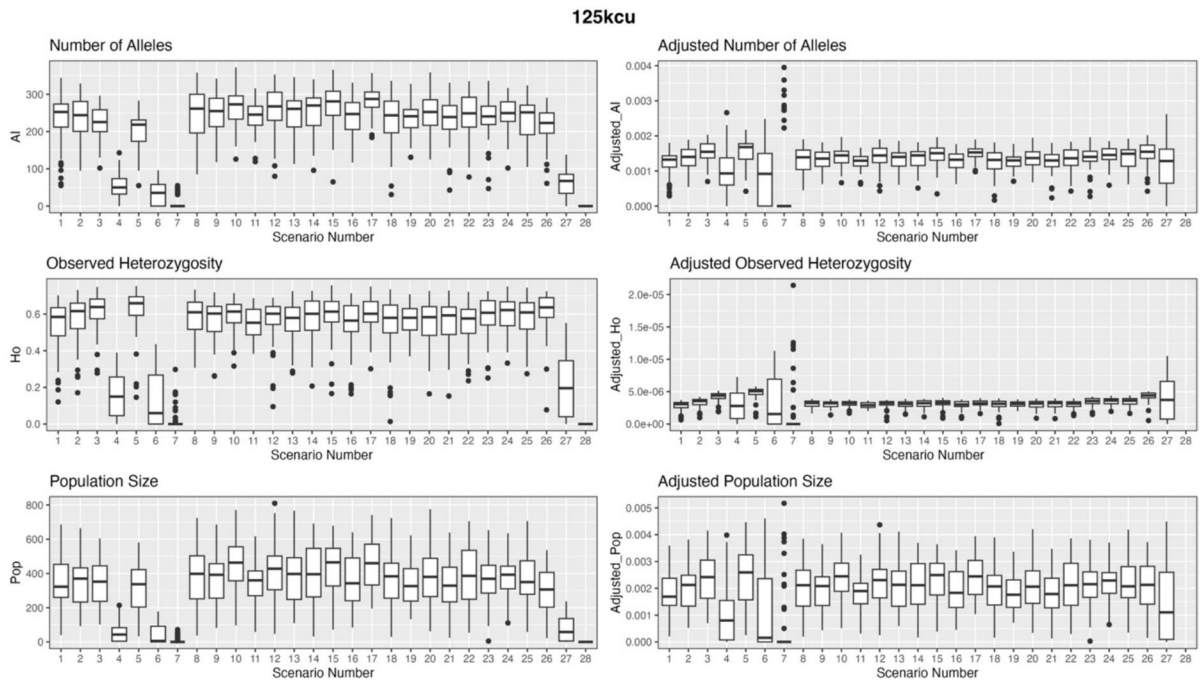


Fig. 2 Boxplots showing the number of alleles, observed heterozygosity, and population size for clouded leopards in each of the 28 scenarios after 100 generations at the 125 kcu dispersal threshold. Plots on the left show the raw measures, while plots

on the right show the measures adjusted for the area of that scenario. Figures displaying results at other dispersal thresholds are available in the Supplementary Information

expectations that larger areas confer greater conservation benefits than small ones.

To assess whether the effects of landscape configuration extend beyond a simple relationship with area, we adjusted the raw measures to provide the total number of alleles, observed heterozygosity, and population size per unit area of the landscape. As shown in Fig. 2, this transformation removes much of the effect observed previously. Nonetheless, area-weighted alleles and area-weighted population size remained significantly and positively correlated with landscape area across all dispersal distances (SI), suggesting that larger areas deliver greater conservation benefits for these metrics even after accounting for area. In other words, larger landscapes appear to yield more efficient conservation outcomes. The pattern for area-weighted heterozygosity, however, was less intuitive: we observed a significant positive relationship at a dispersal threshold of 65 kcu, no significant relationship at 125 kcu, and significant negative relationships at dispersal thresholds of 250 kcu and above (SI).

