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Connectivity conservation to mitigate climate and land-cover change impacts on Borneo

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ABSTRACT

Enhancing connectivity between protected areas is crucial for facilitating species range shifts in response to climate change. Yet spatial planning for this connectivity often overlooks the combined impacts of climate and land-cover change, particularly in tropical regions where habitat loss is a more immediate biodiversity threat.

We explore the need for connectivity between protected areas to mitigate the dual impacts of climate- and land-cover change on Borneo. Using habitat suitability models and combined climate and land-cover change forecasts, we develop connectivity models for present and future scenarios, identifying optimal connections between protected areas for 81 species. By considering restoration and opportunity economic costs, we also explore the cost-benefit trade-offs of implementing connectivity plans.

Connectivity solutions varied among species, but often converged on the same connections between protected areas, with contemporary connections traversing 6 to 40 km and comprising 67 % forest cover, on average. By the 2080s there were fewer connections, and while many were shorter, they also comprised poorer quality habitat, reflecting reductions in forest cover and species distributions. As a result, the economic cost of creating corridors between protected areas was estimated to be 65 % higher in 2080 than in 2020.

Our analysis highlights the urgent need to prioritize connectivity interventions early to maximize long-term benefits for multiple species facing climate-change disruption while minimizing costs. However, conservation planning in tropical regions is complex, given high rates of forest degradation and loss. Implementing our approach at finer spatial scales could help identify cost-effective areas to prioritize landscape connectivity, helping safeguard tropical biodiversity amid changing environmental conditions.

1. Introduction

In past eras of climate change species avoided extinction by either adapting to new conditions or moving to more suitable habitats – typically towards higher latitudes or elevations (Martínez-Meyer et al., 2004). This trend of poleward and upslope terrestrial range shifts is now a prominent feature of the Anthropocene, and expected to continue into the future (Chen et al., 2011; Parmesan, 2006; Warren et al., 2018). Yet, contemporary changes to both climate and land-cover now require species to move much larger distances and more quickly than they would have done in the past (Nogués-Bravo et al., 2018). As species follow major shifts in suitable bioclimatic habitats, the required movements often involve crossing highly modified landscapes, which present suboptimal conditions for wildlife (McGuire et al., 2016; Platts et al., 2019). This poses significant challenges for conservation planning if we are to ensure species have the capacity to track suitable climates between protected areas in response to climate change (Struebig et al., 2015; Ward et al., 2020).

Improving connectivity is frequently invoked as a key climate adaptation strategy in biodiversity conservation (Keeley et al., 2018).

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Landscape connectivity – i.e. the degree to which landscapes facilitate or impede movement – promotes the persistence of populations (Gonzalez et al., 1998), species diversity (Damschen et al., 2006) and dispersal processes (Gilbert-Norton et al., 2010), which in turn can maintain ecological processes over large spatial scales (Heller and Zavaleta, 2009). In practice, this connectivity can be achieved by identifying landscape linkages in the form of corridors, greenbelts and/or stepping stones of habitat patches (Heller and Zavaleta, 2009). However, to ensure connectivity is 'climate wise', landscapes should facilitate animal and plant movements in response to climate change – i.e. be able to connect current habitat to habitat that will remain suitable or become more suitable in the future (Hodgson et al., 2011). Despite the need for such climate connectivity being recognised for some time, only recently have studies examined how this can be genuinely achieved across human-modified landscapes (Keeley et al., 2018; Littlefield et al., 2019).

The study of connectivity – and thus the potential for species movements - from suboptimal to optimal habitats in future environmental conditions has been implemented in multiple ways. A common approach is to characterise structural connectivity (i.e. a landscape-centred analysis), which circumvents the need for species data by defining analogue climates of the contemporary species range, and tracking these conditions in the future (Keeley et al., 2018). For example, accounting for future climates in the modelling proved to be a valuable tool in identifying a limited number of available movement routes across western North America (Littlefield et al., 2017). Other assessments detail the connectivity needs of focal taxa using fine-scale distribution data, assuming that these serve as umbrella species for broader biodiversity interests. In China, for example, five of eight corridors defined for giant panda were found to overlap with those proposed for six sympatric species assessed (Wang et al., 2018). Increasingly, assessments work with modelled distributions of many taxa to define 'meta-corridors' that meet the needs of multiple species for the same conservation investment. For example, Choe et al. (2017) modelled the distributions of 2297 plant species and identified three corridors to link currently inhabited areas to climatically suitable areas in the future for the majority. While multi-species approaches can provide informative insights over large spatial scales, including whole countries and continents, they often miss crucial information on land-cover composition and change, or rely on coarse proxies of how this could influence species movement (Choe et al., 2017; Lawler et al., 2013).

Evidence from movement studies reveals that many species have already changed behaviours in areas of high human impact, and are selecting precarious travel routes (Tucker et al., 2018). In many parts of the world wildlife populations are now poorly placed to make the movements needed to track climatically-suitable habitat, owing to anthropogenic land-uses and/or barriers. This situation is particularly concerning in tropical regions, which continue to experience high rates of forest degradation and loss (Vancutsem et al., 2021). Moreover, future tropical forest landscapes are expected to be more diminished and fragmented (Edwards et al., 2019), emphasizing the need to develop spatial connectivity plans that are robust to future changes in land-cover as well as those in climate. The case for spatial connectivity planning is particularly compelling for protected areas, which remain the foundation of conservation activities across the world, and are crucial for achieving biodiversity targets of the Kunming-Montreal Global Biodiversity Framework (https://www.cbd.int/gbf/targets).

