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Incorporating connectivity into conservation planning for optimal representation of multiple species and ecosystem services

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ABSTRACT

Current conservation planning tends to focus on protecting species ranges or landscape connectivity but seldom both – particularly in the case of diverse taxonomic assemblages and multiple planning goals. Therefore we lack information on potential tradeoffs between maintaining landscape connectivity and achieving other conservation objectives. Here we develop a prioritization approach to protect species ranges, different ecosystem types, and forest carbon stocks, while also incorporating dispersal corridors to link existing protected areas and habitat connectivity for protection of range-shifting species. We apply our framework to Sabah, Malaysia, where the State Government has mandated an increase in protected area coverage of ~305,000 ha but without having specified where the new protected areas will be. Compared to conservation planning that does not explicitly account for connectivity, our approach increased the protection of dispersal corridors and elevational

connectivity by 13% and 21%, respectively, while decreasing the coverage of other conservation features by 0% (vertebrate and plant species ranges; forest types), 2% (forest carbon), and 3% (butterfly species ranges). Hence, large increases in the protection of landscape connectivity can be achieved with minimal loss of representation of other conservation targets.

INTRODUCTION

Protected areas are critical but insufficient for mitigating the impacts of habitat loss, which is the principal threat to global biodiversity (Laurance et al. 2012; Gray et al. 2016). In 2010, signatories to the Convention on Biology Diversity adopted a commitment to protect 17% of global land and inland sea surface area by 2020 (known as Aichi Biodiversity Target 11). As of July 2018, the coverage of terrestrial protected areas had reached 14.9%, which implies that achieving the target requires an additional ~2.8 million km^2 of protected areas globally by 2020 (UNEP-WCMC 2018). Locating new protected areas in the lowland tropics, and especially in Southeast Asia, would contribute disproportionately to global biodiversity conservation through avoided deforestation in biodiversity hotspots (Myers et al. 2000).

Determining the most important areas for additional conservation measures requires prioritizing multiple objectives. Many conservation plans have sought to maximize the representation of species ranges (Pressey et al. 2007). Indeed, powerful and widely-used prioritization tools such as Marxan (Ball & Possingham 2000) and Zonation (Moilanen 2007) have helped planners optimize the selection of new conservation areas on every continent (Sinclair et al. 2018). Other prioritization plans have explicitly focused on landscape connectivity (e.g. Gordon et al. 2009; Lehtomäki et al. 2009; Sirkiä et al. 2012), as this is known to affect metapopulation persistence (Fahrig & Merriam 1994; Hanski & Ovaskainen

2000), the supply of ecosystem services (Kukkala & Moilanen 2017), and organisms' adaptive capacities in the face of climate change (Scriven et al. 2015; Reside et al. 2017). The technical capacity for assessing connectivity and determining optimal locations for habitat corridors is growing rapidly (e.g. Lehtomäki & Moilanen 2013; Pouzols & Moilanen 2014; Brodie et al. 2016; Daigle et al. 2018).

Far fewer conservation plans, however, have attempted to simultaneously optimize landscape connectivity and the representation of multiple conservation features (Reside et al. 2017; Harlio et al. 2019), particularly for multi-species assemblages, over large landscapes, and in the context of diverse planning goals (Magris et al. 2018). Simultaneously accounting for both representation of conservation features and connectivity increased the predicted average population size of Mediterranean fishes by ~66% (Magris et al. 2018) and the average metapopulation capacity (a proxy for population persistence) of Australasian mammals by 5-fold (Strimas- Mackey & Brodie 2018). But jointly optimizing connectivity and representation has seldom been attempted with more diverse taxonomic assemblages and multiple conservation objectives (e.g., species ranges, ecosystem services, habitat types).

Moreover, existing approaches to incorporating connectivity into conservation planning tend to focus on single aspects of connectivity. For example, corridors may be identified so as to maintain dispersal among habitat patches and thereby enhance metapopulation stability (Fahrig & Merriam 1994; Hanski & Ovaskainen 2000), or to provide movement routes by which organisms can shift their distributions in response to climate change (Scriven et al. 2015; Reside et al. 2017). However, simultaneously incorporating the different facets of connectivity into planning has been done much more rarely (Moilanen & Wintle 2007; Lehtomäki et al. 2009), despite each facet being critical to long-term persistence of species in dynamic landscapes.

