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Methodological considerations in reserve system selection: A case study of Malagasy lemurs

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ABSTRACT

Although data quality and weighting decisions impact the outputs of reserve selection algorithms, these factors have not been closely studied. We examine these methodological issues in the use of reserve selection algorithms by comparing: (1) quality of input data and (2) use of different weighting methods for prioritizing among species. In 2003, the government of Madagascar, a global biodiversity hotspot, committed to tripling the size of its protected area network to protect 10% of the country's total land area. We apply the Zonation reserve selection algorithm to distribution data for 52 lemur species to identify priority areas for the expansion of Madagascar's reserve network. We assess the similarity of the areas selected, as well as the proportions of lemur ranges protected in the resulting areas when different forms of input data were used: extent of occurrence versus refined extent of occurrence. Low overlap between the areas selected suggests that refined extent of occurrence data are highly desirable, and to best protect lemur species, we recommend refining extent of occurrence ranges using habitat and altitude limitations. Reserve areas were also selected for protection based on three different species weighting schemes, resulting in marked variation in proportional representation of species among the IUCN Red List of Threatened Species extinction risk categories. This result demonstrates that assignment of species weights influences whether a reserve network prioritizes maximizing overall species protection or maximizing protection of the most threatened species.

1. Introduction

Additions to the current global reserve network must be systematically planned to optimize biodiversity representation and persistence within reserves (Araujo and Williams, 2000; Margules and Pressey, 2000; Sarkar et al., 2006). Reserve selection should be based on specific conservation targets, for example, to ensure adequate areas for threatened species are included within a reserve network (Margules and Usher, 1981; Prendergast et al., 1993; Virolainen et al., 1999; Rosenfeld, 2002; Rodrigues et al., 2004). Algorithms are widely used to assist systematic selection of optimal reserve networks and to ensure that conservation targets are achieved (Margules and Pressey, 2000; Sarkar et al., 2006; Pressey et al., 2007; Cabeza et al., 2008). Inadequacies in taxonomic and distribution data can pose serious problems that hamper the use of algorithms (Csuti et al., 1997), but collection of the required data is costly and time-consuming. International conservation and scientific organizations, in particular BirdLife International, Kew Botanical Gardens, the Global Biodiversity Information Facility, IUCN (the World Conservation Union), Conservation International, the Smithsonian Institution and other prominent museums, along with new collaborative efforts such as the Encyclopedia of Life, have made distribution data available for many species, in the form of maps of species' "extent of occurrence" (Rodrigues et al., 2006). However, the resolution of these species range estimates can be further improved by using widely available land cover and altitude data to eliminate unsuitable regions (Jetz et al., 2008), thereby generating "refined extent of occurrence" maps. Additionally, there is increasing evidence that the ranges of rare and threatened species

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are more likely to be overestimated, especially when limited data are used (McKelvey et al., 2008). Therefore, it is important to assess whether, and how, effort spent in refining extent of occurrence data affects the output of conservation planning algorithms.

Algorithm solutions are further affected by a variety of parameters set by the user. It is increasingly common for species representation targets or preferential weighting schemes to be assigned to threatened or endemic species to prioritize selection of the areas where those species occur (Church et al., 1996; Arthur et al., 2002; Camm et al., 2002; Onal, 2004; Arponen et al., 2005; Kremen et al., 2008) and to maximize the proportions of their distributions represented within a reserve network (Margules and Usher, 1981; Prendergast et al., 1993; Virolainen et al., 1999). However, when threatened species are given preferential targets, or weights, a trade-off occurs such that smaller proportions of non-threatened species ranges may be included in the resulting solutions. The non-threatened species are therefore likely to suffer reductions in ranges, which may ultimately increase their extinction risk status.

In this study we focus on 52 species of lemurs endemic to Madagascar. Worldwide, 9% of primates are Critically Endangered, an additional 21% are Endangered, and 19% are Vulnerable; 18% of those Vulnerable to Critically Endangered species are found in Madagascar (Shipper et al., 2008). The IUCN Red List of Threatened Species categorizes 40% of Madagascar's extant lemurs as Threatened, 5% as Near Threatened, 46% as having insufficient information to complete categorization (Data Deficient); only 7% of lemurs are considered of Least Concern (IUCN, 2008). Lemurs vary in size, ranging from 30 g pygmy mouse lemur (*Microcebus myoxinus*), to the 10 kg Indri (*Indri indri*), and include both nocturnal and diurnal species (Mittermeier et al., 2006). Their diets consist of a variety of leaves, fruit, and flowers, with some omnivorous species also eating insects (Mittermeier et al., 2006). Madagascar's extant lemurs are mostly arboreal and highly forest dependent, and are therefore restricted to the approximately 15% of Madagascar that remains forested (Harper et al., 2007). Lemurs inhabit all of the forest types that exist in Madagascar: tropical rainforest in the east, deciduous dry forest in the west and northwest, and the unique spiny forest in the south. The highest species richness of lemurs is found in the northern and eastern tropical rainforest, which is under intense pressure from development and deforestation (Mittermeier et al., 1992; Harcourt, 1999; Harper et al., 2007).

We used the Zonation conservation planning software (Version 1.0, Moilanen, 2004) to investigate two methodological issues that commonly arise during conservation planning exercises. We compared the effects of: (1) input data quality for Malagasy lemur species, using widely available extent of occurrence data and more detailed refined extent of occurrence data that incorporates additional information on species' habitat dependencies and elevation limits, and (2) species weighting schemes using equal, linear, and logarithmic weights based on the IUCN Red List of Threatened Species Categories (IUCN, 2001). As the refined extent of occurrence reflects the most detailed data about a species location, we define a species' refined extent of occurrence as its range in this paper.

We evaluate the different Zonation outputs with three measures: (1) spatial comparison of the areas of landscape prioritized, (2) species representation within selected areas, and (3) potential Red List Index change, as an indication of the potential extinction risk that would result from implementing individual Zonation solutions. For all comparisons in this study we evaluate the top 10% of the landscape indicated by the algorithm, because the Malagasy government planned to expand its reserve network to 10% of Madagascar (Delaney, 2006). Madagascar has made significant progress towards this goal; however, a recent coup d'etat in 2009 and the ensuing political instability now threatens biodiversity protection (WWF et al., 2009).