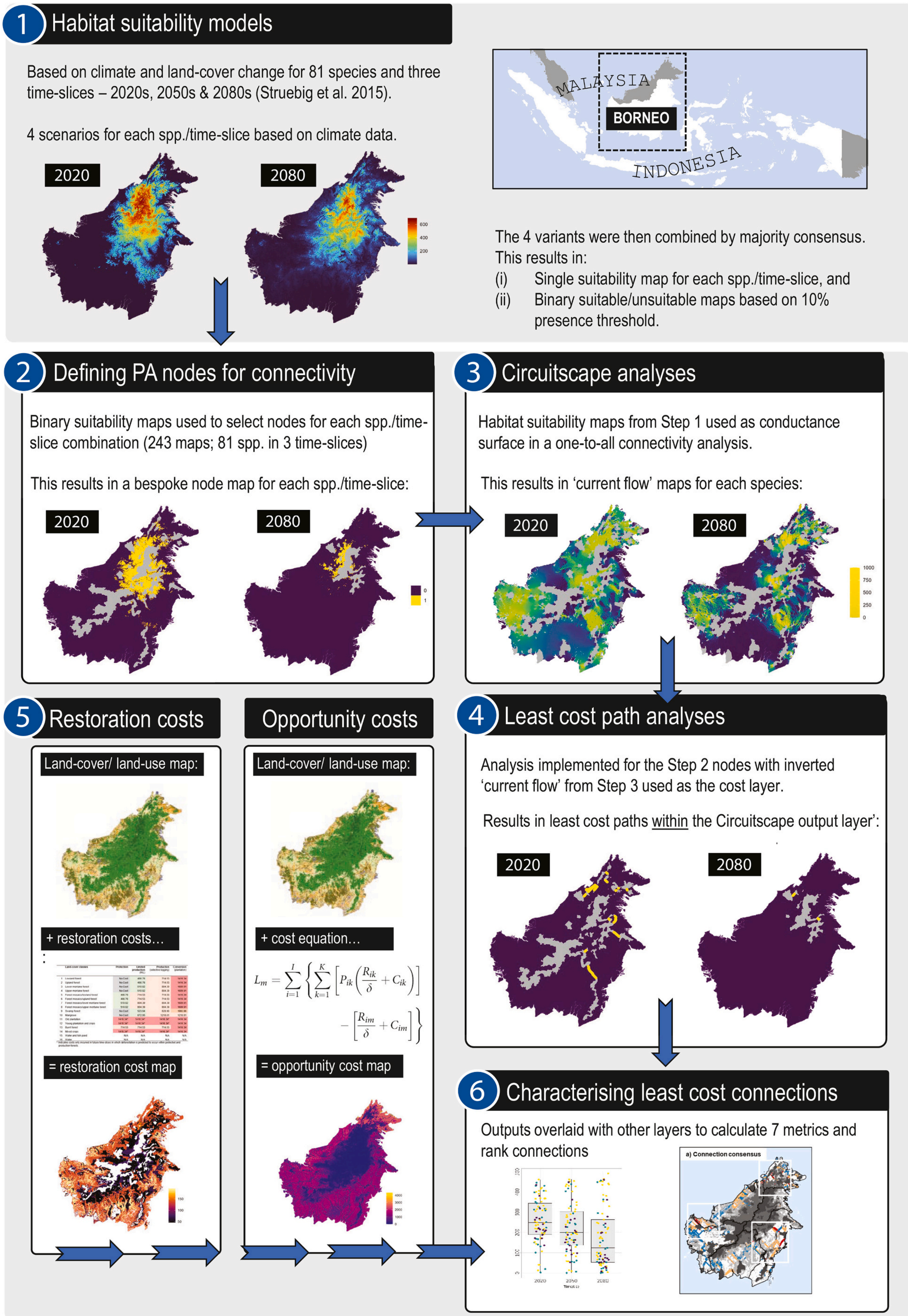
For corridors in tropical countries to be most successful they should provide connections through suitable habitat in current and future conditions, while being affordable to establish, thus freeing up conservation funds to be spent elsewhere. Yet evaluations of the climate connectivity and economic costs of corridors in tropical countries remain scarce. We know from evaluations in temperate regions that protecting movement corridors to connect climatically-suitable areas adds significant costs to conservation (e.g. by at least 18 % in the USA, Lawler et al., 2020). However, many tropical forests are already incapable of facilitating range shifts, and almost a third of climate connectivity was lost between 2000 and 2012 (Senior et al., 2019). The uncertain costs of restoring tropical forests adds to this problem, with upper estimates for merely starting restoration ranging from US$ 3880 to $25,830 per hectare, depending on whether natural or active regeneration is involved (Bodin et al., 2022). It is therefore possible that climate connectivity may be difficult to achieve in some tropical settings, and/or prohibitively expensive to implement. To date, however, few assessments have considered the cost-benefit trade-offs involved in implementing connectivity plans, and those that have worked at large regional scales and relied on crude opportunity cost and carbon payment data (Jantz et al., 2014).

