

**EXTINCTION RISK FROM HABITAT
FRAGMENTATION USING
METAPOPULATION-BASED METRICS**

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ABSTRACT OF THE DISSERTATION

Extinction risk from habitat fragmentation using metapopulation-based metrics

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The world is becoming more developed as the human population steadily grows. With the increase in human influence, anthropomorphic habitat loss will only increase over time. Habitat fragmentation is the leading threat to species globally. Assessing fragmentation and determining sites of the most critical regions is vitally important for conservation efforts. One way of assessing fragmentation is by relating the spatial aspect to the biological aspect, via metapopulation dynamics. Specifically, metapopulation capacity allows for relative valuation of fragmented landscapes. However, a modification is required for it to operate at large-scale landscapes. The modified metric enables relative quantification value of fragmented habitat, with biological relevance for long-term extinction risk. Using the same spatially explicit components of metapopulation theory, we can also create a short-term measure of extinction risk, based on the instantaneous rate of expected decline post-fragmentation. This metric, extrapolated persistence time, along with the modified metapopulation capacity metric, can then be used in a variety of ways to determine high risk species and regions.

Given that bird species are capable of an assortment of dispersal abilities, focusing within phylogenetic groups allows for more relevant comparisons between species. With the use of slopegraphs, we can instantly determine those species, within their families,

with remaining ranges that have extremely low relative values for long or short term extinction risk. Of particular concern are those species considered to be at low risk of threat by the IUCN Red List, yet possess habitats that are critically fragmented. The metrics can be utilized in estimating overall landscape value, and estimating the contribution of specific patches to the overall landscape value; this would be useful in preservation and management decisions. Finally, by focusing on those km^2 that connect large patches, we can determine where restoration of habitat should be prioritized, for anything from the greatest increase in metapopulation capacity to the most number of species with ranges that could be reconnected.

Chapter 2 is in press with Conservation Biology.

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Chapter 1

Introduction

1.1 Extinction

Mass extinctions have occurred throughout history, but the most recent one is happening now. The sixth mass extinction is a compounded result of human activity [40, 10]. The regions of greatest biodiversity are tropical forests, biomes with considerable habitat destruction and subsequent extinction [123, 124, 125, 84], which have significant abiotic impacts globally [1, 34]. It is estimated that without protection, biodiversity hotspots will lose 40% of their species [143]. Species loss will be further compounded by climate change [52, 180, 89] and by success of invasive species [118]. The need for conservation has never been greater.

There are numerous organizations working towards species conservation. The International Union for Conservation of Nature ([85] — <http://www.iucn.org/>), the largest environmental organization and conservation network, compiles data to estimate all species' risk of endangerment, in what is known as the IUCN Red List of Threatened Species, or simply the IUCN Red List (<http://www.iucnredlist.org/>). Data for avifauna risk is contributed by their partner organization, BirdLife International (<http://birdlife.org/>). Some factors that the IUCN incorporates in determining a species' Red List Category include: extent of occurrence, population size, predation/parasitism, anthropogenic activities, and habitat tolerance. Of these, we focus on the extent of occurrence of available habitat.

1.2 Causes of extinction

The factors implicit in extinction risk are multi-fold. One review [82] assembled a number of traits thought to predict species' sensitivity in general: "population size; population fluctuation and storage effect; dispersal power; reproductive potential; annual survival; sociality; body size; trophic position; ecological specialization, micro-habitat and matrix use; disturbance and competition sensitive traits; rarity; and biogeographic position." Birds are one taxon particularly noted in their extinction risk [159, 139, 161].

A number of traits are associated with extinction in birds from fragmentation [149], including: endemism [63], habitat specificity [200, 128, 87, 63, 55], life-history characteristics (e.g., survival rates, clutch size, ground-nesting behavior — [162]), foraging strata [14, 88, 166], body size [101, 200, 88, 147, 55], population size [128, 63, 55], range distribution [14, 87, 88, 63, 147, 55], low dispersal ability [50], diet [200, 14, 87, 88, 166, 147], taxon [87, 147], and association with other species [14, 166].