2. Methods

2.1. Datasets

The extent of occurrence data used in this study are unpublished data for 52 lemur species that were compiled in preparation for the Global Mammal Assessment (Sechrest, 2003). The dataset includes 6 Critically Endangered, 9 Endangered, 17 Vulnerable, 8 Near Threatened, and 6 Least Concern species; the 6 Data Deficient species were excluded from the analyses (IUCN, 2004; Table 1). The Global Mammal Assessment used Geographic Information Systems (GIS) technology to create digital species distribution maps by synthesizing existing data on terrestrial mammal species. Data sources included field and museum locality records, population density and persistence information, and published taxonomic revisions,

Table 1
Lemur species list, and Red List categories (IUCN, 2004).

Genus	Species	IUCN rank[1]
Allocebus	*trichotis*	EN
Avahi	*laniger*	NT
Avahi	*occidentalis*	VU
Avahi	*unicolor*	DD
Cheirogaleus	*major*	LC
Cheirogaleus	*medius*	LC
Daubentonia	*madagascariensis*	EN
Eulemur	*albifrons*	NT
Eulemur	*albocollaris*	CR
Eulemur	*collaris*	VU
Eulemur	*coronatus*	VU
Eulemur	*fulvus*	LC
Eulemur	*macaco*	VU
Eulemur	*mongoz*	VU
Eulemur	*rubiventer*	VU
Eulemur	*rufus*	NT
Eulemur	*sanfordi*	VU
Hapalemur	*aureus*	CR
Hapalemur	*griseus*	LC
Hapalemur	*occidentalis*	VU
Indri	*indri*	EN
Lemur	*catta*	VU
Lepilemur	*dorsalis*	VU
Lepilemur	*edwarsdsi*	NT
Lepilemur	*leucopus*	NT
Lepilemur	*mustelinus*	NT
Lepilemur	*ruficaudatus*	NT
Lepilemur	*septentrionalis*	VU
Microcebus	*berthae*	DD
Microcebus	*griseorufus*	DD
Microcebus	*murinus*	LC
Microcebus	*myoxinus*	EN
Microcebus	*ravelobensis*	EN
Microcebus	*rufus*	LC
Microcebus	*sambiranensis*	DD
Microcebus	*tavaratra*	DD
Mirza	*coquereli*	VU
Phaner	*electromontis*	VU
Phaner	*furcifer*	NT
Phaner	*pallescens*	VU
Phaner	*parienti*	VU
Prolemur	*simus*	CR
Propithecus	*candidus*	DD
Propithecus	*coquereli*	EN
Propithecus	*deckenii*	VU
Propithecus	*diadema*	EN
Propithecus	*edwarsdsi*	EN
Propithecus	*perrieri*	CR
Propithecus	*tattersalli*	CR
Propithecus	*verreauxi*	VU
Varecia	*rubra*	CR
Varecia	*variegata*	EN

CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient.

up to 2004. The project adhered to the IUCN definition of extent of occurrence as "the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy" (IUCN, 1993). The extent of occurrence polygons were created by designating minimum estimates of species' ranges while following a rule allowing interpolation of occurrence between known locations if the locations shared similar habitat features, but prohibiting extrapolation beyond known locations (Global Amphibian Assessment, 2004).

The refined extent of occurrence polygons are versions of the extent of occurrence polygons that have been reduced according to the upper and lower recorded elevations and habitat dependence of each species, using data collected in preparation for the Global Mammal Assessment. Therefore, the refined extent of occurrence polygons are always smaller than the extent of occurrence polygons.

Steven Goodman of the University of Antananarivo, The Field Museum of Chicago, and the World Wildlife Fund reviewed tables of habitat dependency and altitudinal limits, and advised modifications for refining the species' extent of occurrence polygons based on extensive literature review (Goodman and Ganzhorn, 2004) and field experience (Goodman, 1993, 1996; Goodman and Langrand, 1996; Goodman, 1997; Langrand and Goodman, 1997; Ratsirarson and Goodman, 1998; Goodman, 1999a; Goodman, 1999b; Goodman and Schütz 1999; Rasolooarison et al., 2000; Yoder et al., 2000; Goodman et al., 2001, 2003, 2004; Goodman and Ganzhorn, 2003).

The Taxonomic Working Group for the Système d'Aires Protégées de Madagascar, the group responsible for planning the protected areas expansion, refined the extent of occurrence polygons with altitude and habitat data at a workshop funded by World Wildlife Fund and led by Tom Allnutt, in June, 2004, in Antananarivo, Madagascar. For the habitat refinements the group used forest cover for the year 2000, digitized by Conservation International (Harper et al., 2007). The resulting refined extents of occurrence were used extensively by the Taxonomic Working Group for the Système d'Aires Protégées de Madagascar for planning the protected areas expansion over a four year period from 2004 to 2008.

Primate taxonomy has undergone significant changes in recent years, although taxonomists do not agree on many of the revisions. The authoritative text on mammal taxonomy lists 60 species of extant lemurs (Wilson and Reeder, 2005). The IUCN Red Listings are regularly updated and as a result of recent taxonomic revisions (Andriaholinirina et al., 2006; Kappeler et al., 2005; Louis et al., 2006a,b; Olivieri et al., 2007; Rabarivola et al., 2006; Ravaoarimanana, 2004), the IUCN (2008) now lists 92 extant lemur species. Although this indicates potential to eventually include more species in this analysis most (46%) of the species on the revised Red List are listed as Data Deficient (including 34 out of the 41 new species) on the basis that "further information is required to determine the taxonomic validity of this species, its limits of distribution, and its population status", and the altitude limit data that is necessary to make the range refinements is also unavailable for most of the new species. The aim of this paper is not to present a prioritization for Madagascar, but a study of effect of range refinement and species weighting on conservation plans.

2.2. Zonation algorithm

We used Zonation (Version 1.0) conservation planning software to select priority reserve sites (Moilanen, 2004). For computational efficiency, and to maintain a degree of landscape connectivity, Zonation works from the edge of the given landscape and iteratively removes grid cells of lowest priority, ranking them sequentially. Grid cells of increasingly higher value are removed as follows: (1) start from the full landscape, (2) calculate the marginal loss, δ_i, that would result from the removal of each edge grid cell i, (3) remove the cell with smallest δi, (4) return to step 2 if there are any cells remaining in the landscape.

At the start of any one iteration Zonation defines marginal loss caused by the loss of cell i as:

$$\delta_i = max_j(Q_{ij}(S)w_j/c_i) \quad (1)$$

In Eq. (1), $Q_{ij}(S)$ is the proportion of the range of species j remaining within the remaining set of grid cells S that lies within the single cell i, wj is the weight of species j, and c_i is the cost of adding cell i to the reserve network.