Here we characterise climate connectivity and the cost-benefit trade-offs that may arise in Borneo. This megadiverse island, shared by three countries, exemplifies many of the challenges faced in connectivity planning in tropical regions. In addition to transboundary challenges, the protected area system is also large, scattered and fragmented, which is especially problematic for species expected to experience significant climate- and land-cover change impacts (Struebig et al., 2015). Indeed, spatial analyses of Indonesia's protected areas showed human pressures such as forest conversion and infrastructural expansion increased outside parks in recent years, particularly in the lowlands of Kalimantan (Dwiyahreni et al., 2021). In a previous study (Struebig et al., 2015) we generated habitat suitability maps for 81 mammal species, and used these data to identify 28,000 km^2 of forest to help safeguard biodiversity from future environmental change. Here, we build on those analyses to identify areas that could maximize connectivity between protected areas on Borneo, and be used as potential pathways to facilitate range shifts for multiple species responding to climate change. Potential connections between protected areas were identified for the 81 taxa by combining the species distribution information under environmental change forecasts with connectivity models. Among the many potential connections available, we identified those that had the greatest value for multiple species in the assessment. We first asked whether the areas delineated to enhance connectivity between protected areas in current environmental conditions would continue to provide this function under forecasts of climate- and land-cover change. Given the many potential connectivity solutions, but limited funds for implementation, we then integrated habitat quality and cost information to help prioritize the most effective connections for long-term biodiversity conservation and climate-change mitigation efforts on Borneo.

2. Methods

2.1. Areas of suitable habitat for Bornean mammals

Our assessment was based on three mammal taxonomic groups (13 primate species, 23 carnivores, 45 bats; 81 in total), for which sufficient distribution information was available and previously published (Struebig et al., 2015). These included specialists and generalists, threatened and non-threatened taxa, and several conservation flagships. We previously delineated areas of suitable habitat for these species under multiple climate- and land cover change forecasts (Fig. 1; Supplementary materials; Struebig et al., 2015). Briefly, under this framework a baseline distribution model based on 2020 bioclimatic data was generated for each species using 10-years of location records, and projected into future climates for the 2050s and 2080s at 1-km^2 resolution. Each output was then refined using a habitat suitability index based on land-cover and human population information to define the extent of potential suitable habitat (from poor to high, 0–1) for each species in the future. We used binary habitat suitability maps (10 % presence threshold, distinguishing between suitable and unsuitable habitat) to ensure that species-specific connectivity models were restricted to only those protected areas where a species was expected to be present (i.e. the maximum area of extent). Our full assessment utilised predictions from several climate and land-cover change scenarios to account for



$$L_m = \sum_{i=1}^{I}\left\{\sum_{k=1}^{K}\left[P_{ik}\left(\frac{R_{ik}}{\delta}+C_{ik}\right)\right] - \left[\frac{R_{im}}{\delta}+C_{im}\right]\right\}$$

(caption on next page)

Fig. 1. Analytical workflow to identify protected area connections that help maintain connectivity and facilitate range shifts for mammal species in Borneo. Maps for each step represent a typical restricted-range species (Hose's civet, *Diplogale hosei*) and are shown for 2020 and 2080 only. The habitat suitability maps for each species (Step 1) were generated in an earlier study (Struebig et al., 2015), and used here to define protected area nodes (Step 2) for Circuitscape (Step 3) and least cost path analyses (Step 4). The outputs of these connectivity analyses were overlaid with estimated economic cost maps (Step 5) to characterise each connection in terms of its species representation, landscape characteristics and cost (Step 6).

uncertainty in the environmental forecasts (Struebig et al., 2015). For the connectivity analyses presented here, we combined information from each of the thresholded habitat suitability maps (i.e. a majority consensus) for each species to generate a single predicted presence-absence map for each species and time-slice depicting the combined effects of climate and land-cover change. The connections delineated can therefore be viewed as potential pathways to facilitate species movements in response to climate change, while also accounting for deforestation predictions.

2.2. Connectivity modelling

Connectivity between suitable protected areas was first delineated for each species using Circuitscape version 4.0.5 (McRae et al., 2008) and then further refined using a least cost algorithm implemented in R via the gdistance package (Van Etten, 2017). The Circuitscape algorithm uses electronic circuit and random walk theories to simulate animal movements between suitable patches or points across areas of variable landscape conductance. The resulting 'current flow' maps can be viewed as potential movement patterns between source and target nodes for random individuals of a species (Littlefield et al., 2017).

We constructed two layers required for running Circuitscape for each of the 243 species/time-slice combinations: one defining the source/target nodes for which connections were to be established, and a second defining landscape conductance (i.e. the permeability of the landscape for animal movement) (Fig. 1). Source/target nodes were set as the protected areas (national parks, wildlife reserves and other protected forest areas, https://www.protectedplanet.net), combined with the additional 28,000 km^2 of upland forest prioritised in our previous spatial conservation planning assessment (Struebig et al., 2015). For the conductance layer we utilised the habitat suitability maps previously produced for each species and time-slice. Thus, the resulting connectivity network was designed to facilitate species movements between important conservation areas within a time-slice (2020s, 2050s, 2080s), and involved 243 Circuitscape models (i.e. 81 species in three time-slices).