When evaluating the 5 specific hypotheses outlined in Table 1, we found strong support for Hypothesis 1, which posits that the full design performs better than any other scenario. When considering the raw response variables, 60–100% of predictions supported this claim (Table 2). However, this pattern largely disappeared when accounting for the spatial extent of the conserved area: none of the predictions showed any improvement for area-weighted alleles or area-weighted population size. Notably, 60% of predictions showed a significant improvement in weighted observed heterozygosity. This effect appears to be influenced by dispersal ability, with higher dispersal thresholds associated with stronger support for the hypothesis (SI).

Hypothesis 2 predicted that the loss of smaller patches from the network would have limited impact on the response variables. The contrasts relevant to this hypothesis revealed a complex pattern: 67%, 53% and 40% of comparisons showed significant differences for the raw response variables (alleles, heterozygosity, and population size respectively), while

Table 2 Proportion of predictions significant at alpha 0.05 level for the three response variables across the five overall hypotheses. Results are shown for both raw response variables and area weighted response variables. Full tables of sig-

nificance of contrast tests are available in the Supplementary Information. Note that hypothesis 2 predicts no differences between pairs of scenarios, thus values of $\alpha < 0.05$ would suggest that this hypothesis should be rejected

Hypothesis	Alleles	Observed heterozygosity	Population size	Weighted alleles	Weighted observed heterozygosity	Weighted population size
1. Conserving the full network is best	100%	80%	60%	0%	60%	0%
2. Small patches have limited benefits	67%	53%	40%	33%	66%	7%
3. The largest patch of core area in a network dominates	100%	100%	100%	90%	85%	100%
4. Corridors do not mitigate for the loss of core areas	48%	64%	40%	36%	40%	24%
5. Overall area of the network dominates	90%	80%	83%	60%	90%	83%
6. Corridors enhance measures of population and genetic diversity	16%	25%	20%	4%	4%	7%

33%, 66%, and 7% of comparisons were significant for the area-weighted variables (Table 2). Since this hypothesis predicts no difference between contrasts, these results do not provide strong support. A closer inspection shows no significant differences when only the smallest patch is removed, but moderate effects when either the medium-sized patch, or both the small and medium patches are excluded (SI).

Hypotheses 3, which proposes that the largest patch of core area dominates the effect, was strongly supported. All predictions showed significant improvements for the raw response variables, while between 85 and 100% of predictions demonstrated significantly improved outcomes for the area-weighted response variables (Table 2).

For Hypotheses 4, which posits that corridors do not mitigate against the loss of core areas, we found moderate support. Specifically, this hypothesis compares the full network of core areas without corridors (Scenario 22), with all scenarios in which core habitat is lost, irrespective of whether corridors are retained. Scenario 22 outperformed the others in 40–64% of predictions. When adjusting for the spatial extent of the conserved area, this support was lower, with significant improvements observed in 24–40% of predictions (Table 2).

We found strong support for Hypothesis 5, which posits that the overall area of the network is the dominant factor. Between 8 and 90% of predictions showed significant improvements for the raw response variables, while 60–90% of predictions indicated improvements in the area-weighted measures (Table 2). These

results are consistent with our earlier finding that both raw and area-weighted response variables are significantly and positively correlated with landscape area (SI).

We found limited support for Hypothesis 6, which posits that corridors enhance measures of population and genetic diversity. A small proportion of the predictions were supported for the raw response variables (16–25% Table 2). However, when we adjusted for the spatial extent of the conserved area, only 4% of predictions showed a significant improvement for alleles and observed heterozygosity, and just 7% of predictions showed a significant improvement in population size. Moreover, the effect of corridors appeared to be linked to the dispersal ability of the species: across all three response variables—and for both raw, and area-weighted measures—a higher proportion of predictions were supported at the 500 kcu threshold than at the 65 kcu level (SI).