Our species range inputs were binary values (1 indicated presence and 0 indicated absence), for w_j we used species-specific weights based on the current IUCN threat categories of each species (see section on species weights below), and we set $c_i = 1$ for all cells to isolate the effects of data quality and species weights.

Eq. (1) thus integrates the priority (weight) given for the species and how much of the range of each species has already been omitted during the course of the algorithm. Zonation optimizes the solution by capitalizing on the natural patterns of species co-occurrences in the landscape to include the maximum possible proportion of each species distribution within the solution (Moilanen et al., 2005). In the early stages of removal, the lowest-priority cells are those that do not have occurrences of any species of importance, and cells that have occurrences of highly-weighted species receive the highest priority. The critical part of Eq. (1) is $Q_{ij}(S)$; when a substantial part of the range of a species has been removed by the algorithm, $Q_{ij}(S)$ increases the value of the remaining cells where that species occurs. Consequently, Zonation retains representation of all species with non-zero weights until the end of cell removal. Even for initially common species, which are often allocated low weights, the last remaining cells will have high value so they will receive some protection. In situations when species are weighted equally, species with small ranges usually receive relatively high proportions of protection up until the final stages of removal as their ranges are often nested within other species ranges (e.g. in areas of high endemicity). However, if these narrow range species are highly weighted, the algorithm will allocate them relatively high proportional protection, even if they are located in geographical isolation and are not nested within other species ranges.

2.3. Species weights

To address the issue of prioritization among species, species area targets are frequently used in popular conservation planning algorithms such as Marxan (Ball and Possingham, 2000). Although target-based algorithms are rapid and powerful decision support tools, producing a solution that meets all targets within a given budget or area constraint is often impossible. In these cases, target revision is required, a process which demands significant time from experts, and can be politically challenging, as it either involves eroding all targets at a similar rate, or trading off target reduction between species.

In contrast, the weighting mechanism of Zonation automates the process of eroding all species targets at the same rate while also allowing for species to be weighted separately according to their conservation value. Zonation continuously reduces the proportional representation of each species, within the hierarchical nested solution, thereby allowing the user to focus on a given percentage of landscape to protect as the overall target. Species are represented within this targeted percentage in higher or lower proportion to each other, as their specific weights dictate. A distinct advantage of the algorithm is that it aims to maximize

Table 2
Three weighting schemes for IUCN Red List categories; used to weight species for Zonation, and to derive Red List Indices.

IUCN Red List category	*n*	Equal weights	Linear weights	Log weights
Extinct[a] (EX)	0	1	5	1
Critically Endangered (CR)	6	1	4	0.5
Endangered (EN)	9	1	3	0.05
Vulnerable (VU)	17	1	2	0.005
Near Threatened (NT)	8	1	1	0.0005
Least Concern (LC)	6	0	0	0

[a] No lemurs were listed as extinct, and none are predicted to go extinct under the scenarios considered, but this weight is necessary (W_{EX}R) in the RLI calculation.

Table 3
Red List categories (IUCN, 2004) and criteria (2001 Version 3.1) used to determine categories of species from the extent of occurrence and refined extent of occurrence.

IUCN Red List category	Criterion A(1): reduction in extent of occurrence (%)	Criterion B(1): extent of occurrence size (km^2)
Critically Endangered	90	<100
Endangered	70	<5000
Vulnerable	50	<20,000

The IUCN Red List specifies criteria only for Critically Endangered, Endangered and Vulnerable categories. A species is categorized as Extinct when "there is no reasonable doubt that the last individual has died" and Near Threatened when it is "close to qualifying for or is likely to qualify for a threatened category in the near future" (IUCN, 2001).

representation across all species at each percentage ranking (e.g. 1%, 2% ... *x*% of the total land area preserved); it is therefore a practical approach that adapts well to political constraints.

We weighted each species according to its Red List category; Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), or Least Concern (LC) (IUCN, 2004). We compared three numerical species weighting schemes: (1) equal weights, (2) linear weights, and (3) log weights (Table 2). The equal weighting scheme allocates all threatened and Near Threatened species weights of 1. The linear weighting scheme prioritizes species in higher risk categories, and maintains an equal interval (of 1) between successive categories; this is the same as the "equal-step" approach used by Butchart et al., 2004. The log weighting scheme prioritizes species in higher risk categories by increasing the weights on a logarithmic scale, so that each successively higher Red List category receives a weight ten times higher than the previous category, which matches the geometric mean of "extinction risk" weighting used by Butchart et al. (2004).

For each of the above weightings, we weighted Least Concern species as 0 because the IUCN assessment determined that they are not globally threatened. Least Concern species are often widespread or opportunist species that successfully compete in disturbed habitats, and so may occur in developed areas that may not be in need of strict protection. The 0 weighting emulates this assumption, which is common among conservation planners who regularly omit these species from conservation planning exercises. With weights of 0, these species did not influence the priorities identified by Zonation, but we still evaluated the proportions of their ranges that would be incidentally protected by the Zonation solutions using the output generated by Zonation. We did not include Data Deficient species in the analysis because their ranges are not sufficiently known to rely upon this type of analysis to meaningfully represent or assess them.

2.4. Potential Red List Index change

To evaluate the overall potential effectiveness of our solutions, across all lemur species, we estimate the potential extinction risk that could result from the proposed Zonation solutions using Red List Index change as in Butchart (2007). This method assumes that any portion of a species' range that is not incorporated in the Zonation solution would suffer habitat transformation and become unsuitable for the species.

The IUCN Red List criteria allocate species to categories of extinction risk, through detailed assessment of information against a set of objective, standard, quantitative criteria based on population sizes, population decline rates, range areas, and range declines. We use 2004 Red List categories (IUCN, 2004) to compare the 2004 Red List Index (which we refer to as the current Red List Index) with the potential Red List Index for each Zonation solution. We assess the change in the Red List Index that would occur with the implementation of each Zonation solution. The rate of Red List Index change indicates the rate at which species are slipping towards extinction at a particular point in time (Butchart et al., 2004), and has been used to assess historical change in extinction risk (Brooke et al., 2008; Butchart et al., 2004, 2005). Here, for the first time, we explore its use in assessing the value of possible future conservation scenarios.

