Reserve design to optimize the long-term persistence of multiple species

Matthew Strimas-Mackey [iD][1,3] and Jedediah F. Brodie[2]

[1]*Cornell Laboratory of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, New York 14850 USA*
[2]*Wildlife Biology Program, University of Montana, 32 Campus Drive, Missoula, Montana 59812 USA*

Abstract. Protected areas form the cornerstone of global efforts to conserve biodiversity. Most current methods for designing reserve networks focus on maximizing the representation of species, but with no assurance that those species will persist in the protected landscapes into the future. We present a new strategy for reserve design that combines metapopulation theory with spatial conservation prioritization to estimate conservation solutions that minimize extinction risk across numerous species simultaneously. Our framework optimizes the spatial configuration of reserves to maximize metapopulation persistence for an entire assemblage of species by accounting for both species representation and landscape connectivity. As a case study, we design a reserve network for 114 terrestrial mammal species in Indonesian New Guinea. Our approach builds on Marxan, the flagship representation-based reserve design tool, improving estimated persistence (metapopulation capacity) by an average of 4.6-fold across species, without increasing the socioeconomic cost. We suggest that enhancing species persistence, rather than protecting arbitrary proportions of species' ranges, should be the ultimate objective of conservation planning.

Key words: biodiversity conservation; habitat fragmentation; Marxan; metapopulation; protected areas; rainforest; tropical ecosystems.

Introduction

Protected areas are a key component of global efforts to conserve biodiversity. Over the last 30 yr, the terrestrial protected area network has expanded substantially, from 3.5% of global land area in 1985 (Zimmerer et al. 2004) to nearly 13% today (IUCN and UNEP-WCMC 2016). However, reserve coverage is highly non-representative across biomes and taxa, and many biodiversity features remain unprotected or poorly protected by reserves (Rodrigues et al. 2004). Protected areas tend to be significantly biased toward land with low economic value with little pressure for conversion to agriculture (Joppa and Pfaff 2009). The result is a mismatch between the location of reserves and the spatial distribution of biodiversity. For example, Venter et al. (2014) found that 17% of threatened vertebrate species do not occur within any protected area, and 85% are not afforded sufficient protection by existing protected areas to ensure their long-term persistence.

Systematic conservation planning offers a structured, transparent, and scientifically defensible approach to designing new reserve networks that efficiently meet conservation objectives while minimizing socioeconomic cost (Margules and Pressey 2000). The fundamental objective of conservation planning is to ensure the long-term persistence of biodiversity (Cabeza and Moilanen 2001); however, under the current paradigm, conservation planning rarely accounts for persistence explicitly (Cabeza and Moilanen 2001, Nicholson et al. 2006). Rather, reserve design typically focuses on maximizing the representation of species within reserves, i.e., ensuring that a desired (but necessarily arbitrary) proportion of a species' distribution falls within protected areas.

But this approach gives no assurance that the reserves will ensure the long-term persistence of the species (Cabeza and Moilanen 2003, Nicholson et al. 2006). Indeed, a vast literature has shown that "extinction debts" are common in reserves or habitat patches that are too small or isolated (Tilman et al. 1994). Therefore, simply protecting a given proportion of a species' range does not mean that the species will not go extinct, even in the near term.

Some reserve design tools do address the issue of species persistence, but only indirectly. For example, Marxan (Ball et al. 2009), the most widely used conservation planning tool, can produce more compact and less fragmented spatial configurations of protected areas by minimizing the cumulative perimeter of the reserve network. Species-specific habitat requirements can also be incorporated in the form of minimum patch sizes (Smith et al. 2010), and the risk of simultaneous stochastic extinctions can be reduced by specifying the minimum number of patches and minimum separation distance between them (Ball et al. 2009). However, the relationship between patch size or configuration and local or regional persistence is never explicitly incorporated into these analyses; therefore, none of these approaches assess the population ecology of the focal species in a process-based fashion.