We then implemented a least-cost path analysis on each of the current flow outputs for each species and time-slice to delineate potential linkages between the protected areas. For this we used the gdistance package with the 'shortestPath' function. We restricted the analysis to potential paths in human-modified landscapes, since protected areas within the central region of Borneo are already connected by forest. Further details on connectivity procedures are described in the Supplementary materials Appendix 1.

2.3. Economic cost of corridors

To estimate the potential economic cost of implementing corridors, we estimated the forest restoration costs for each least-cost path identified, as well as opportunity costs of forgone development to other major land-uses: oil palm agriculture, timber plantations, and logging. These economic costs were linked to a Borneo-wide land-use map, and extracted per km^2 grid cell for each connection path generated for each species. The economic cost estimates were generated and mapped as follows:

Restoration cost was based on the standard expenses of restoring a forest, as prescribed by the Indonesian Ministry of Environment and Forestry, and supplemented by additional technical reports, government regulations and personal communications (Budiharta et al., 2018, 2014). Restoration included expenses associated with planting activities and maintenance, and for degraded peatlands included the cost of hydrological rehabilitation (Table S1). To demarcate potential restoration costs, we combined land-cover information with a land-use map compiled for the three nations of Borneo. Forest was categorised into four classes depending on whether it was assigned for protection, production (selective logging), limited production (using reduced impact logging techniques) or conversion to other land-uses (Table S2). Forested land in protected areas was assigned zero cost, since this land is already formally assigned for conservation. For future time-slices we applied a deforestation model (Struebig et al., 2015) to produce the expected land-cover map for that period together with its associated restoration costs.

To estimate opportunity costs we used the following equation from Runting et al. (2015) to calculate cost for each land-use category:

$$L_m = \sum_{i=1}^{I} \left\{ \sum_{k=1}^{K} \left[P_{ik} \left(\frac{R_{ik}}{\delta} + C_{ik} \right) \right] - \left[\frac{R_{im}}{\delta} + C_{im} \right] \right\} \quad (1)$$

where L_m is the opportunity cost of land-use m (L_m is ≥ 0), P_{ik} is the probability that cell i will be converted to land-use k (the outcome of the deforestation model used to forecast land-cover changes in future time-slices – Supplementary materials), R_{ik} is the average annual profit/loss associated with land-use k for parcel i, δ is the discount rate, C_{ik} is the profit/loss from converting cell i to land-use k, R_m is the average annual profit from land-use m for cell i and C_{im} is the profit/loss from converting cell i to land-use m.

We assumed that the most lucrative land-use of forests would be reduced impact logging (RIL), and in deforested areas it would be oil palm plantation. Therefore, in forested areas we used the net present value (NPV) of RIL, defined as annual profits discounted into perpetuity, less the NVP of the selected land-use within the corridor. In deforested areas we used the NPV for oil palm production (average yearly profit discounted into perpetuity, plus profits from the timber harvest when forest was converted) less the administrative costs of conversion as well as the NPV of the selected land-use. A full description of the information used to parameterize the cost analyses is provided in Runting et al. (2015). A 10 % discount rate was set throughout and costs were defined in US dollars in 2020.

2.4. Ranking corridors

There are multiple ways that connections could be prioritised, for example, based on species representation, logistical and/or political constraints, or potential economic cost. However, for corridors to be an effective return on conservation investment it is important to ensure they fulfil biodiversity objectives as a first step. Therefore, among the possible connections where corridors could be established, we ranked them according to the number of species represented, to identify a portfolio of primary linkages which, if targeted, could benefit the most species. We then implemented a second ranking based on potential economic cost to identify the cheapest investments for connectivity.

3. Results

Connectivity solutions varied substantially among the species assessed, but many converged on the same protected area connections (Fig. 1). Based on the habitat suitability information for 2020, between 3 and 462 connections were selected across the 81 species (median across species =250) from 10 to 376 protected area nodes (median = 244)