Exploring the relationship between habitat fragmentation and measures of population and genetic diversity, we found that all three response variables – total number of alleles, observed heterozygosity, and population size were positively associated with the overall area of the scenario, regardless of the level of fragmentation. However, beyond this area effect, we also found that evidence that habitat configuration plays a critical role. Specifically, scenarios characterized by more compact, less subdivided, and less elongated habitat patches consistently produced better outcomes for population size and genetic diversity (Figures S13–S19 in SI).

Discussion

Land use change through habitat loss remains one of the most severe threats to biodiversity, yet the specific impacts of fragmentation are still not well understood (Fahrig 2017; Riva et al. 2024). In response, many conservation strategies aim to achieve the twin goals of protecting habitat and maintaining connectivity between habitat patches. These goals are encapsulated in the UK government's Lawton Report, which advocates for conservation that is "more, bigger, better and joined" (Lawton et al. 2010), and are central to the GBF's aspiration to set aside 30% of Earth's area as connected protected areas by 2030 (CBD 2022). Despite this, considerable uncertainty persists about how best to design protected area networks, and how to balance or prioritise habitat area versus habitat connectivity (Fahrig 2017; Fletcher et al. 2018; Brodie et al. 2025). This study addresses these questions using Sunda clouded leopards on the island of Borneo as a case study.

When considering the straightforward relationship between habitat area and measures of population and genetic diversity, we find clear evidence that landscapes containing more habitat provide greater benefits for the Sunda clouded leopard than those with less. Our finding that overall habitat extent is associated with higher levels of allelic richness, observed heterozygosity and population size is consistent with a neutral model of genetic diversity (Kimura 1991) and is not unexpected. However, the effects of landscape configuration independent of habitat area-*fragmentation* per se- are both more complex and more contested (Fahrig 2017; Fletcher et al. 2018; Riva et al. 2024; Gonçalves-Souza et al. 2025). Notably, we demonstrate that larger areas are associated with higher levels of allelic richness and population size even when normalised for the spatial extent of the scenario. This suggests that larger habitat areas are more efficient, yielding disproportionately greater increases in population size and allelic richness relative to their size. This pattern holds across all dispersal thresholds, reinforcing our conclusion about the outsized importance of large habitat patches on network design. Fahrig (2017) reviewed ecological response to habitat fragmentation and found that, after accounting for habitat area, most studies reported no significant impact of habitat fragmentation per se, and where significant effects were detected, they

were more often positive than negative. Our result—that larger patches provide a disproportionate benefit – therefore contributes further evidence of a negative impact of fragmentation.

Interestingly, while observed heterozygosity was positively correlated with the overall area of the scenario, area-weighted heterozygosity generally was not. In fact, at higher dispersal thresholds, area-weighted heterozygosity showed a weak but significant negative correlation with area. A similar pattern was reported in Macdonald et al. (2018b), who found that the relationship between landscape resistance (measured using cumulative resistant kernel values) and observed heterozygosity was steeper than that between resistance and allelic richness. Both findings suggest that heterozygosity is particularly sensitive to landscape resistance, and that at of 125 *kcu* and above, all areas of our modelled landscape are effectively connected by dispersal. This pattern is consistent with the importance of large patches of habitat but also suggests that this effect asymptotes such that beyond a certain threshold, further increases in the extent of connected habitat do not yield additional gains in heterozygosity. This observation has important implications for less mobile species, which are likely to experience more pronounced reductions in heterozygosity in response to habitat loss and fragmentation.

Across all metrics, we found that allelic richness, observed heterozygosity, and population size all increased with dispersal ability. This suggests that species with greater dispersal capacity are likely to exhibit lower vulnerability to habitat loss and fragmentation, as they are able to maintain larger, more genetically diverse populations across fragmented landscapes. This is particularly true under model assumptions such as those used here, where dispersal and establishment do not incur additional mortality risk as a result of habitat degradation. However, as highlighted by Cushman et al. (2010) and Kaszta et al. (2019), this positive relationship between dispersal ability and population performance can be misleading in real-world contexts where habitat loss and fragmentation are accompanied by increased mortality risk in the landscape (see also Cushman 2006; Ash et al. 2022; Vasudev et al. 2023). To account for uncertainty in the dispersal ability of the Sunda clouded leopard, we ran our models at a range of dispersal thresholds, however this finding also raises

the importance of future research to refine these estimates.