The location, spatial configuration, and connectivity of reserve networks play critical roles in shaping the population dynamics, and hence the persistence, of species in a landscape (Cabeza and Moilanen 2001). Metapopulation theory provides a framework within which to study these spatial population dynamics, and to estimate how alternative reserve configurations affect species persistence (Hanski 1999, Hanski and Ovaskainen 2000). However, despite substantial interest in both metapopulation theory and systematic conservation planning, exceedingly few attempts have been made to combine them. One of the only examples of such a synthesis was provided by Nicholson et al. (2006),

who developed a method for reserve selection based on minimizing the expected number of extinctions across multiple species. While their approach did explicitly account for species persistence, it was based on spatially explicit, stochastic, metapopulation models (Frank and Wissel 2002) that require parameters such as home range size, which is unknown for most species. This greatly limits the set of species that can be considered, often excluding important rare or threatened species that have been poorly studied. In addition, Nicholson et al. (2006) constrained the application of their method to a fixed landscape of only 39 forest fragments, whereas most real-world reserve design problems divide landscapes into many thousands of planning units. Therefore, our approach builds upon that of Nicholson et al. (2006) by increasing both the number of species and the number of planning units that can be considered.

We present a method for systematic reserve design that explicitly maximizes regional persistence for a large assemblage of species. Our approach is based on maximizing metapopulation capacity, a relative, asymptotic metric of landscape-scale persistence derived from a spatially explicit metapopulation model (Hanski 1999, Hanski and Ovaskainen 2000). This metric requires few parameters to calculate and incorporates the size and spatial configuration of reserves as well as species-specific dispersal dynamics among them. We use simulated annealing, an optimization heuristic widely used in conservation planning, to maximize metapopulation capacity and, by extension, species persistence. We demonstrate our approach with a reserve planning exercise for 114 terrestrial mammal species in Indonesian New Guinea (Fig. 1). This approach is intended to complement and build upon traditional representation-based reserve planning exercises such as those performed by Marxan.

Methods

Planning for persistence

As with other systematic reserve design tools such as Marxan (Ball et al. 2009), ours requires dividing the study area into planning units that are candidates for protection. The objective was to find the set of planning units that maximizes persistence across a suite of species for a fixed cost. We used metapopulation capacity to estimate species persistence for candidate protected area networks and simulated annealing to perform the optimization. This reserve design approach was implemented using R (R Core Team 2018) and is available in a newly available R package (metacapa; Strimas-Mackey and Brodie 2018).

Metapopulation capacity

Metapopulation capacity is a relative, asymptotic approximation of the ability of a network of habitat patches to support a viable metapopulation of a species (Hanski and Ovaskainen 2000). We used this metric because it is a proxy for species persistence that accounts for metapopulation processes such as dispersal and local persistence as well as landscape structure (Hanski and Ovaskainen 2000). This contrasts with graph theory
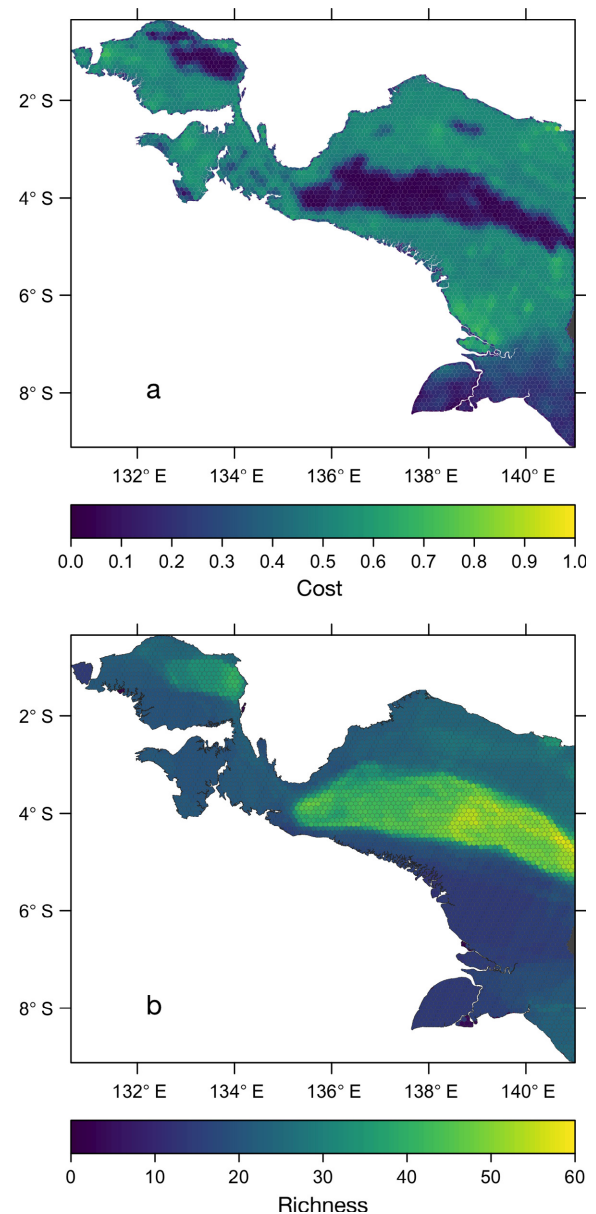