Because we can only assess our conservation solutions by the area of each species' current range that would be protected by each potential Zonation solution, we evaluate them using only Red List criteria A and B, which relate to thresholds of range reduction and minimum range remaining. In our analysis of future scenarios, a species was allocated a higher Red List category when: (1) the protected proportion of a species' range within a Zonation solution fell below the IUCN Red List Criterion A threshold for proportional range reduction or (2) the total size of the area remaining was reduced below the IUCN Red List Criterion B threshold for minimum range size (Table 3). Red List categories are determined through detailed data involving additional criteria beyond range size and range contraction. Our assessment of increased extinction risk is limited by the use of only two Red List criteria (A and B) and the fact that range refinements reduced the current range estimates. The application of only Criteria A and B to the current refined ranges categorized eleven Vulnerable species, seven Near Threatened species, two Least Concern, and all six Data Deficient species in higher risk categories than the IUCN had categorized them. In these cases we used the new, higher, categories as current categories in the Red List Index calculations. The Red List Index for current conditions and for each Zonation solution were each derived according to Eq. (2a).

$$\mathrm{RLI}_t = 1 - \frac{\sigma_{s=1}^{n} W_{c(t,s)}}{W_{FX} * N} \tag{2a}$$

When RLI_t = Red List Index for time *t*, W_{EX} = the maximum possible weight, *N* = total number of species assessed, $W_{c(t,s)}$ = weight according to Red List category for species *s* at time *t*. RLI values are low when many species are threatened; consistent with this, RLI_t approaches 0 when species threat increases maximally under the proposed reserve design, and approaches 1 when all species remain at current threat levels under the proposed design.

The extinction risk (E_t), predicted by proportional change in the Red List Index, is calculated according to Eq. (2b).

$$E_t = (\mathrm{RLI}_{t-1} - \mathrm{RLI}_t)/\mathrm{RLI}_{t-1} \tag{2b}$$

In calculating the RLI for each Zonation solution the numerical values representing the extinction risk for a given Red List category, $W_{c(t,s,)}$, were the same as the log weights used in Zonation, which are referred to as the geometric mean of "extinction risk" by Butchart et al. (2004).

2.5. Methodological comparisons

2.5.1. Data type comparison

We used each of the three species weighting schemes, equal, linear and log, to run Zonation for the two data types, extent of occurrence and refined extent of occurrence. Solutions generated using refined extent of occurrence data are assumed to be more accurate than solutions from the unrefined data, and this comparison focuses on quantifying the benefits of using refined data for conservation planning.

We compared the reserve solutions generated by extent of occurrence versus refined extent of occurrence data in three ways. First, we determined the overlap between the top 10% of the landscape selected for inclusion in reserves by each data type. Second, we calculated the Red List Index change to assess the potential increase in extinction risk that could occur if each solution were implemented. Third, we examined the proportions of species' ranges (refined extent of occurrence) that would be protected by each reserve solution.

2.5.2. Comparison of species weighting schemes (equal, linear and logarithmic)

The effects of the three weighting schemes were compared as above, using: (1) the spatial overlap between the three Zonation solutions, (2) potential Red List Index changes, and (3) the proportions of species' ranges protected under the three different weighting schemes. Additionally, to compare how effectively species in the different IUCN categories are protected by different weighting schemes, we calculated the proportion of species' refined extents of occurrences that were protected for each of the five IUCN categories.

3. Results

3.1. Data type comparison

Comparisons between the pairs of Zonation solutions identified using the extent of occurrence data and the refined extent of occurrence data show only 32%, 32%, and 35% spatial overlap for the equal, linear and log weightings respectively.

The potential Red List Index changes for equal, linear, and log weights are 3.2%, 8.1%, and 8.9%, respectively, for the extent of occurrence solutions, and 1.7%, 1.7% and 1.8%, respectively, for the refined extent of occurrence solutions (Fig. 1a).

Fig. 1b shows that the minimum and mean proportions of species' ranges that are protected are significantly higher under the solutions generated using the refined extent of occurrence data (Mann–Whitney Test, equal weights: $U = 500$, $p < .0001$; linear weights: $U = 452$, $p < .0001$; log weights: $U = 394$, $p < .0001$).

Solution quality can also be evaluated for each threat category by comparing the pairs of graphs in the rows of Fig. 2. These graphs show the proportion of lemur species' ranges represented in the solution. How well all species' ranges are protected and how well the threatened species are represented is shown respectively by how much of the total bar area and how much of the shaded bar area is found to the right of the graphs. All three solutions derived from the refined extent of occurrence data (Fig. 2b, d, and f) protect the entire ranges of all the Critically Endangered species, and also protect larger proportions of species' ranges in all categories. The increases in the mean proportions of species' ranges protected by solutions derived from refined data, compared to solutions derived from unrefined data are: Endangered 32–47%, Vulnerable 45–71%, Near Threatened 62–68%, Least Concern/Data Deficient 52–68%.

These comparisons all demonstrate that using refined extent of occurrence data provides a substantial improvement in the potential performance of the resulting Zonation solutions. We therefore used only the refined extent of occurrence data for the remainder of our analyses.

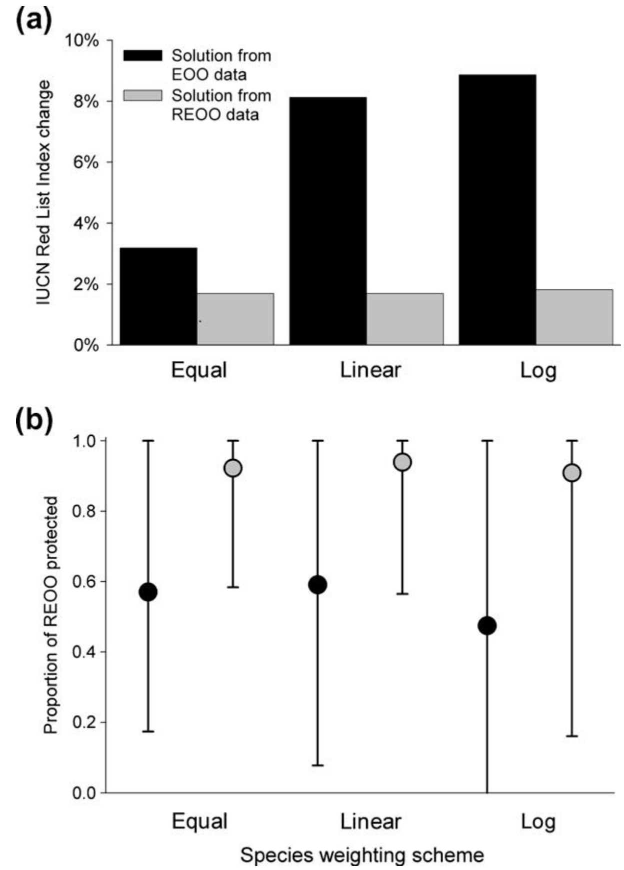

Fig. 1. (a) Increase in extinction risk indicated by the IUCN Red List Index change for Threatened species (CR, EN, VU, NT) and (b) minimum, mean, and maximum proportions of species refined extent of occurrences protected when using two data types (Extent of Occurrence=EOO, and Refined Extent of Occurrence=REOO) and three different weighting schemes (Equal, Linear, and Log).