Multi-faceted conservation optimization always has the potential to involve tradeoffs. Trying to protect one conservation feature can decrease protection of another feature that is uncorrelated or negatively correlated with the first. The inclusion of connectivity in spatial prioritization involved relatively small tradeoffs with habitat quality in a semi-arid grassland site in Europe (Harlio et al. 2019) and with estimated current and future species ranges of tropical vertebrates in Australia (Reside et al. 2017). But we have little understanding of connectivity tradeoffs in prioritization analyses involving more diverse taxa and conservation objectives. For example, it remains important to assess how the addition of connectivity to multi-objective spatial planning in complex systems would affect the areal representation of species ranges, habitat types, and ecosystem services. Indeed, the lack of evaluations of connectivity in the context of complex, multi-faceted spatial conservation planning may have contributed to the only slight improvements in landscape connectivity that have accompanied recent increases in the coverage of protected areas (Saura et al. 2018).

Here we designed an analysis to simultaneously prioritize species ranges, ecosystem services (aboveground forest carbon storage), and two types of landscape connectivity. We then assessed whether the inclusion of connectivity compromised the achievement of the other conservation objectives. Our approach explicitly incorporated *(i)* specific locations of dispersal corridors based on animal movement models and *(ii)* connectivity of habitat along elevational gradients to enhance climate change resiliency and facilitate species range-shifting. We applied this prioritization approach to recommend new areas for protection of rainforest in the state of Sabah in Malaysian Borneo, where the state government has mandated an increase in the coverage of terrestrial Totally Protected Areas (TPAs; e.g., State Parks or Class 1 Forest Reserves) of ~305,000 ha. The locations of the forest areas to be designated for protection have not yet been chosen, and here we present the analytical method that we developed to aid the Sabah Forestry Department in this decision making.

METHODS

Study system and objectives

Sabah is in the north of Borneo, which is a global biodiversity hotspot based on high levels of endemism and rapid land conversion (Myers et al. 2000). Rates of land use change in this region have been among the fastest in the world (Langner et al. 2007; Miettinen et al. 2011), often driven by the expansion of industrial-scale tree and agricultural (mainly oil palm) plantations (Gaveau et al. 2018). Until the 1970s, most of Borneo was covered by primary rainforest (Bradshaw et al. 2009); by 2010, just over 50% of the island remained forested, with much of that commercially selectively logged and fragmented (Gaveau et al. 2014). The Sabah Forest Policy directives call for an increase in the coverage of terrestrial TPAs to 30% by the year 2025 (SFD 2018), requiring a minimum of 304,708 ha of additional land area to be protected. For our conservation planning exercise, we were asked by the Sabah Forestry Department to prioritize 410,000 ha for protection, as this would allow decision-makers flexibility in choosing the final configuration of new TPAs.

Within the study area, we restricted our analysis to mainland Sabah in areas with forest cover (Fig. 1; Appendix S1). We determined the remaining forested area of Sabah, excluding mangroves, by applying a threshold of 40 Mg ha^{-1} of aboveground forest carbon, as determined from a recent high-resolution mapping study (Asner et al. 2018). This followed similar forest delineation guidelines used elsewhere (Rosoman et al. 2017) and was selected to be low enough to include areas of minimally degraded forest capable of regeneration, whilst excluding most oil palm and short-rotation tree plantations.

We employed a conservation planning framework with three underlying objectives. First, we aimed to ensure that the areas of forest recommended for protection covered distributional ranges for a variety of taxa for which such data were available – plants, butterflies, and several vertebrate groups (amphibians, birds and mammals). We included only restricted-range or threatened species to ensure that we prioritized species of highest conservation value; overall we included 149 range-restricted plants (trees, shrubs and orchids), 77 range-restricted butterflies, and 83 threatened vertebrates (IUCN status of Vulnerable, Endangered, or Critically Endangered; Appendix S2).