Fig. 1. (a, b). Map of the study area in Indonesian New Guinea, showing 4,399 hexagonal 100-km² planning units. (a) Cost of planning units, composed of current and 2,050 potential oil palm yield (IIASA/FAO 2012), percent crop cover (Ramankutty et al. 2002), and population density (CIESIN/IFPRI/WB/CIAT 2011). Each of the four components are normalized to 0–1, then averaged. (b) Richness of 114 terrestrial mammal species used in this study based on IUCN Red List range polygons (IUCN 2015). The low cost, high richness area at the center of the island corresponds to the New Guinean Highlands, which is largely unsuitable for oil palm due to the high elevation.

metrics, which typically only address proximate correlates of persistence such as total landscape connectivity, and purely spatial metrics of landscape fragmentation (i.e., that do not consider population processes) such as those available in FRAGSTATS (Calabrese and Fagan 2004). Visconti and Elkin (2009) found that metapopulation capacity performs well compared to other measures of landscape connectivity in ranking habitat patches according to their contribution to population viability.

Metapopulation capacity is defined as the dominant eigenvalue, λ, of the landscape matrix $\mathbf{M}$ with elements $m_{ij} = f(d_{ij})A_j A_i^{0.5}$, where A_i is the area of patch i and d_{ij} is the edge-to-edge distance between patches i and j. In the context of reserve design, we define a patch as a group of contiguous selected planning units. $f(d_{ij})$ is the species-specific dispersal-survival function, which indicates the proportion of individuals leaving patch i that successfully reach patch j at distance d_{ij} away. In this study, we used a negative exponential dispersal-survival function, parameterized using species specific maximum dispersal distances. Thus, the only species-specific parameter required to calculate λ is maximum dispersal distance, which can be estimated even for data-poor species using body-size allometries (Santini et al. 2013).

The original formulation, $m_{ij} = 0$ for $i = j$, leads to the undesirable behavior that single-patch landscapes have $\lambda = 0$ regardless of patch size. To address this, we followed Schnell et al. (2013) in allowing for self-colonization (i.e., within patches) by setting $m_{ij} = A_j A_i^{0.5}$. Furthermore, since metapopulation capacity is a relative metric, which can vary by several orders of magnitude between species, to facilitate aggregation across different species we scaled λ to be between 0 and 1 by dividing by its maximum possible value, which is attained when the entire study area is protected. This normalization results in a metric that assesses alternative reserve configurations based on relative, rather than absolute, differences in metapopulation persistence. Without the normalization, this reserve selection method would prioritize common, widespread species with overall high metapopulation capacity at the expense or rare, range-restricted species.

Simulated annealing

Simulated annealing is a stochastic metaheuristic for approximating global optima of complex functions (Kirkpatrick et al. 1983). This method is widely used for reserve design problems, notably by Marxan (Ball et al. 2009). In this context, simulated annealing can be used to find a near-optimal set of planning units that minimizes a given objective function encapsulating the conservation objective. We used the implementation of simulated annealing provided by R (R Core Team 2018).

Given some initial starting set of planning units to include in the candidate reserve network, simulated annealing works by switching the status of a random planning unit from selected to not selected, or vice versa. Changes that improve the objective function are always kept, while changes that worsen the objective function are sometimes kept, with a probability that decreases as the heuristic progresses. This probabilistic acceptance ensures that the heuristic avoids getting trapped in local minima.

Simulated annealing typically uses a random starting point; however, we used Marxan (Ball et al. 2009) to generate the starting reserve network. This approach greatly reduces the number of simulated annealing iterations required by assuming that a Marxan-generated solution does a reasonable job of ensuring metapopulation representation. Our approach can therefore be seen as building upon Marxan-generated solutions by improving species persistence through the incorporation of landscape connectivity

into the site-selection algorithm (which is otherwise based strictly on representation).