3.2. Species weights comparison

Fig. 3 shows maps of the Zonation solutions for equal (Fig. 3a), linear (Fig. 3b), and log weights (Fig. 3c) using refined extent of occurrence inputs. The spatial overlaps between these solutions are 75% (equal-log), 85% (equal-linear), and 88% (linear-log).

Despite these spatial differences the potential Red List Index change for the refined extent of occurrence Zonation solutions (light bars in Fig. 1a) are very similar (1.7%, 1.7%, and 1.8%).

In Fig. 2, comparisons between the three graphs in the right column indicate the differences between weighting schemes for the three solutions (shown in Fig. 3) derived from refined range inputs. Darker shading and taller columns towards the right of the graphs indicate better protection of threatened species. Critically Endangered species are fully protected by all three solutions, even by the equal weights scheme. The difference between the three weighting schemes (Figs. 2b, d, and f) is largely reflected in the Endangered species, more of which are better protected as you move from equal, through linear, to log weights (number of species with >90% of their distributions protected: equal 4, linear 8, and log 9). The log weighting solution (Fig. 2f) also better protects more Near Threatened and Least Concern species (number of species with >90% of their distributions protected: equal 6, linear 3, log 10), but trades off protection of other less threatened species

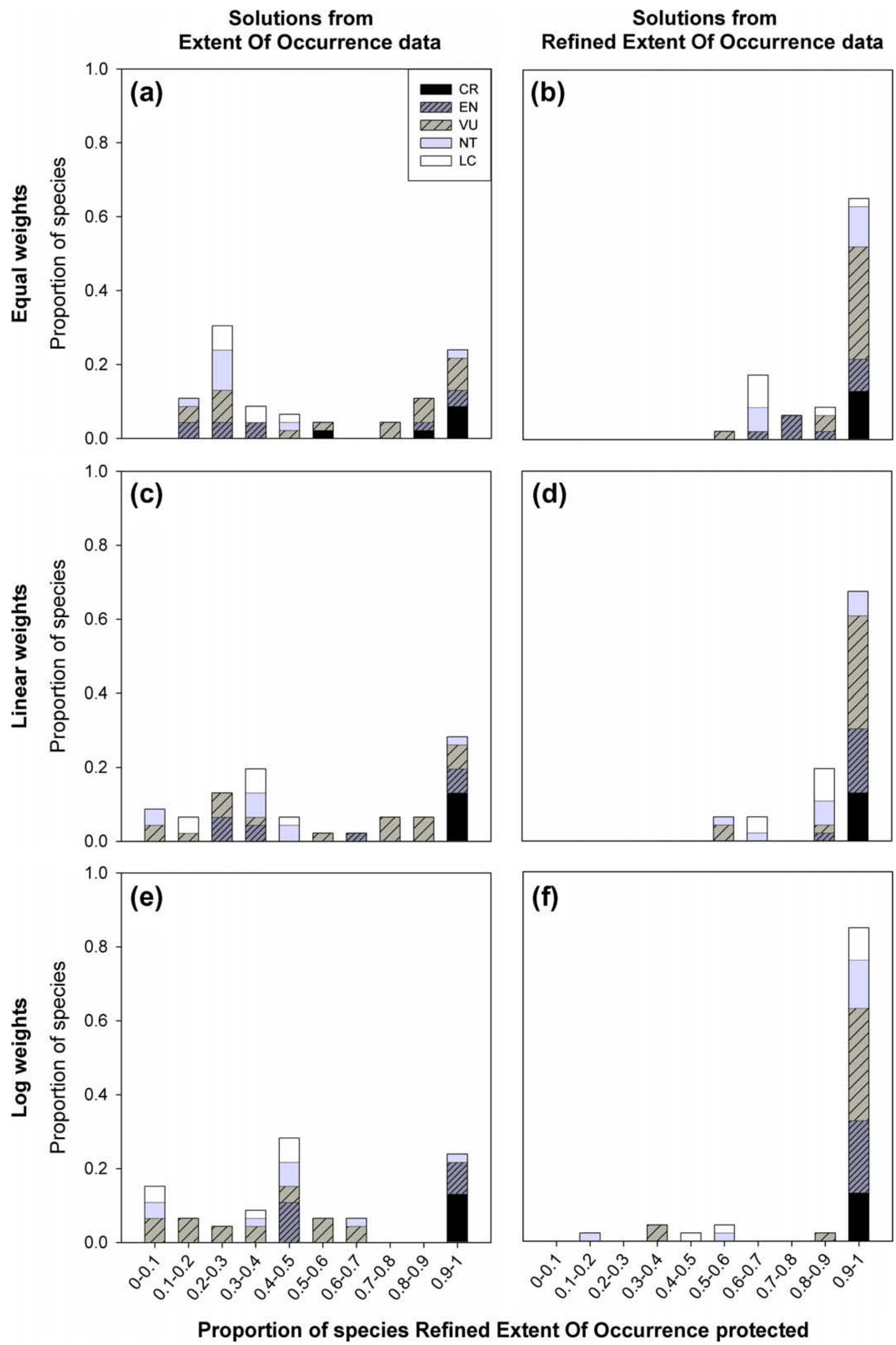

Fig. 2. The proportion of species protected by having different proportions of their ranges remaining in the top 10% of the Zonation solution. The two columns allow comparison between the solutions from extent of occurrence (a, c, e) and refined extent of occurrence (b, d, f) data. The three rows allow comparison between the equal (a and b), linear(c and d), and log (e and f) weighting schemes. The IUCN Red List categories, which determined each species' weight, are indicated by the color gradient. When reserve solutions are effective for all species, more of the total bar area will be found toward the right side (larger proportions of species' ranges) of the graph. When reserve solutions are effective for threatened species, more of the darker shaded bar area will be found on the right side of the graph.

and has the most species with low percentages of their ranges protected as compared to the equal and linear solutions (number of species with <50% of their distributions protected: equal 0, linear 1, log 2).