Recent bird studies have shown fragmentation to interact complexly with extirpation. For example, ground nesting birds are particularly vulnerable to habitat fragmentation, with the increase in edge and exposure to predators [91, 112]. Neotropical migrants were found more sensitive than residents to forest fragmentation [116]. Forest fragmentation can increase hunters' accessibility to larger birds [137]. New World species were more sensitive to fragmentation than Old World species, due to the historical duration of forest degradation, while pairing success was most closely linked to fragmentation [94]. Secondary forest regrowth could improve species richness by connecting patches with contiguous forest [168]. Understory birds decreased with edge proximity [95]. The higher instability of smaller forest fragments was found due to higher levels of colonization rates [19]. Conversely, [92] found increased patch size correlated with decreased emigration in movement models, but in the bush cricket.

1.3 Habitat fragmentation

Habitat loss, and subsequent fragmentation, is the greatest cause of species extinction in the world [143]. The primary effects of fragmentation are decreased patch size, increased

edge, and decreased connectivity between patches [59, 99]. Forest fragmentation has been demonstrated to have dire consequences for biological community dynamics [4]. Birds are highly vulnerable to habitat disturbances and these consequences have been heavily studied [105, 14, 177, 128, 15, 176, 116, 4, 66, 83, 185, 97, 62, 22, 104, 56, 164, 19, 9, 138, 129]. Climate change will further exacerbate habitat fragmentation [132].

1.4 The Atlantic forest

The biodiversity hotspots [126] of the world include 44% of the world's plants and 35% of terrestrial vertebrates in just 1.4% of the land area [27]. One of these, the Atlantic Forest of Brazil, is simultaneously one of the most diverse and threatened habitats for species. The original, intact form of Brazil's Atlantic rainforests covered 1.0-1.5 million km² [44]. An estimated 1-12% of that eastern coastal habitat is all that remained two decades ago [122, 126, 154], although latest estimates have narrowed this down to 7-8% [148]. Remaining patches of the Atlantic Forest consist of humid evergreen forest isolated amidst drier (caatinga, cerrado, and chaco) habitats that historically allowed for unique speciation [135], the majority of which are very small [62, 172, 148]. One estimate is that 48% of the rain forest fragments are less than 10 ha, while only about 7% are greater than 100 ha [145]. Despite this extreme overall decline, deforestation has not ceased [121, 126].

These insufficient patches contain 75.6% of Brazil's threatened endemic species [114], or comprise of 20% of all plant and 16% of all vertebrate species worldwide [126]. Birds are chief among them as they suffer severely when their habitat is fragmented and lost [114]. Because of the clear threat that has been documented, many studies have focused on the declines and extinctions of the avifauna of the Atlantic forest of Brazil [174, 64, 26, 135, 31, 115, 149].

1.5 Metapopulation theory

Metapopulation dynamics [102, 103, 71] provide us with an efficient means of relating spatially explicit geographical information and known ranges to species' extinction risk,

via spatially realistic metapopulation theory [75]. The potential for a rescue effect [32] between patches means that isolated populations can persist longer as a whole species. While metapopulation dynamics dictate the local scale, it is increasingly important to account for the landscape level, as climate change and fragmentation impact upon species' ranges [132]. Currently, however, no measures of landscape connectivity exist that can be applied to many species across a single ecosystem and still have biological significance. Ideally, this is what would be required for an effective risk classification system [183, 37, 150].

The world is large enough that species still remain unknown. An earlier review on bird extinctions advocated that conservationists must maximize preservation of land to benefit the most number of species, and that the spatial configuration of the preserved area would be an important component as well [175]. Given the finiteness of available funds and support for conservation, it would be extremely beneficial to be able to prioritize the most important areas for a species within its range [152, 151, 86]. Without prioritization, management attempts can be ineffective, or, at best, inefficient. Conservation efforts would be greatly optimized if they were directed to preserve the best habitat areas for endangered species.

Forest dependent birds are significantly affected by both forest patch area and isolation, suggesting that the distribution of these birds is highly related to forest patch area and limited by dispersal ability [3]. Furthermore, it should be noted that there can be an extinction debt with habitat loss; that is, a delay in the detrimental effects observed that would be expected based on the loss in habitat area [48, 30, 93, 120, 196]. Indeed, the highest levels of extinction debt in Brazil seem to be in the southeastern portion — effectively, the Atlantic forest [196]. This means that a strong understanding of the spatial landscape is key in determining the optimal habitat for species' persistence there.