Mathematical formulation

We formulated the conservation objective (to maximize persistence across species for a fixed cost) mathematically as an optimization problem. In particular, given a set of m planning units, with costs c_j, and n species the objective was

$$\text{Maximize} \sum_{i=1}^{n} b[\lambda_i(\vec{x})] - blm \cdot P(\vec{x}) \text{ subject to } \sum_{j=1}^{m} c_j x_j \leq B$$

where x_j is a binary indicator variable specifying whether planning unit j is included or excluded from the candidate protected area, $\lambda_i(\vec{x})$ is the metapopulation capacity (scaled to 0–1) for species i and reserve configuration $\vec{x}$, b is the benefit function, $P(\vec{x})$ is the outer perimeter of the reserve network, blm is a scaling factor analogous to the boundary length modifier in Marxan analyses, and B is the total conservation budget.

The benefit function, b, translates changes in metapopulation capacity to a measure of the conservation benefit associated with that change. We used a logarithmic benefit function $\log(100\lambda + 1)/\log(101)$ in this study; this preserves the 0–1 range of the scaled metapopulation capacity, while prioritizing changes that benefit species with low metapopulation capacity. This benefit function ensures that simulated annealing does not favor changes to the reserve configuration that benefit species with already high persistence at the expense of species with low persistence. To explore the effect of the benefit function, we performed a sensitivity analysis comparing prioritizations with and without the benefit function. We found that the logarithmic benefit function produced more compact solutions with a higher metapopulation capacity on average (Appendix S1).

The above formulation consists of maximizing an objective function subject to a budgetary constraint; however, simulating annealing is significantly more efficient without explicit constraints (Nicholson et al. 2006). Therefore, we modified the objective function to incorporate the constraint directly

$$f(\vec{x}) = \sum_{i=1}^{n} b[\lambda_i(\vec{x})] - blm \cdot P(\vec{x}) - \delta \cdot \max\left(0, \sum_{j=1}^{m} c_j x_j - B\right)$$

where the final term is a penalty for exceeding costs and δ measures the relative importance of staying within budget vs. increasing metapopulation persistence. It is this objective function that we sought to maximize with simulated annealing.

Case study

To demonstrate the use of our persistence-based reserve design approach, we applied it to the western half of the island of New Guinea, which is composed of the Indonesian states of Papua and West Papua. New Guinea has extremely high biodiversity and endemicity (Myers et al. 2000), and the world's third largest remaining area of contiguous

tropical rainforest. The region is also experiencing high rates of deforestation (Shearman et al. 2009) and increasing pressure for conversion of forest to oil palm plantations (Obidzinski et al. 2014). Thus, New Guinea presents an interesting case study since it contains large areas of currently pristine habitat supporting high biodiversity, many species of which are endemic, with high land conversion pressures in the near term.

We divided the study region into 100-km^2 hexagonal planning units ($n = 4,399$). This planning unit size is arbitrary, but represented a balance between computational feasibility and planning flexibility, and is on a spatial scale relevant for this study, given the low population density of many tropical rainforest mammals (for example, Brodie and Giordano 2012). Within each planning unit, we estimated the cost for protection by combining four factors: current oil palm yield, predicted 2,050 oil palm yield, population density, and percent crop cover. While there are clearly other costs that could have been incorporated as well, we kept ours cost assessment simple as our analysis is a proof of concept. Moreover, the oil palm expansion is arguably the single biggest threat to biodiversity in this region. Oil palm yield came from the Global Agro-Ecological Zones dataset (GAEZ; IIASA/FAO 2012) and represents the opportunity cost for protection, assuming that the most lucrative alternative land use is oil palm cultivation (Runting et al. 2015). Population density and percent crop cover were used as metrics of current land use intensity and were derived from the Global Rural-Urban Mapping Project (GRUMP; CIESIN/IFPRI/ WB/CIAT 2011) and EarthStat Cropland and Pasture Area dataset (Ramankutty et al. 2002), respectively. These four cost metrics were normalized to 0–1, then averaged to produce a final measure of cost of protection within each cell (Fig. 1a).