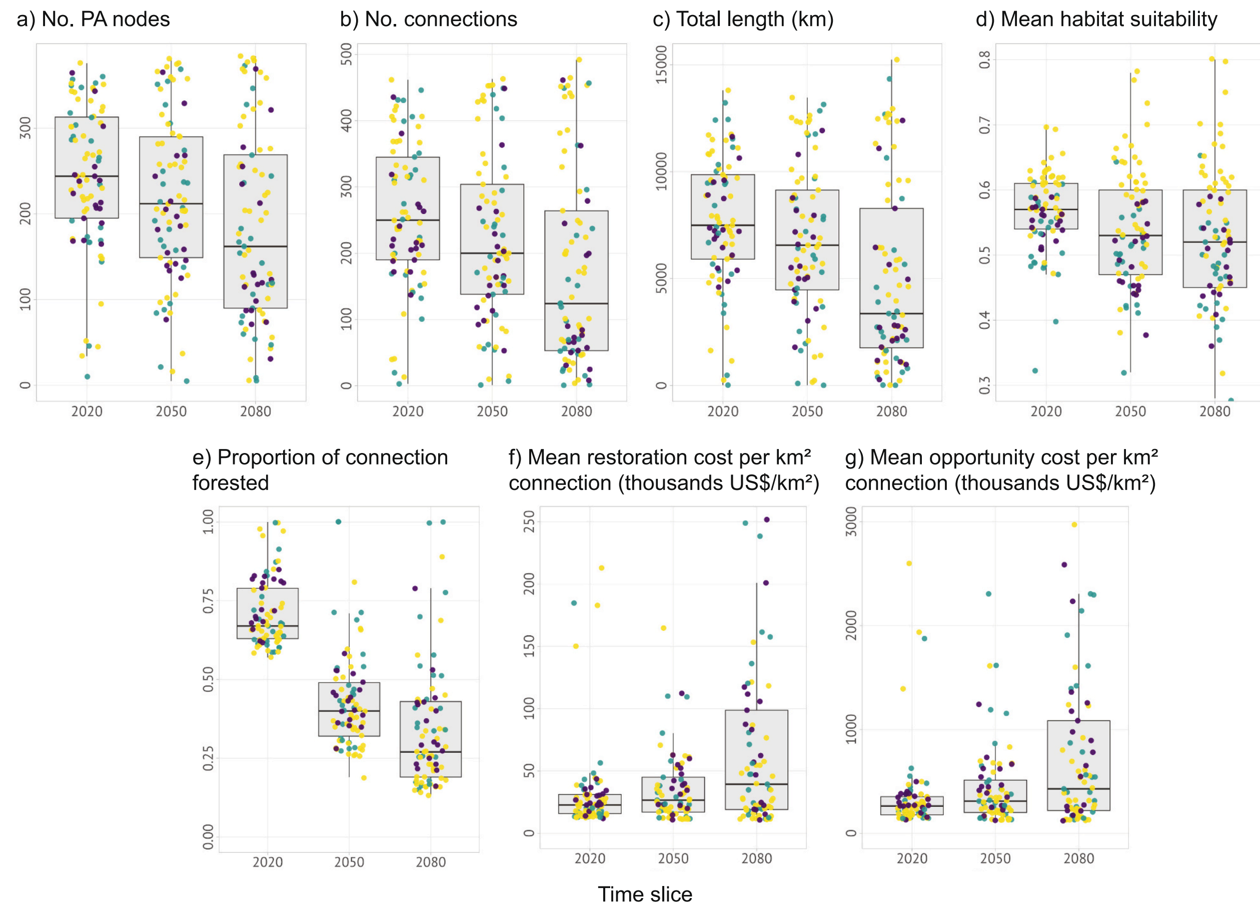


Fig. 2. Characteristics of connections delineated to accommodate range shifts between protected areas in Borneo for 81 mammal species. (a) the number of forest nodes to connect; (b) the number of resulting connections identified between nodes; (c) total length of all connections identified; (d) average proportion of $1km^2$ cells within connections that are forested; (e) mean habitat suitability of connection across species; (f) mean implementation cost per corridor; (g) mean opportunity cost per connection. Connection solutions were sought separately for each species between protected areas and climatically suitable areas delineated under a combined land-cover and climate change scenario. Boxplots show the median, range and interquartile range of values for the 81 mammal species (blue points, bats; green, carnivores; yellow, primates). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 2). Connections through human-modified landscapes ranged from six to 40 km in length (median across all species possibilities, 30 km) and were typically 67 % forested (range, 57–100 %).

In contrast, the 2080 configuration was based on fewer protected areas to connect (i.e. fewer nodes; median = 162) and typically comprised around half the number of connections (median = 124) as a result of reduced forest extent and subsequent range contractions predicted for many of the species by the end of the century (Fig. 2). Many connections were shorter, and comprised less suitable habitat compared to connections selected in 2020; average habitat suitability for species within connections was marginally lower in 2080 than in 2020. Similarly, the amount of each connection expected to be forested in 2080 was much lower than in 2020 (median = 27 %). While the extent of these changes varied among species, the overall trends were consistent among the three taxonomic groups assessed (Supplementary material, Appendix 3). We reran the analyses to generate connections based on present-day habitat suitability data modelled for future time-slices, and vice-versa, and came up with similar findings. Therefore, we limit our reporting to model outcomes specific to each time-slice here.

Given the large differences in forest cover within the potential connections identified, the estimated restoration costs to establish corridors within these areas were also highly variable. Each species connectivity model generated a least-cost path between protected area nodes for which costs could be estimated by overlaying our cost maps. The restoration costs associated with implementing the corridors identified for 2080 were 72 % higher than those for 2020 (median: 22,800 vs. 39,310 US$ /km), reflecting the logistical burdens of restoration in highly deforested regions (Fig. 2). This preponderance of connections through suboptimal mosaic habitat also led to much higher opportunity costs for foregone agricultural development, increasing by 64 % from 2020 to 2080 (median: 263,220 US$ /km in 2020 versus 432,600 in 2080). Combined, the restoration and opportunity costs of creating corridors were 65 % higher in 2080 than in 2020. Thus, overall, and given the reduction of viable corridor options and increasing cost, it is better to tackle connectivity now rather than in the future.

Of the 669 possible connections identified in analyses, 358 represented fewer than 50 % of the species evaluated in each time-slice, and thus were deemed the lowest priority for immediate conservation investment (Blue; Fig. 3). Conversely, only 19 connections would represent >75 % of the species evaluated in each timeframe. These primary connections, distributed across the island, ranged in length from <1 km in Sabah to 122 km in East Kalimantan (Table 1). Some would be highly costly to implement, but would yield high returns for biodiversity (e.g. Tawau Hills to Ulu Segama linkage in Sabah). Yet, others could still be important for many species at much lower cost (e.g. Lesan to Jele to Mengapoh, in East Kalimantan). Importantly, costs for corridors implemented in these areas would be comparable now and in the future, and all would contribute to species connectivity objectives.