Fig. 4a shows the minimum, maximum, and mean proportions of species' ranges that would be protected, per Red List Category, under each solution. The proportion of species' ranges protected in different categories mirrors the design of each weighting

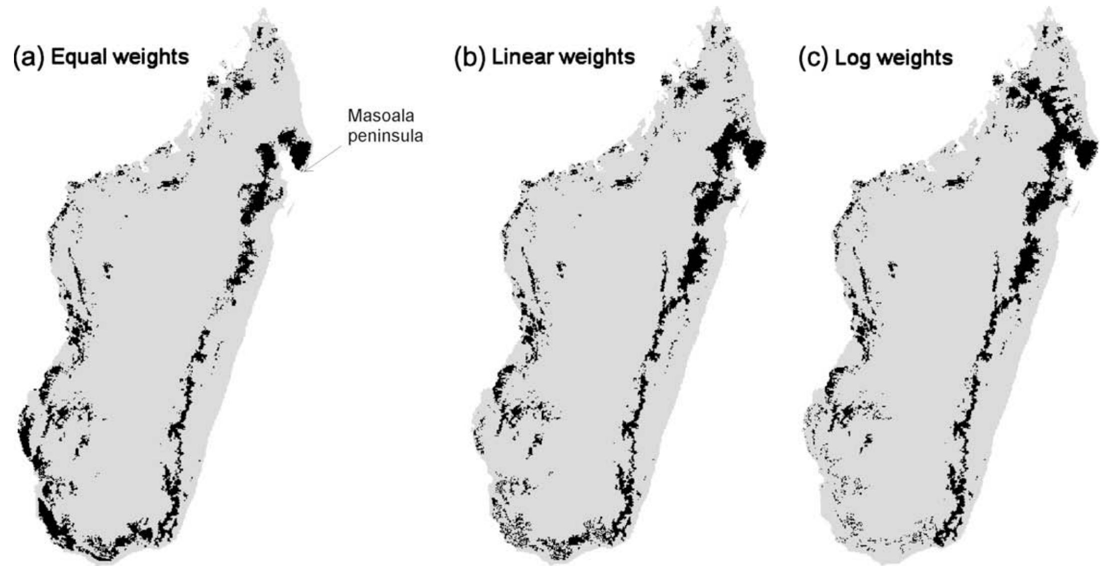

Fig. 3. The top 10% (black) from Zonation solutions generated using and refined extent of occurrence inputs with: (a) equal, (b) linear and (c) log species weighting schemes.

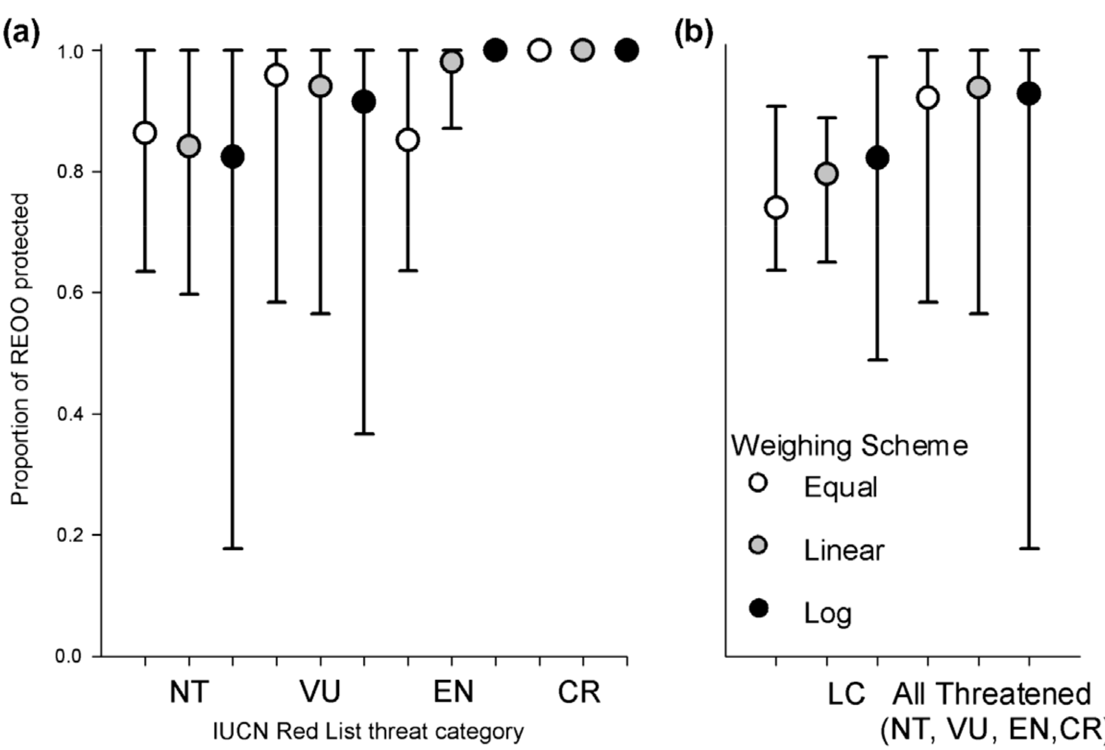

Fig. 4. Minimum, mean, and maximum proportions of species refined extent of occurrences (REOO) protected by the top 10% of Zonation solutions, created from refined extent of occurrence data, using three different weighting schemes, and organized by IUCN Red List category: (a) NT = Near Threatened (n = 8) ; VU = Vulnerable (n = 17); EN = Endangered (n = 9); CR = Critically Endangered (n = 6). (b) LC = Least Concern (n = 6), All Threatened = NT, VU, EN, CR (n = 46).

scheme. All the Critically Endangered species are fully protected under each of the three weighting schemes. In general all the weighting schemes show a progression of low to high mean proportion protected, moving through successively more threatened categories (from NT, to VU, to EN, to CR), although the equal weighting scheme shows a low mean level of protection among the Endangered category. As the higher threat categories are increasingly prioritized (i.e. moving from equal to linear to log weightings), the mean representation of the Endangered species is increased, which comes at the expense of the representation of the Vulnerable and Near Threatened species. The trade-off in protection among categories is also demonstrated by the range of minimum representation as the log weighting scheme produces the lowest minimum representation for the lowest threat category, and the highest minimum representation for the Endangered category.