We used all native terrestrial mammal species for which body mass could be estimated (114 total) as the conservation features (Fig. 1b). Range polygons for these species came from the IUCN Red List (IUCN 2015). Most of these polygons are based on expert opinion because data are lacking for so many tropical species. While range estimates almost certainly have inaccuracies for any particular species, we had no reason to expect any systematic bias when combining estimates across so many taxa. Body masses for these species were taken from the PanTHERIA mammal trait database (Jones et al. 2009) and used to estimate maximum dispersal distance via the allometric body size relationships developed by Santini et al. (2013). Maximum dispersal distances were used to parameterize dispersal survival functions, which in turn were used to calculate metapopulation capacity (Data S1).

We used Marxan to generate a candidate reserve network to serve as both a starting point for the persistence-based reserve design and as a baseline for comparison of the performance of the method. In contrast to our persistence-based approach, Marxan requires representation targets for each species being considered. We set these targets to 20% of each species' current range. Ideally, species-specific targets would be set in a systematic fashion through viability analysis or elicitation of expert opinion (Ardron et al. 2010); however, since this case study is meant as a proof of concept, we felt that a 20% target for all species was a reasonable starting

point. (We also note that, with so few demographic data available for tropical animals, viability analyses are impossible for the vast majority of species and so our representation targets are likely no more subjective than those of many other Marxan-based exercises.) To set the Species Penalty Factors (SPFs) and Boundary Length Modifier (BLM) we followed the best practices for calibration outlined in the Marxan Good Practices Handbook (Ardron et al. 2010). We used a BLM of 0.0316 after exploring a range of values and selecting that which achieved a significant decrease in boundary length (i.e., producing more compact reserves) with minimal increase in cost. We ran Marxan for 100 simulated annealing runs, each of 2 million iterations, followed by a round of iterative improvement. We used the best solution (i.e., the one with the lowest objective function) as the starting point for the persistence-based selection. To aid comparison between approaches, the cost of this best solution was used to set the budget for our method. We used the R package marxan (Hanson and Watts 2015) as an interface to the Marxan command-line tool (Ball et al. 2009).

Finally, we ran the metapopulation capacity-based reserve design method for 5,000 simulated annealing iterations using an Amazon Web Services EC2 cluster. Simulated annealing exercises without starting values (i.e., where the whole landscape is a "blank slate" in terms of situating reserves) typically require more iterations to reach an optimal solution. But given that we started with a sensible Marxan solution rather than a random starting point, and that the study was intended to provide a proof of concept rather than precise conservation recommendations, our simulated annealing runs were sufficient to provide optimal solutions and demonstrate the utility of the method.

Sensitivity analysis

The objective function used in this study requires setting two scaling parameters, δ and blm, that control the relative importance of reserve cost and compactness, respectively, compared to metapopulation capacity. We performed a sensitivity analysis to explore how these parameters affect the behavior of the objective function. For all combinations of $blm = 0$, 0.0001, 0.001, 0.0025, and 0.005 and $\alpha = 0.1$ and 0.05, we ran metapopulation capacity-based reserve design analyses using 5,000 simulated annealing iterations. Based on this analysis, we chose $blm = 0.0025$ and $\alpha = 0.05$ to yield solutions that maximizing metapopulation capacity, while producing compact and cost effective solutions. The results of this sensitivity analysis are available in Appendix S1.

RESULTS

Comparison of the best reserve output solution from Marxan with the results from our persistence-based optimization showed that substantial gains in metapopulation persistence can be achieved with minimal or no increase in socioeconomic cost (Table 1). On average, scaled metapopulation capacities were 4.6 times higher across species in the reserve output from our method than the Marxan solution.

The spatial configuration of the candidate reserve (Fig. 2) revealed that our persistence-based method refined the

TABLE 1. Comparison of reserve performance using Marxan and our persistence-based method.

Method	Cost	Area (km²)	λ	Range protected (%)
Marxan	289.1	81,853	0.17 ± 0.25	36 ± 22 (20–100)
Maximize λ	290.4	103,401	0.46 ± 0.34	58.8 ± 29 (14–100)

Notes: The reserve selection methods are representation-based selection using Marxan and our approach maximizing metapopulation capacity. Cost is the sum of the normalized cost across all selected planning units. The parameter λ is the mean scaled metapopulation capacity, which ranges from 0 (no protection) to 1 (entire study area protected). The percentage of range protected refers to the percentage of planning units that the species occurs in that are protected. Values are mean ± SD; values in parentheses are the range.