Our second objective was to ensure that landscape connectivity was conserved. Landscape connectivity was measured in two different ways, reflecting its different ecological benefits. First, we sought to protect forest areas that provide linkage between existing TPAs, specifically allowing for regular population exchange of highly mobile species, for example clouded leopards (*Neofelis diardi*) (hereafter, dispersal corridors). Second, we aimed to conserve forest areas that spanned elevational gradients between TPAs so as to provide range shifting routes for less mobile species (e.g., a forest dependent butterfly) in the face of climate change (hereafter, elevational connectivity).

Our final objective was to maximize representation of different forest types (excluding mangroves and beach forest), as a proxy for facets of biodiversity that we did not capture with our species ranges, and to protect forest areas that store particularly large amounts of aboveground carbon, so as to contribute to state and national commitments to climate change mitigation. For forest types, we used data from the Sabah Forest Research Centre with a classification of the state's forest types based on the pre-development spatial distribution of each. The 22 forest types (Appendix S3) were distinguished by species groups, edaphic characteristics, and land formations. Details of the different types of feature layers (species ranges, dispersal corridors, elevational connectivity, forest type, and aboveground carbon) are provided in the online Supplementary Material (Appendix S1).

Estimation of connectivity

To determine the location of dispersal corridors, we simulated the movements of individuals across the landscape using correlated random walk models to identify forest areas that may be the most important for animal movement between existing TPAs. Within these simulations, we incorporated biologically-relevant parameters to generate movement scenarios commonly associated with transit or dispersal as exhibited by wide-ranging mammals and birds. We varied starting locations within areas of high-quality forest habitat as well as the resistance to movement through suboptimal habitat (non-forested areas). This technique estimated the flow of dispersers across all potential corridors on the landscape, or the 'centrality' of each linkage (Brodie et al. 2016). We weighted each landscape unit according to its spatial position relative to its two nearest TPAs as well as the size of the TPAs – previous research in the system has suggested that short corridors linking two large habitat patches are the most important to metapopulation persistence (Brodie et al. 2016). The output value from the movement simulations was the total use of each cell in the landscape by all dispersing individuals that successfully reached a new habitat patch. The most important corridors were then generated by iteratively selecting the highest value cells across the landscape until a corridor across the landscape was reached. By integrating animal movement and location weighting, we generated a connectivity metric that incorporates movement stochasticity and metapopulation dynamics to identify corridors of contiguous planning units (see Appendix S1 for more details).

To assess elevational connectivity, we used 'Condatis' models (Hodgson et al. 2012), based on circuit and metapopulation theories, to identify the most important forested areas connecting each lowland (source) TPA to higher elevation (target) TPA grid-cells: those that would have equal or lower mean annual temperature in 2061-2080 (based on Relative Concentration Pathway 8.5, the 'business as usual' emissions scenario) than the source TPA's current mean annual temperature. Identifying the most important forest areas was achieved by progressively dropping unprotected forest from the landscape (Hodgson et al. 2016) and monitoring the decline in the conductance between the source and target TPAs, which indicated the rate at which organisms could cross the landscape (see Appendix S1 for more details).

Conservation prioritization

Our framework employed systematic conservation planning using integer linear programming based on specified objectives, input conservation features, targets, and land budget. This was implemented with the package priotritizr (ver. 4.0.2; Hanson et al. 2017) in the program R (R Core Team 2015); the analysis code is available at github.com/williash23/SEARRP-UMT-Prioritization. As our aim was to incorporate several types of conservation features, each with varying numbers of raw feature layers, we developed a two-step prioritization process (Appendix S4). First, we prioritized the input features for each of seven categories (i.e., plants, butterflies, vertebrates, aboveground carbon, forest types, elevational connectivity, and dispersal corridors) that addressed our three ecological objectives and our budgeted land area, with the objective of maximizing the number of features that meet a specified target without exceeding a land area budget. This produced a single prioritized output layer per feature category (Appendix S4). Second, we used these seven feature category layers (e.g., a single prioritized layer for butterflies instead of 77 individual species layers), all weighted equally and with equal representation targets, as input features to create one overall output layer. We used a boundary length modifier (Appendix S1) to clump the prioritized areas spatially. Existing TPAs were ensured of being included in the conservation solution. Thus, our solution found the optimal area (up to 410,000 ha) outside of existing TPAs that maximized the representation of species ranges, forest type diversity, aboveground carbon density, dispersal corridors, and elevational connectivity across Sabah. Prioritization was implemented across 100 ha planning units covering the current extent of forested areas in the state.