The goals of this dissertation research are: 1) to devise a spatially explicit metapopulation metric for quantifying extinction risk based on large-scale fragmentation; 2) to determine risk for threatened and non-threatened species based on said metric; 3) to prioritize areas within ranges that contribute the most to overall capacity of the range;

4) to locate where specific km^2 provide the greatest benefit for restoration. We test the applications of our metric with refined range data on forest-endemic birds within the Atlantic forest.

Chapter 2 is in press.

Chapter 2

Estimating extinction risk with metapopulation models of large-scale fragmentation

2.1 Summary

Habitat loss is the principal threat to species. How much habitat remains — and how quickly it is shrinking — are implicitly included in the IUCN’s Red List determination of a species’ risk of extinction. Many endangered species have habitats that are not merely small, but fragmented to different extents. Ideally therefore, fragmentation would be quantified in a standard way in risk assessments. While mapping fragmentation from satellite imagery is easy, efficient techniques for relating maps of remaining habitat to extinction risk are few. Purely spatial metrics from landscape ecology are hard to interpret and do not address extinction directly. Spatially-explicit metapopulation models do link fragmentation to extinction risk, but standard models work only at small scales. They predict that a species in a large, contiguous habitat fares worse than one in two tiny patches, because of a small extinction probability but no colonization to rescue it. We propose models with an area-weighted self-colonization term, reflecting re-population of a patch from a remnant of individuals that survive an adverse event. This solves the ‘few large patches’ problem. For four ecologically comparable bird species of the Central American Highland forests, our predictions put species deemed at least risk on a par with those ranked as threatened, suggesting that fragmentation has harmed them to an unappreciated degree.

2.2 Introduction

Habitat destruction is the most severe threat to species’ survival [144, 155]. It causes both loss of area and fragmentation — the distribution of what habitat remains into small, often widely-separated patches [15, 4, 45]. Not surprisingly, habitat extent and decline play an important role in the IUCN’s Red List determination of a species’ risk of extinction, both through the “A” criteria relating to population size and the “B” criteria relating to geographic range. In both cases, recent habitat loss forms just one basis for inferring small size or declining trends in these other variables, but the accompanying written justifications show that it is by far the most frequently invoked. This is likely a combination of the relatively well-understood relationship between habitat loss and extinction risk, and the fact that habitats are easier to assess than populations.

Until recently, species ranges in the Red List have typically been presented as continuous and with smooth edges — the kind of extent of occurrence (EOO) that field guides display. Previously, a study showed that after sub-setting these field guide ranges by known elevational limits and by broad habitat choices, extents of suitable habitat [13, 33] are often much smaller, especially for species in mountains [81]. For birds, Birdlife International makes the risk assessments, continually updating them on their website (<http://www.birdlife.org>). Recent inspection reveals that some, but not all, of their maps are now subset by at least elevation.

In producing more realistic range maps, one quickly uncovers how fragmented they are. Fragmentation especially threatens tropical forest species, as unbroken canopies become tiny, isolated fragments that include just a few percent of the original forest [14, 185, 56]. While the increased extinction risk in isolated small fragments is fairly well understood (e.g., [56, 98], species can persist on fragmented landscapes if dispersal between patches is sufficient [102, 103]. However, navigating between isolated patches can have high cost [18], even for relatively mobile birds [12].

Accurate assessments of extinction threat under habitat loss require we evaluate species’ remaining habitat distribution, and its effect on extinction risks, in a practical and consistent way. The current Red List guidelines say “A taxon can be considered

to be severely fragmented if most ($> 50\%$) of its total area of occupancy is in habitat patches that are (1) smaller than would be required to support a viable population, and (2) separated from other habitat patches by a large distance.” Thus, a binary decision (fragmented or not) is based on another set of binary decisions about what size is too small, what distance is too large, and so on. In this paper, we will argue that there are more consistent ways to incorporate the spatial information provided by updated, realistic habitat maps.

One approach to assessing fragmentation is purely spatial. For example, the popular software package FragStats [117] calculates a variety of statistics related to spatial patterning. More recent approaches borrow from graph theory [157] or circuit theory [119]. They are essentially non-biological, can sometimes be difficult to interpret, and provide no direct assessment of extinction risk. At the other extreme, large-scale, spatially-explicit implementations of population dynamic models allow for a great degree of realism but are complex, with many parameters, and have been studied mainly for their heuristic value (e.g., [11]). Our goal is a metric that can be applied in a wide range of real-world circumstances, using commonly available data.