Marxan solution by connecting the discrete reserves in the center of the study area into one large contiguous reserve spanning much of the high-diversity highlands along the spine of New Guinea. Compared to the Marxan results, the refined reserve was 26.3% larger in area but only 0.5% higher in cost (Table 1), showing that low-cost, marginal planning units were added to form connections between formerly unconnected reserve patches.

Explicitly accounting for persistence in the reserve selection process led to an increase in metapopulation capacity for all but two species over the Marxan solution (Fig. 3; Data S1). Metapopulation capacity for *Ratus praetor* (IUCN least concern) decreased by 2.8% and for *Thylogale browni* (IUCN vulnerable) by 31%. The former is widespread, but does not occur in the high richness, low cost highlands that our solution favored, while the latter occurs primarily in Papua New Guinea (east of our study area),

only extending into our area in a small portion of Northwestern Indonesian New Guinea, an area that happens to be of high cost and low richness.

The distribution of changes in metapopulation capacity was distinctly bimodal (Fig. 3), suggesting two categories of species: those for which persistence-based reserve design, such as ours, is important and those for which traditional representation-based approaches, such as Marxan, may be sufficient. One potential factor underlying this difference is the variation in species ranges, which span several orders of magnitude (16–40,000 km²). Range-restricted species experienced a greater increase in metapopulation capacity using our method (as opposed to a Marxan-only solution) than did widespread species (Fig. 4) and are therefore better candidates for the persistence-based planning that we demonstrate here.

DISCUSSION

We developed a novel method for systematic reserve design that explicitly maximizes long-term species persistence, as opposed to traditional conservation planning strategies that focus solely on species representation. Our approach is grounded in ecological theory (Hanski and Ovaskainen 2000) and accounts for the interaction between the spatial configuration of reserves across the landscape and the metapopulation dynamics of numerous species. This contrasts with the majority of systematic conservation planning approaches that focus on meeting species representation targets and either ignore the spatial configuration of habitat or account for it very indirectly via simple landscape metrics that are unrelated to ecological
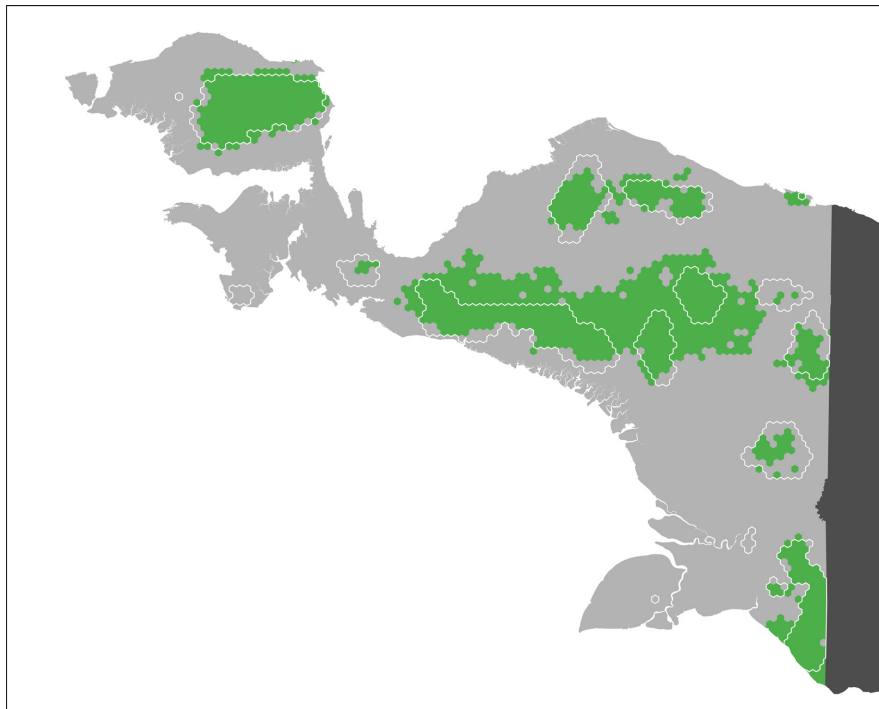