Evaluation of the conservation prioritization

We computed the total proportion of each feature layer that was covered by the prioritized area, both excluding and including existing TPAs. For our first assessment, excluding existing TPAs and evaluating only the additional area prioritized for conservation, the 410,000 ha land budget accounted for approximately 5% of the total land area of mainland Sabah. Thus, we measured the success of the 410,000 ha of prioritized new areas by assessing the number of raw feature layers for which the overall prioritization solution reached a coverage of at least 5%. Note that it is also important to consider that many of the best areas are already protected by the existing TPA network, so reaching this level of coverage for each of the raw features is more difficult in the remaining available forested area of Sabah.

For our second assessment, the total area of our full prioritized solution (i.e., our land budget plus existing TPAs) was 32% of the total land area of mainland Sabah. Thus, to measure the efficacy of our prioritization analysis, we determined how many raw input features reached at least 32% coverage through the full prioritization solution.

We determined how the results of our overall prioritization compared to those generated from a more typical systematic conservation planning exercise that did not explicitly incorporate connectivity. As a measure of this more typical analysis, we ran the same prioritization analysis using the five feature layers not related to connectivity (i.e. plants, butterflies, vertebrates, forest types, and aboveground carbon) but excluded dispersal corridors and elevational connectivity. Finally, we assessed the sensitivity of our overall prioritization results to each input feature layer (Appendix S1).

RESULTS

The total area available for conservation in our analysis covered 2,288,426 ha, of which 1,879,238 ha were in existing TPAs on mainland Sabah that were forced to be included in the solution. Our two-step analysis prioritized an additional 409,187 ha for conservation (hereafter, prioritized area). The prioritized area (Fig. 1B) was concentrated largely in several clumps including *(i)* southwestern Sabah, which had high species richness of butterflies and vertebrates and important dispersal corridor connections to Sarawak and Kalimantan, *(ii)* the Upper Kinabatangan, which was important for plants, vertebrates, and elevational connectivity, and *(iii)* areas east of the Crocker Range that were important for all taxa and contained a diverse range of forest types (Appendix S4). All of these areas were also relatively high in aboveground carbon density, generally above 200 Mg C ha^{-1} (Appendix S4).

In our assessment of how well the 410,000 ha prioritized area covered each of the raw input conservation features outside of existing TPAs, 200 out of the 246 raw input features (excluding the restricted plants species that had limited point locality data) reached the ≥5% benchmark. On average, raw input features reached over 12% coverage (Fig. 2), demonstrating that our prioritization analysis provided a conservation solution that was far better than what would have been achieved by randomly selecting new conservation areas. Connectivity features had the lowest coverage of the seven input features of the final prioritization (these features were generated by analyses that focused explicitly on locations outside the existing TPA network, so existing TPAs added no coverage for these features.)

For our assessment of how well the full conservation solution (i.e., the prioritized area plus existing TPAs) covered the raw input features, an average of 37% coverage was reached for species ranges and forest types (Table 1). The mean coverage for all seven feature categories was ≥40% (Fig. 2). Coverage was achieved most successfully for butterflies and forest types (58% of the input features for each). Coverage was least successful for vertebrates (43% of input features), though even for this feature, the fact that coverage was so far above the 32% benchmark suggests, again, that the prioritization analysis provided a substantially better solution than randomly choosing conservation areas would have done.

Compared to the analysis that excluded the two connectivity features (i.e., a more typical systematic conservation planning approach), our prioritized area had no change in the protected coverage of vertebrates, plants, and forest types, a 3% decline in coverage for butterflies, a 2% decline in coverage for aboveground carbon, a 12.5% increase in coverage of elevational connectivity, and a 21.4% increase in the protection of dispersal corridors (Table 1).