Fig. 4b shows the proportion of range remaining for Least Concern species, which are not currently threatened, and received a weighting of 0 in all weighting schemes. If any of the solutions were implemented, the mean range protection for Least Concern

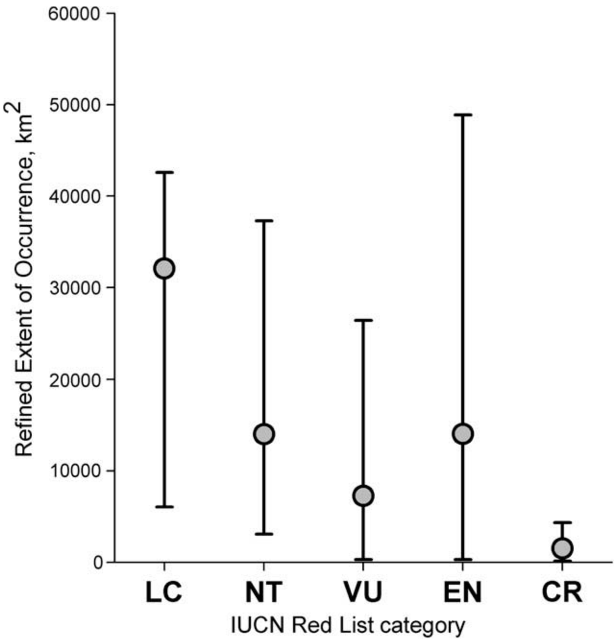

Fig. 5. Minimum, mean, and maximum refined extent of occurrence for lemur species within each IUCN Red List threat category.

species would be 11–20% lower than the ranges of all threatened species (CR, EN, VU, NT; Fig. 4b). The original range sizes of species in the different threat categories are compared in Fig. 5.

4. Discussion

4.1. Data type comparison

The quality of distributional data input into an algorithm dictates the location of priority areas as well as the protection afforded to individual species. For lemurs, simple range refinements using altitude and habitat dependency resulted in an average of 71% range reduction (range 2–97%, $n = 52$). This is almost double the difference reported by Jetz et al., 2008 for bird species extent of occurrence data, who reported an average overestimation of 38% (range 0–91%, $n = 1158$) using a similar refinement process.

When the less accurate extent of occurrence data are used, the algorithm converges on apparently optimal priority areas for lemur conservation. However, when additional information regarding altitude and habitat requirements is taken into account, between 65% and 68% of those priority areas are no longer among the top 10% of the solution.

While there are potential sources of error in the refined data, including remote sensing error in habitat classification, and insufficiencies in field survey data to accurately determine altitude limits, the low agreement between the priority areas identified using the two different data types indicates that a large advantage can be gained from the small additional effort required to refine by habitat and altitude. The potential changes in the Red List Index further suggest the importance of using refined data, as potential extinction risk is markedly higher for the three solutions generated from unrefined data (Fig. 1a). Although the directionality of this result is pre-determined by the comparison of both data types to the refined data, the magnitude and significance of the result clearly demonstrate the importance of using refined data.

Investing conservation funds in conducting the extent of occurrence refinement exercise, which is based on data that are relatively easy to collate, is clearly preferable than risking poorly allocating approximately two thirds of a reserve network. In the case of Madagascar's planned protected area expansion, this would equate to 4 million hectares being sub-optimally allocated.

Further refinements of the species ranges, to account for extirpation in regions of high hunting pressure or areas with greater potential for habitat change as a result of anthropogenic pressures, would further increase their utility for conservation planning. Availability of this data is limited for many lemur species and is often not geo-referenced in a format conducive to spatial analyses. While we expect that the effort required to collect these data will result in diminishing returns in the application of conservation planning algorithms, ideally, these data ought to be a factor in conservation planning. It might be more efficient to factor in the effects of hunting by developing a hunting pressure layer derived from combined estimates of hunting pressure, across all lemur species, which could be utilized in the form of a cost layer in Zonation.

4.2. Species weights comparison

The objectives of a reserve network, including which species are to be prioritized, should always be explicit (Kershaw et al., 1995; Pressey et al., 1996; Margules and Pressey, 2000). Species can be prioritized according to their IUCN Red List Categories, as in this study, or according to a wide range of other criteria, such as whether a species is a charismatic species that generates tourism revenue, a keystone species (Caro and Doherty, 1999), a provider of ecosystem services (Chan and Daily, 2008), or is more likely to provide potential for future evolution (Forest et al., 2007). Many studies have discussed the potential uses of species-specific targets or weighting systems in conservation planning algorithms in order to prioritize threatened species (Church et al., 1996; Arthur et al., 2002; Camm et al., 2002; Onal, 2004), but few have explored the effects of different targets or weighting schemes. Our different species-specific weighting schemes are designed to explore the potential effects of the common practice of preferentially weighting species that have already suffered population reductions from habitat destruction or exploitation.

We found an overlap of 75–88% between sites selected using different weighting schemes, which is broadly consistent with the 60–80% overlap reported by Arponen et al., 2005. However, our overlap in weighting schemes must be interpreted within the context of lemurs' preference for forested habitat and the forested area remaining in Madagascar. Because lemurs are forest dependent they are particularly vulnerable to habitat destruction, and a high proportion (82%) are threatened. From 1950 to 2000, Madagascar's forest cover decreased by nearly 40% and estimates show that less than 15% of Madagascar remains covered in forest (Harper et al., 2007). If all 52 lemurs' refined extent of occurrence polygons are overlaid, they are entirely contained within this remaining forest, and their total area encompasses 13% of Madagascar's surface area. Therefore, the minimum possible overlap between any two randomly generated top 10% solutions within this 13% of the land surface would be 54% (or 5.4% of the entire land surface). This indicates that the differences between the solutions from the two most extreme weighting schemes (25% difference between the equal and log weighting schemes) diverge considerably when compared to what is practically possible (46%) within the confines of the remaining forest cover. Therefore, although the convergence of forest-dependence and deforestation results in largely overlapping spatial requirements for protecting lemurs in general, the potential exists for a spatial divergence of reserve priorities, which can require difficult decisions from conservation planners. In this case, the greatest difference between the solutions occurs in the connectivity of the northwest Masoala peninsula to northern transitional forests (Fig. 3). This is of particular note as the northern forests are currently suffering heavily from illegal logging in the wake of the 2009 coup (Patel, 2007; Black, 2009).