FIG. 2. Candidate reserves resulting from our reserve selection method maximizing metapopulation capacity. Green regions indicate planning units selected by our persistence-based approach, while the white lines indicate the boundary of the reserve generated by Marxan.
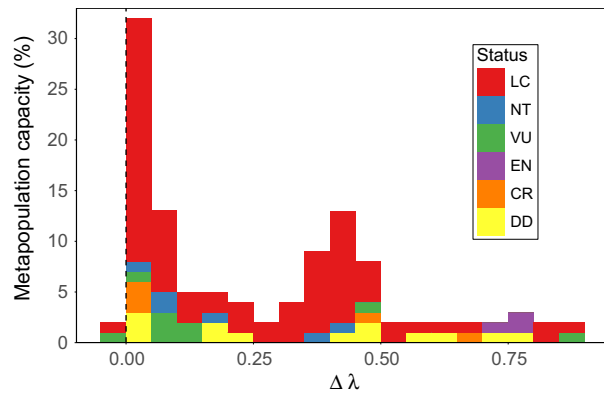
Fig. 3. Distribution of the differences in species-specific scaled metapopulation capacity between candidate reserves from a Marxan analysis vs. our persistence-based selection approach. Positive values indicate an improvement in metapopulation capacity. Bars are colored according to species' IUCN Red List status. LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; DD, data deficient

processes (Saura and Pascual-Hortal 2007). Indeed, we suggest that facilitating species persistence, rather than protecting an arbitrary proportion of species' ranges, should be the ultimate goal of systematic conservation planning.

Addressing spatial configuration in reserve design is challenging because suitable metapopulation models are often difficult to parameterize (Nicholson et al. 2006) and because computational limitations preclude them from inclusion in an optimization framework. We overcame these challenges by using metapopulation capacity, which requires few species-specific parameters and offers a balance between ecological realism and computational efficiency.

While our method led to a substantial overall increase in mean metapopulation capacity across an entire mammal assemblage, at the level of individual species we identified two distinct groups: those that experienced significant
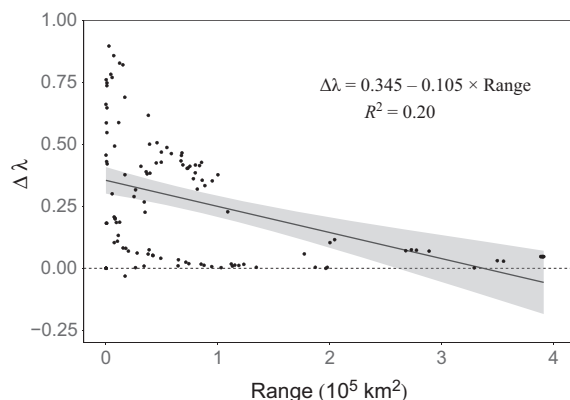

Fig. 4. Relationship between change in scaled metapopulation capacity (between −1 and 1) and range size (from IUCN distribution polygons) within Indonesian New Guinea for each of the 114 mammal species in the case study. The y-axis shows the difference in scaled metapopulation capacity between candidate reserves from Marxan and our persistence-based selection method. Range-restricted species see a greater improvement in metapopulation capacity compared to widespread species.

benefits from our persistence-based approach and those for which the Marxan solution was approximately as good. This pattern is partly explained by differences in range sizes between species, with range-restricted species apparently exhibiting a greater need than wide-ranging taxa for persistence-based planning. Range-restricted species are nearly always at higher extinction risk than those that occur broadly (Cardillo et al. 2005), so utilizing a persistence-based planning approach is likely to be warranted in most systems.

The main differences in the final solutions between our persistence-based method and the original Marxan-only, representation-based methods was that the former linked several groups of close, but unconnected, reserves into very large reserves. These findings are consistent with a study by Brodie et al. (2016) suggesting that linking large patches together into "super-patches" greatly enhanced metapopulation persistence and metacommunity stability. Starting from the Marxan solution, our approach connected the chain of five large reserves along the center of the island into a single reserve (Fig. 2), and the two reserves in the north into another large reserve. Thus, these findings reinforce the importance of integrating reserve design with landscape-scale wildlife corridors designed to improve connectivity between reserves (Beier et al. 2011).