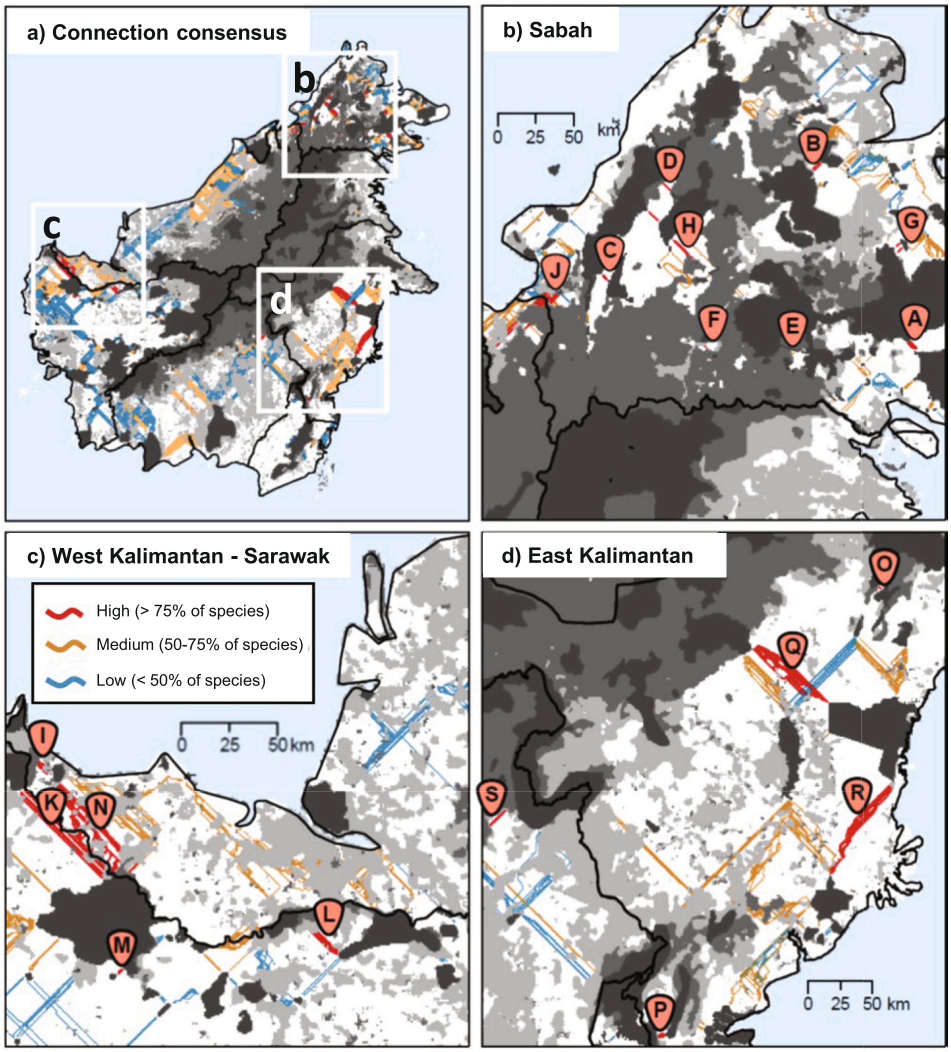


Fig. 3. The highest ranking connections based on species representation to help maintain population connectivity for mammals among Borneo's protected areas, and facilitate range shifts in response to climate and land-cover change. Map (a) shows connectivity patterns over Borneo derived using a combination of circuit theory and least-cost analysis. All potential connections are presented as the consensus of connectivity analyses implemented for each species-timeframe combination. Connections are colour coded based on quartiles of the species numbers represented in each one. For example, red depicts the connections derived for at least 75 % of all species in the analysis for all timeframes (182 of 243 possibilities in 2020, 2050 and 2080) – i.e. the 19 primary connections that will serve at least 75 % of species both now and in the future (see Table 1 for further information). Maps b–c show the primary connections in various parts of Borneo with labels referring to connections in Table 1. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

4. Discussion

We present a broad appraisal of multi-species connectivity opportunities across Borneo, and demonstrate that future reductions in suitable habitat, particularly in the coastal lowlands, will lead to reduced landscape connectivity for multiple taxa. The costs associated with developing new connections between protected areas will be high, particularly in highly modified parts of the island. Such an analysis is highly scale dependent, and so the connections we identify should be viewed as approximate, from which more detailed landscape-level appraisals will be required to prescribe specific connectivity interventions. These interventions might include linear corridors of natural habitat, but also "stepping-stones" or pattern-based linkages with the aim to promote connectivity by improving the permeability of the landscape for movement and dispersal (Ng et al., 2021).

Species ranges have shifted, and will continue to shift, to more suitable elevations and latitudes in response to climate change. The size of the range shift needed is particularly challenging for many tropical species that are already near their thermal optima, and have little capacity to track shallow latitudinal gradients in temperature (Colwell et al., 2008; Mata-Guel et al., 2023). Habitat loss adds to this problem by further hindering the dispersal abilities of climate-affected species (Newbold, 2018; Struebig et al., 2015). Maintaining habitat connectivity across landscapes will therefore be vital to facilitate species range shifts and avoid extinctions, particularly among protected areas. Yet, globally fewer than 10 % of protected areas are structurally connected via intact land (Ward et al., 2020).