DISCUSSION

Systematic conservation planning is important for identifying the most important areas for new protection in order to stem extinctions driven by habitat loss. The Convention on Biological Diversity's Aichi Target 11 calls for at least 17% of the world's land to be covered by well-connected protected areas or other effective area-based conservation measures by 2020 (CBD 2010). Globally, protected area coverage is ~14.7%, but only about half of that area is considered well-connected (Saura et al. 2018). But while numerous conservation planning exercises have sought to optimize the representation of conservation features or the connectivity of the landscape, few have sought to do both, especially in the context of multi-species assemblages and diverse conservation objectives. Here, we prioritized multiple conservation features (ranges for a diverse array of species, ecosystem types, and forest carbon storage) across a large landscape, while also incorporating the protection of landscape connectivity. This approach greatly enhanced the protection of dispersal corridors and elevational gradients along which species could move in response to warming temperatures, with no additional cost in terms of land area requirements, and limited costs in terms of poorer representation of other conservation features. This is consistent with other studies, which had less diverse conservation objectives, that also show relatively limited tradeoffs between the protection of connectivity and species ranges (Reside et al. 2017; Harlio et al. 2019). Part of the reason why these studies and ours may have been able to achieve multiple benefits with limited costs is that at least some of the input features were spatially correlated (see Appendix S4, for example). At least in our case, this is unlikely to represent systematic collection bias because we included a wide range of taxa representing data assembled from multiple sources as input features. Applications of these methods to other systems with less input feature correlation, for example where species were strongly clustered into distinct, non-overlapping habitat types, could increase the difficulty in simultaneously achieving different conservation objectives.

The locations selected for conservation generally contained several conservation features, but full representation of all seven conservation features was only achieved across the suite of areas. Some of the hyper-endemic plants (where we used point locality information instead of predicted species ranges) were not included in our prioritized area (Table 1), and may require additional conservation measures in particular localities. The most important part of the state for dispersal corridors was southwestern Sabah, where connectivity is needed to link the cluster of protected areas in the central part of Sabah to protected forests in Sarawak and Indonesia (Brodie et al. 2016). Several areas were critical for elevational connectivity, including the Upper Kinabatangan in central Sabah and areas around Kinabalu Park that would increase its connection to the lowlands. The Kinabalu area was also identified as a priority area in a conservation analysis focused on mammals (Struebig et al. 2015). These three areas were also rich in vertebrates (southwest Sabah, Deramakot), butterflies (southwest Sabah), plants (Deramakot, Kinabalu Park vicinity), forest types (southwest Sabah, Kinabalu Park vicinity), and aboveground carbon (southwest Sabah, Deramakot) (see Appendix S4).

In Sabah, the protection of the prioritized area identified by our analysis would provide important conservation benefits. The prioritized area has been presented to the Sabah Forestry Department, which has initiated a round of free, prior informed consent consultations with indigenous peoples, local communities, and other stakeholders who may have overlapping rights and interests in the locations identified for enhanced conservation. Outcomes of this process will inform subsequent revisions of the prioritization analysis. We will continue with this iterative process to seek consensus on the final recommendation for the designation of new protected areas. The conservation influence of this and other planning measures could be enhanced further via cross-border coordination with governments in Brunei Darussalam, Kalimantan (Indonesia), and Sarawak (Malaysia; van Paddenburg et al. 2012; Runting et al. 2015).

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TABLE 1: Targets and achievement in coverage of raw input features of the overall prioritized solution (existing totally protected areas plus areas prioritized for new conservation) both with (no brackets) and without (square brackets) explicit incorporation of dispersal corridors and elevational connectivity.

Input feature categories	No. of raw input features for round one of prioritization	Targets for round one of prioritization	Proportion of raw input features protected by overall prioritized solution			Number of raw input features that reached 32% coverage
			Mean	Range	Total	
Vertebrates	81	43.5%	0.39 [0.40]	0.00 - 1.00 [0.00 – 1.00]	—	34 [36]

Invertebrates	77	43.5%	0.32 [0.32]	0.25 - 0.42 [0.25 – 0.43]	—	35 [37]
Plants	66[a]	43.5%	0.39 [0.39]	0.12 - 0.88 [0.11 – 0.89]	—	33 [33]
Forest types	19	50%	0.44 [0.45]	0.00 - 0.94 [0.00 - 0.96]	—	11 [11]
Aboveground carbon	1	52.5%	—	—	0.49 [0.50]	—
Elevational connectivity	1	31%	—	—	0.17 [0.14]	—
Dispersal corridors	1	99%	—	—	0.17 [0.14]	—

[a] An additional 83 plant species (331 locality records) with extremely limited distributions were included in this category, represented as 0.05 ha localities that were either included or excluded in their entireties in the prioritized area.