The findings for Hypothesis 1, which proposed that the full network design would outperform other scenarios, were mixed. While a large proportion of predictions supported this claim when considering the raw response variables, this pattern largely disappeared when adjusting for the total area conserved. This suggests that the apparent benefits of the full network design may be primarily attributable to the overall extent of habitat, rather than the specific configuration of that habitat. This highlights the overriding importance of habitat area in conservation outcomes (Haddad et al. 2015).

Hypothesis 2, that the loss of smaller patches would not have significant impact on the response variables, received mixed support. Overall, there was limited support for the hypothesis: 40–67% of predictions showed significant differences for the raw response variables, and 6–66% showed significant differences for the area-weighted response variables.

However, when examining individual predictions, the pattern appears to be driven by the loss of either the intermediately sized patch (P2.02, SI) or both smaller patches combined (P2.03, SI). We found no evidence that the loss of the smallest patch alone affected conservation outcomes, even when adjusting for area (P2.01, SI). Taken together with the results from Hypothesis 3, these findings suggest that the impact of patch loss correlates with patch size, even when controlling for the area of the patch.

Hypothesis 3, which predicted that the largest patch of core habitat would dominate conservation outcomes was strongly supported. A large majority (85–100%) of predictions showed significantly improved values for the area-weighted response variables when the largest core area was included. This finding aligns with research highlighting the disproportionate importance of large, intact habitat patches in supporting viable populations and maintaining genetic diversity (e.g. Brooks et al. 2002; Gonçalves-Souza et al. 2025), and provides further evidence of the negative effects of habitat fragmentation (Fahrig 2017).

Hypothesis 4, which proposed that corridors would not mitigate the loss of core habitat, received intermediate support. Scenario 22, comprising the full network of core areas without corridors, showed significant benefits in 24–40% of predictions when

compared to scenarios that lost core habitat, regardless of corridor presence. This suggests that while landscape corridors may provide some conservation value, they cannot fully compensate for the loss of large, contiguous habitat patches.

Hypothesis 5, positing that the total area of the network would be the dominant factor, received strong support. Across both the raw and area-weighted measures, 60–90% of predictions showed significant improvements with increasing total conserved area. This underscores the fundamental role of habitat amount in shaping conservation outcomes, consistent with the habitat amount hypothesis (Fahrig 2013).

Finally, Hypothesis 6, which posited that habitat corridors would enhance measures of population size and genetic connectivity, received only limited support. The data indicate that only a modest proportion of the predictions were significant for the raw response variables, and this effect largely disappeared when accounting for the spatial extent of the conserved area. This suggests that, within the context of this study, the apparent benefits of corridors are primarily attributable to the increased habitat area they contribute, rather than to connectivity per se. Notably there was a clear relationship between dispersal ability and the area-weighted effectiveness of corridors: a greater proportion of predictions were supported at higher dispersal thresholds, indicating that corridors become more important when dispersal is high enough to enable substantial exchange through the corridors among the habitat patches. While other studies have demonstrated the potential value of corridors (e.g. Fontoura et al. 2022), their overall effectiveness remains under-evaluated (Cushman 2006), and these findings highlight that both ecological context and spatial scale are critical in determining their impact.

Our findings about the relationship between levels of habitat fragmentation and measures of population and genetic diversity add important nuance to these results. Specifically, these analyses reaffirm the above relationship between landscape area and conservation outcomes but also highlight the importance of landscape configuration. We show that more compact, less subdivided, and less elongated patches lead to better outcomes for population size and genetic diversity (e.g. Figures S15–S17). Corridors, being typically small, narrow, and elongated, tend to perform worse than expected based on area alone. Our results

emphasize the importance of total habitat area, with allelic richness, heterozygosity (H_o), and population size increasing as habitat area increases. However, they also show that landscape configuration contributes in addition to area, with more compact, less subdivided, and less elongated patches again associated with better outcomes. Adding narrow, elongated habitat areas, such as corridors, increases population size, heterozygosity and allelic richness less than would be expected based on the additional area alone. In other words, long, narrow habitat patches such as corridors provide less benefit than if the equivalent area were aggregated onto the edges of larger habitat blocks. Area is the dominant factor, but compaction enhances outcomes. This is likely because elongated patches are less efficient for key population processes such as dispersal and mating. It is easier to find a mate and an available home range within a compact habitat block than across long, complex, branching, and narrow patches.