Pantropical analyses have demonstrated that species can be expected to experience a temperature increase of ∼4 °C in areas with limited structural connectivity, compared to 2.6 °C in complex habitats where they are able to disperse (Senior et al., 2019). Consequently, efforts to promote structural complexity and contiguous forest cover will have disproportionate benefits in human-modified tropical landscapes where connectivity is typically low. Such improvements, through conservation set-asides or habitat restoration, can benefit some specialist, highly forest-dependent species, many of which are threatened (Deere et al., 2022), and are also sensitive to shifts in microclimate (Jucker et al., 2020; Sunday et al., 2014). Recent studies have demonstrated that as

Table 1
Characteristics of the 19 most important connections between protected forests of Borneo. Connections were identified from connectivity analyses for 81 mammal species to account for changes in land-cover and climate change between 2020 and 2080. Priority connections include all those with viable habitat for at least 75 % of all species in 2020 and 2080, and are presented in order of species representation for each administration. Costs are presented for the entire potential corridor as an average across all potential connections identified for that route through the modelling. The location of each connection is shown in Fig. 3.

				2020					2080				
		Forest blocks connected	Length (km)	% species present	% forested	Mean habitat suitability	Mean opportunity cost (1000s USD)	Mean restoration cost (1000s USD)	% species present	% forested	Mean habitat suitability	Mean opportunity cost (1000s USD)	Mean restoration cost (1000s USD)
Sabah, Malaysia:													
A	16_22	Tawau Hills to Ulu Segama	6.1	0.94	0.06	0.55	23,846	1362	0.93	0.11	0.56	22,787	1302
B	405_444	Bidu-Bidu to Bukit Kuamas	5.8	0.91	0.04	0.41	16,757	1257	0.86	0	0.4	16,815	1181
C	19_370	Crocker Range to Tenom	3.2	0.86	0	0.36	4864	979	0.88	0	0.37	4865	979
D	19_442	Crocker Range to Tambunan	8.5	0.88	0.15	0.45	22,538	1891	0.86	0.12	0.45	22,594	1963
E	16_322	Ulu Sungai Napagon to Gunung Magdelina	0.8	0.84	0.50	0.69	1488	284	0.79	0.43	0.71	2570	339
F	298_309	Sungai Siliawan to Sungai Sansiang	9.0	0.85	1.71	0.68	12,386	1507	0.70	0.33	0.62	12,622	1552
G	16_365	Malua to Lamag	2.9	0.90	0	0.34	12,907	745	0.60	0	0.42	12,326	702
H	349_442	Tambunan to Milian-Labau	19.0	0.86	0.23	0.55	60,089	3267	0.72	0.16	0.54	60,269	3349
Sarawak Malaysia:													
I	14_238	Gunung Gading to Samunsam	12.0	0.83	0.52	0.57	17,816	2600	0.79	0.31	0.52	17,588	2484
J	21_339	Ulu Temburong	65.3	0.90	0.69	0.71	106,081	10,389	0.86	0.49	0.67	99,673	10,701
West Kalimantan, Indonesia:													
K	14_457	Gunung Nyiut to Gunung Melintang	65.7	0.88	0.30	0.6	95,248	13,442	0.86	0.08	0.53	95,513	12,587
L	203_204	Nangahemara to Gunung Kumbu	26.6	0.88	0.48	0.63	67,002	4800	0.74	0.16	0.56	65,268	4657
M	191_457	Gunung Empoho to Gunung Setutuk	3.1	0.88	0	0.48	7314	700	0.67	0	0.53	7365	700
N	238_457	Gunung Nyiut to Gunung Gading (Sk)	66.3	0.83	0.44	0.71	131,490	13,375	0.79	0.12	0.6	115,366	11,962
East Kalimantan, Indonesia:													
O	228_241	Sungai Lesan to Sungai Jele to Sungai Mengapoh	2.0	0.88	0.74	0.67	6315	304	0.79	0.95	0.71	6301	258
P	8_125	Gunung Lumut to Sungai Samu	5.5	0.85	0.02	0.56	12,659	885	0.80	0.08	0.59	11,758	841
Q	212_456	Kutai to Mahakam	77.8	0.85	0.06	0.57	153,536	10,891	0.68	0.02	0.61	153,929	10,591
R	116_212	Kutai to Bukit Soeharto	92.7	0.85	0.17	0.59	171,845	17,872	0.67	0	0.6	170,887	16,802
Central Kalimantan, Indonesia:													
S	24_145	Bukit Sapat Huwung	32.4	0.72	0.51	0.63	48,003	3232	0.86	0.44	0.65	48,006	3205

well as adding to habitat area, linear forest remnants help buffer microclimatic extremes experienced in open cultivated areas (Williamson et al., 2020; Zhang et al., 2023), and thus offer some potential as refuges and movement corridors for wildlife (Gray et al., 2022), even if only temporary.