In evaluating the methodological decisions in the use of Zonation, we aimed to understand the trade-offs inherent in conservation planning algorithms. Our results largely indicate that the selection of an optimal solution requires value judgments and trade-offs in prioritization in order to minimize extinction risk. In our case, the potential Red List Index change is nearly identical regardless of weighting scheme, but our supplementary assessments of proportional protection demonstrates that there are significant trade-offs occurring between the solutions.

The optimal solution generated could be evaluated with respect to minimal extinction risk across all species. However, Akçakaya et al. (2006) have warned that it is difficult to attach estimates of extinction risk to IUCN Red List Categories. To conduct a completely rigorous Red List assessment for the future scenarios, we would ideally have compared the range area at the start of each species area loss trajectory (the historical range) with the future range under the potential protected area solution. However, since the historical range areas are not adequately known, we could only compare the current range with the potential protected area solution, which results in underestimates of Red List Index change for the potential protected area solutions. The relative contributions of the unknown portions of each species' range loss trajectory (historical range loss) would vary among the three Red List Index change results due to the different species weights used in Eq. (2a) (equal, linear, log). Species in lower threat categories are more likely to have under-contributed to the potential Red List Index change results than the species in higher threat categories, and species in higher threat categories may over-contribute to potential Red List Index change if they experience a relatively low decrease in range but cross a threshold barrier. For example, a Least Concern species, which may have already experienced as much as 49% historical range loss (Table 3), would not contribute to the Red List Index change results, but a Vulnerable species with a range size slightly over 5000 km^2 whose range drops just below 5000 km^2 would contribute to increase extinction risk.

Our results demonstrate that different weighting schemes distribute species protection differently across the Red List threat categories. The trade-offs in setting representation targets, or selecting species weighting schemes, are inherent in conservation planning, and in the absence of methods to predict exact probability of extinction, the assignment of species weights is likely to be a value judgment. The overall cost or benefit of any weighting system is likely to vary depending on the proportions of species that fall into each threat category, and according to natural variation in patterns of species richness and endemicity. However, comparing a range of targets or weights allows their consequences to be assessed, and the methods we have outlined should be within the capabilities of conservation planning groups operating with limited data and low budgets in developing countries. Where possible, we recommend conservation planning be conducted in consultation with regional and taxonomic experts and include a variety of weighting schemes to investigate the trade-offs specific to a regions and taxa. The graph illustrations we present provide a simple way of presenting the results to decision makers, to highlight the choices faced in spreading risk across all species or optimizing the solution for some species at the cost of others.

4.3. Non-threatened species protection

Due to the high degree of forest-dependence among lemurs we expected Zonation solutions for threatened lemur species to provide a relatively high degree of protection for non-threatened lemur species. The refined ranges of the 52 lemur species occupy 86% of Madagascar's remaining forest cover, 97% of this occupied area contains 2 or more species. Therefore, even if forested grid cells were randomly selected almost every cell would benefit more than one of our 52 species and we expect that incidental protection of the relatively widely distributed species in the Least Concern category (Fig. 5) would be high relative to other taxa in Madagascar or elsewhere. In other taxa, which may have less overlap in habitat suitability, protection of only threatened species could expose non-threatened species to even higher extinction risk.

Our results demonstrate that not including species of Least Concern in the prioritization, under the assumption that they will receive sufficient incidental protection, results in relatively poor proportional protection of their ranges (Fig. 2b, d, f and 4b), even when these species share very similar life history and habitat requirements with the highly-weighted species. However, the difference between the mean proportions of range protected for the threatened species and the Least Concern species (Fig. 4b) can largely be attributed to the larger original range sizes of Least Concern species (Fig. 5). The average area protected for Least Concern species is 3.2–3.3 times greater (comprising an average of 38–42% of the Zonation solution, $n = 6$) than the average area protected for all threatened species (12–13% of the Zonation solution, $n = 40$). However, of the six species currently categorized as Least Concern, only one species (*Eulemur fulvus*) would increase to Endangered under the equal weights solution, none would change category under the linear weights solution, and only one species (*Cheirogaleus major*) would increase to Vulnerable under the log weighted solution. This shows that while the solution incidentally offers a large area of protection to these non-threatened, un-weighted, species, it is possible for some to fall through the gap and suffer substantial increases in their extinction risk.

We advise that conservation planning exercises should evaluate the probable long-term consequences for non-threatened species when planning is based primarily on threatened species. Having demonstrated how the relatively cheap and simple, expert driven process of range refinement can improve conservation planning results, we suggest that the same expert review process could provide some additional opportunities for efficiency. In particular, the tolerances of non-threatened species to hunting and other forms of disturbance, typical of different land management and protection strategies (e.g. the newly created community managed forest blocks in Madagascar) could be estimated. This might allow the protected area requirements for some of these species to be relaxed, which could allow increased prioritization of other less disturbance-tolerant species.

5. Conclusions

The quality of distributional data and species weights input into an algorithm dictate the location of areas prioritized and the quality of protection afforded individual species. Therefore, assessment of the relative costs and benefits of investment in data quality and the consequences of species weighting systems is of vital importance. As these are likely to vary between regions and taxa, we recommend that these should always be explored during quantitative conservation planning exercises.

Data refinement according to species altitude and habitat preferences is a highly recommended investment of time and money because it leads to more efficient solutions. Our exploration of different numerical weighting schemes demonstrates the trade-off between protection across the range of threat categories, and highlights the choice between minimizing overall species extinction risk and minimizing the risk to more threatened species.

Our examination of the degree of incidental conservation afforded to non-threatened species, which were not weighted in the prioritization, leads us to recommend that, to minimize overall extinction risk, conservation planners should make case by case assessments to determine the potential benefits of including non-threatened species in the weighting scheme, as taking care to ensure their representation may be as important as choosing an overall weighting scheme. We demonstrate that a post optimization assessment of the protection that un-weighted species would receive is a simple way of determining whether they might require weighting and active prioritization in conservation planning exercises.

We present a thorough exploration of two common methodological issues in conservation planning. To clearly present the effects of range refinement and weighting schemes many other important factors (such as pre-existing protected areas, legal availability of land, habitat quality, cost, threat from hunting, logging and other anthropogenic activities) were excluded, and the results are not intended as a finalized conservation planning solution for Madagascar's lemurs.

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