Collectively, these findings underscore the complex and multi-dimensional influence of landscape configuration on biodiversity outcomes. The consistent importance of total habitat amount, and the disproportionate value of large core areas suggest that conservation planning should prioritise the protection and restoration of extensive, contiguous habitats wherever possible. These results reinforce the central tenets of Systematic Conservation Planning (Moilanen et al. 2009), which emphasise representation, persistence, and efficiency in reserve design, and align closely with Target 3 of the post-2020 Global Biodiversity Framework (CBD 2022), which calls for 30% of land and sea areas to be conserved through well-connected systems of protected areas and other effective area-based conservation measures. To maximise the ecological impact of such efforts, our findings suggest that a focus on habitat quality and spatial configuration—particularly the retention of large core patches – should be a core focus of these goals. Using corridors to enhance connectivity between patches of core habitat remains a useful tool for conservationists in contexts where retention and expansion of large patches is not possible, but tailoring network design to species' ecological traits and dispersal abilities will be critical to ensuring that limited conservation resources are directed strategically and effectively.

The evidence presented here, and elsewhere (e.g. Gilbert-Norton et al. 2010; Riva et al. 2024),

underscores the complexity of the debates surrounding habitat area, configuration, and connectivity. Our study focussed on a specific set of response variables in the context of a single species. While this approach was appropriate for our objectives, it represents just one lens through which the impacts of habitat fragmentation can be assessed. Fahrig's review (2017) included multiple ecological response variables (e.g. abundance, species richness etc.) across a variety of contexts and found examples of where fragmentation had positive, non-significant, and negative impacts. Our study, framed through the lens of modelling the genetic response of a single species offers an example where fragmentation had a negative impact, but also illustrates how the scale of the analysis (single- vs multi-species) and the choice of response variables critically shape interpretation (Brodie et al. 2025). As with any modelling exercise, our work necessarily involved a set of assumptions and simplifications. We sought to ensure that these were realistic (e.g. the use of resistance surfaces from Macdonald et al. (2018b)), valid (e.g. through sensitivity testing of dispersal thresholds), and analytically appropriate (e.g. by excluding peripheral areas to aid interpretability). Nonetheless, the scenarios modelled here should not be interpreted as direct conservation prescriptions for the Sunda clouded leopard on Borneo. Rather, they serve as a theoretical exploration into the relative importance of different design principles for conservation network planning.

Conclusion

A central debate in conservation planning concerns the relative importance of habitat area versus habitat configuration and connectivity. This study contributes valuable insights to that debate by evaluating alternative counterfactual scenarios for the conservation of Sunda clouded leopards on Borneo. Our results show that habitat area is the principal driver of conservation outcomes in this context. Simulation models revealed a non-linear relationship between habitat area and measures of population size and genetic diversity, with larger areas conferring disproportionately greater benefits than expected from a simple proportional increase. Habitat connectivity played a secondary role, becoming consequential only at the highest dispersal thresholds, where fragmented

patches effectively function as a single, connected landscape. These findings highlight the paramount importance of maximising the size of protected areas in conservation planning. They also suggest that investments in connectivity—particularly through movement corridors—should be strategically targeted to highly mobile species. Given the persistent constraint of limited conservation resources, prioritising the protection, consolidation and expansion of core habitat areas may offer a more efficient and impactful strategy for biodiversity conservation than approaches focussed primarily on enhancing connectivity.

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Data availability The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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