Meta-community models demonstrate that short corridors connecting large patches benefit more species in the long-term than longer corridors or smaller patches (Brodie et al., 2016). Intuitively, these shorter corridors would be less expensive to implement than longer ones. Yet, because the impacts of climate- and land-cover habitat suitability and species distributions accrue over time, we show that longer connections between protected areas will be needed in the future, bringing additional economic costs. The onus should therefore be on conservation to secure climate connectivity early when it has the greatest long-term benefits and is less expensive to implement, especially given that funding is limited and that preserving all possible connections between protected areas is an unrealistic goal. There is a significant trade-off between these two objectives: the highest priority connections for biodiversity value are not necessarily the cheapest to implement. Nevertheless, seeing the relative value of various potential connections available provides an important step in prioritising connectivity interventions.

An important caveat in our study is the additional costs associated with restoring degraded peatlands, which make connections through peatland habitat exceedingly expensive and seemingly low priority. However, protecting or enhancing structural complexity in these habitats brings additional benefits, such as maintaining key carbon stocks (Budiharta et al., 2018; Girkin et al., 2022; Law et al., 2015) and minimizing the probability, frequency and intensity of fire (Harrison et al., 2024), which are not captured within our analysis. The coarse scale of our study also limits the ability to model fine scale features, such as roads or rivers, which may act as barriers to movement, especially for non-volant species, and require further restoration and/or mitigation, such as artificial canopy bridges (Chan et al., 2020). The responses, and mitigation of these potential barriers are likely to be highly site- and species-specific (Brunke et al., 2019), thus requiring fine scale local assessments to direct connectivity initiatives on the ground.

We identified several important connections with high consensus among species (i.e. important for >75 % of species assessed (Fig. 3). One such connection in the southeast of Sabah connects Tawau Hills and Ulu Segama protected areas, and has recently been designated as a wildlife corridor by the Sabah Forest Department. We also identified at several important connections within the vicinity of Indonesia's planned new capital city in East Kalimantan, providing an opportunity for developers to mitigate the expected impact of the new capital's development (Spencer et al., 2023) by fostering improved landscape permeability in this region. There has been previous concern of greenwashing and wasteful conservation resources in the implementation of corridors in Southeast Asia, and it is clear that significant green investments are needed to ensure success. For example, the locations of underpasses and corridors in Malaysia in the early 2000s were largely defined by river or topographic features, rather than ecological modelling, and have since experienced very limited success in facilitating species movement (Jain et al., 2014). Nevertheless, early insights from wildlife overpasses across urban infrastructure in Singapore suggest some success in maintaining wildlife connectivity over short distances (Elangovan, n.d.).

Connectivity assessments typically focus on single species, commonly those that can serve as umbrellas for other taxa. For some species the umbrella status can be justified (e.g. giant panda, Wang et al., 2018), but in other cases there is limited transferability of corridors designed for one species to another (e.g. in Gabon, Vanthomme et al., 2019). Our multi-species modelling provides some assurance that many connections between protected areas have the potential to benefit a large number of species. However, implementing connectivity interventions within these areas may enable species dispersal but it does not guarantee it. Other factors, such as edge tolerance and pressure from the surrounding matrix, may impede the ability of species to disperse (Gray et al., 2022). Advances in spatially-explicit individual based models offer powerful planning tools to designate conservation linkages to provide functional connectivity (Seaman et al., 2024). Although future research may take advantage of these advances, for Borneo much of the information on species dispersal behaviour and demography is lacking. Increasing our understanding of species dispersal and movement behaviour, particularly in heavily modified landscapes (e.g. for clouded leopards, (Kaszta et al., 2024), should therefore be a priority for future research.

Given the pace of climate- and land-cover change, establishing effective policy and initiatives aimed at promoting functional connectivity should be a priority to facilitate species range shifts and safeguard Borneo's biodiversity into the future. Acting now to establish connectivity will not only benefit Borneo's biodiversity, but also reduce the monetary and opportunity cost. We should also expect connectivity interventions to help further the core objectives of protected areas, which have slowed deforestation in Borneo (Morgans et al., 2024), but experienced heightened anthropogenic threats along their borders (Dwiyahreni et al., 2021). Such pre-emptive action is necessary to ensure sufficient time for restoration plantings to mature before the impacts of climate change intensify species' range shifts. In fact, capitalising on global impetus for restoring forests may be a useful way to help finance connectivity initiatives, especially since restoration objectives often enhance biodiversity conservation when implemented systematically (Tobón et al., 2017). Swift action is especially important for corridors in deforested areas (relative to moderately or lightly degraded forest), as restoring structural complexity to facilitate animal movement will require additional time. Ultimately, the successful establishment of wildlife corridors in priority areas will require more fine-scale, detailed assessments to inform and implement site-specific conservation actions.

CRediT authorship contribution statement

Matthew J. Struebig: Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Moritz Wenzler:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis. **Rebecca K. Runting:** Writing – review & editing, Formal analysis. **Elizabeth Law:** Writing – review & editing, Investigation, Formal analysis, Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft. **Sugeng Budiharta:** Writing – review & editing, Methodology, Data curation. **David Seaman:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Stephanie Kramer-Schadt:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Conceptualization.

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Declaration of competing interest

The authors of this manuscript have no conflicts of interest to disclose.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110838.

Data availability

Example data and analytical scripts associated with this manuscript can be accessed at https://github.com/EcoDynIZW/Struebig_2024_BIOCON.

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