FIGURE LEGENDS

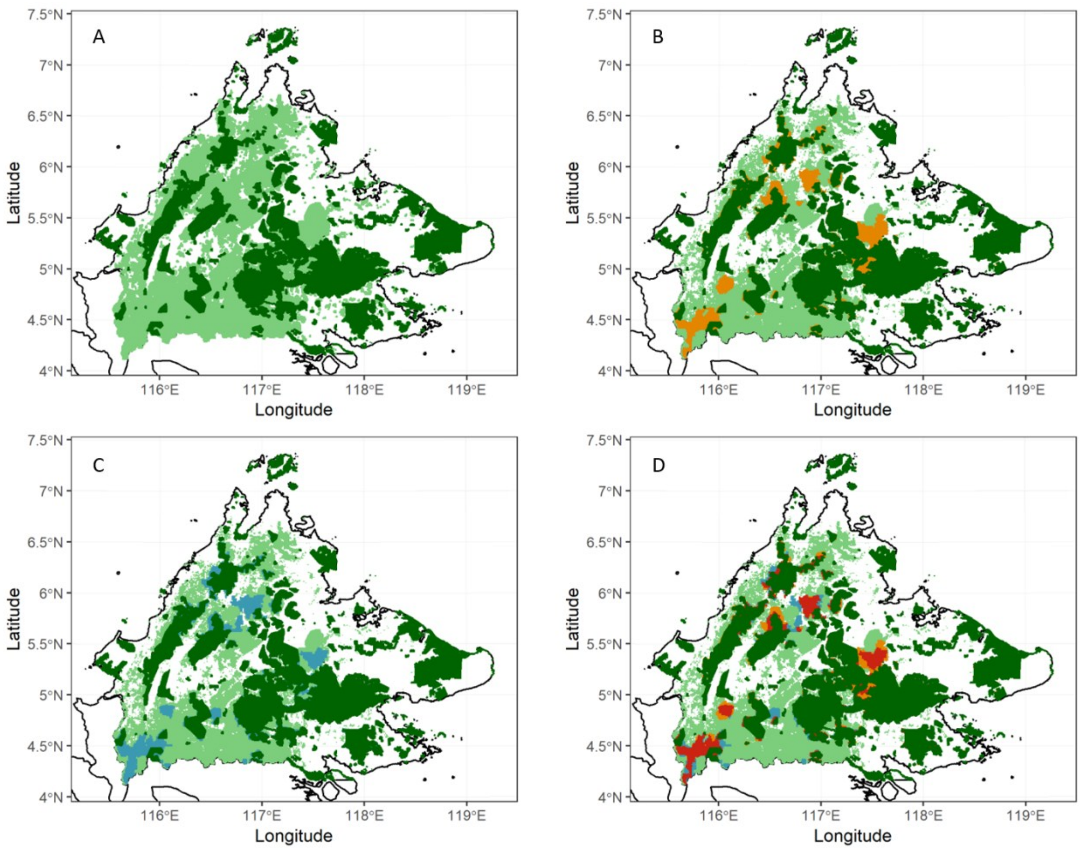

Figure 1: Study area on mainland Sabah, Malaysian Borneo, showing existing protected areas (dark green), the remaining forested areas (A; light green), and areas prioritized for additional protection (B: orange; C: blue), both with (B) and without (C) explicit incorporation of dispersal corridors and elevational connectivity. Panel D shows where the prioritized areas in B and C overlap (red).

Figure 2: Proportion of the conservation features (input feature data layers) protected by the overall conservation solution, with (A) and without (B) explicit incorporation of dispersal corridors and elevational connectivity.