Underlying this reserve design method is a set of assumptions resulting from the use of metapopulation capacity as a persistence metric. The metapopulation capacity metric is based on a simple spatially explicit metapopulation model consisting of colonization and extinction within a network of habitat patches embedded in a matrix of non-habitat (Hanski 1994, Hanski and Ovaskainen 2000). Apart from differences in size and isolation, all patches are assumed to be identical in terms of habitat quality, and colonization and extinction rates. Furthermore, this model assumes that the unprotected matrix is homogenous and permits dispersal, but cannot support populations of species. In reality, there is considerable heterogeneity in the landscape that is not captured by this binary patch-matrix dichotomy, yet may have an impact on metapopulation dynamics (Moilanen and Hanski 1998, Prevedello and Vieira 2009). More complex metapopulation models that address these issues have been developed; however, as noted above, computational and data limitations make them unsuitable for the present application. Finally, metapopulation capacity is based on a model that assumes the landscape has reached colonization–extinction equilibrium. Therefore, our method should be used to predict long-term persistence, but could be biased in the immediate aftermath of fragmentation.

Two other factors are critical to consider in their impacts on reserve design: socioeconomic cost and comparisons across species. In our case study, the optimal solution suggested reserves should be located almost entirely in low-cost areas. This could be driven by inherent cost–benefit trade-offs, or by the fact that our system exhibited a (likely idiosyncratic) negative correlation between socioeconomic cost and species richness. Meaningful, "apples-to-apples" comparisons of persistence across species are difficult because species exhibit such variety in life-histories and conservation status. We felt that our normalization method dealt with these differences in a fair and transparent way, but have built flexibility

into the R package metacapa to allow users to choose other normalization methods that might better suit their systems.

Our use of a Marxan-like boundary length minimizing term in the objective function was necessary to ensure our method produced compact solutions; however, this term is not grounded in ecological theory and introduces an arbitrary element into our method, which is otherwise entirely based on metapopulation theory. Future extensions of the prioritization method presented here could address this by drawing on our knowledge of the ecological effects of fragmentation (Laurance et al. 2002) to incorporate species-specific edge effects metrics into the objective function.

Finally, uncertainty in our knowledge of the species under consideration can clearly affect the robustness of the model results. To calculate metapopulation capacity, we used estimates of species-specific maximum dispersal distance (Santini et al. 2013). The error associated with this estimation propagates into uncertainty in the outcome of the reserve selection exercise. However, Nicholson and Possingham (2007) found that rankings of different reserve configurations based on metapopulation metrics changed little in response to variation in parameter estimates, thus conservation planning strategies should be fairly robust to uncertainty (Brodie et al. [2016] found a similar result).

Our results were also affected by issues of spatial correlation in the pattern of diversity. The 114 species in this study were not independently distributed across the study area; rather most species occurred in the central highlands (Fig. 1b). Thus, this region was overrepresented in the final reserve configuration, which consisted primarily of one contiguous "super-reserve" spanning the high diversity highlands (Fig. 2b). Species occurring outside of this high diversity region may experience shortfalls in protection. This suggest that our approach may be a good candidate for a focal species approach in which a subset of representative species is chosen based on geographical distribution and life history characteristics (Nicholson et al. 2013). This approach would have the dual benefit of working with a spatially independent set of species and reduced computation time due to fewer species under consideration.

In our case study, there was one threatened species that saw a decrease in metapopulation capacity relative to the Marxan solution. This scenario is likely to occur when certain planning units are critical for the protection of a single species, but of limited value to remaining species. To address this, we recommend identifying range-restricted species that are at high risk of extinction, and locking their ranges into the final solution. Alternatively, species-specific weighting factors (equivalent to species penalty factors in Marxan) could be included in the objective function, and higher weights could be given to threatened species that are experiencing declines in metapopulation capacity.

Despite these caveats, our approach demonstrates that incorporating metapopulation theory into conservation planning can greatly enhance long-term species persistence at no additional cost. For many species, the dominant paradigm of representation-based reserve design may yield reserve networks that do not adequately ensure long-term persistence because they do not protect sufficiently large population sizes or because they do not ensure connectivity. Computational limitations so far preclude the method we have described in

this study from being used for highly complex reserve design problems. However, in cases where persistence cannot be explicitly incorporated into the optimization framework, metapopulation capacity can still be a valuable tool in reserve design (Schnell et al. 2013), for example as a means of ranking different reserve configurations output from tools such as Marxan. We also highlight the importance of effective wildlife corridor design to ensure landscape connectivity (Beier et al. 2011, Brodie et al. 2016).

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