Occupancy-based, spatially explicit metapopulation (SEM) models (Hanski 1994) specifically predict extinction risk in fragmented systems, are relatively simple to parameterize, and have been studied and developed extensively. They have not, however, been applied at large spatial scales because of a key difficulty. Analyses generally address equilibrium occupancy or some derived measure of the long-term behavior of a highly fragmented system of small patches [77, 75]. Such metrics behave oddly for systems with a few, large patches. In the extreme, a single large patch has zero long-term value because it has a small but non-zero extinction probability with no colonization to rescue it. This would lead to the conclusion that a large, contiguous habitat is riskier for a species than were it confined to a few tiny patches, which goes against the available evidence.

We overcome this behavior by modifying the standard SEM to include *self-colonization*. By this, we mean the re-colonization of a patch *from within* by a small

number of individuals that survived whatever catastrophe affected the patch — something particularly likely for large patches. This is reasonable on ecological principles alone, and as we will show, also corrects the previously described non-intuitive behavior of occupancy-based models when applied at large scales. Using range data on four forest endemic bird species from the highlands of North Central America, we used two metrics, metapopulation capacity [77] and extrapolated persistence time (defined below), to quantify fragmentation and consequent extinction risk for an entire habitat patch network, both before and after recent forest loss.

2.3 Methods

2.3.1 Spatially explicit metapopulation models for large-scale landscapes

The spatially explicit metapopulation (SEM) model [72] incorporated concepts from island biogeography [107, 106]. Area and connectivity functions determine colonization and extinction rates, and therefore occupancy dynamics, for individual patches [76, 77]. The basic formulation follows the original [102, 103] model except that there is a separate expression for each patch:

$$\frac{dp_i}{dt} = \text{Col}_i (1 - p_i) - \text{Ext}_i p_i \quad (2.1)$$

where p_i is the occupancy rate of patch i . In most formulations the extinction rate term Ext_i is an inverse function of patch area:

$$\text{Ext}_i = \frac{E}{A_i^x} \quad (2.2)$$

where E and x are constants. x is typically set to 0.5 for many taxa, and this is supported for tropical forest birds by Ferraz et al. (2003). That same paper suggests a value for E of 0.07.

The colonization rate Col_i is the sum of the incoming rates from all other occupied patches. These rates increase with the size of the colonizing patch and decline with inter-patch distance according to simple functions. With their various constants, we

write the functions:

$$\text{Col}_i = C \sum_{j \neq i} f(D_{ij}) A_j p_j \quad (2.3)$$

where C is a constant, A_i is the area of patch i , $f(D_{ij})$ is a function of the distance between patches i and j , and p_j is the occupancy rate of patch j (as only an occupied patch can provide colonists).

At large scales, and when dealing with complex patterns of fragmentation, habitat patches may be large relative to their separation distances. Here, we take the distance value D_{ij} to be the minimum distances between patch edges, rather than centroid-to-centroid distances (unlike [134]).

The dispersal survival function $f(D_{ij})$ gives the proportion of individuals leaving patch i that will make it to a patch j , D_{ij} distance units away. The function commonly presented is an exponential decay $e^{-\alpha D_{ij}}$, where $1/\alpha$ is the average inter-patch survival distance. This function implies vanishingly small survival at long distances. This contradicts the evidence that, while most birds make short movements most of the time, they can travel long distances when necessary [190, 68]). Instead, we use a function [190] proposed based on bird movements from habitat fragments in the Amazon, to which the best fit was a heavy-tailed log-sech function. This is a probability distribution of movement distances, not a survival rate function, so we convert it into one by integrating over distances from D_{ij} to ∞ :

$$f(D_{ij}) = \int_{D_{ij}}^{\infty} \frac{2/(\pi b r)}{(r/a)^{1/b} + (r/a)^{-1/b}} dr = \frac{2 \arctan \left[(a/D_{ij})^{1/b} \right]}{\pi} \quad D_{ij} \geq 0 \quad (2.4)$$

where a and b [or a and β where β is the ‘tail’ function and $b = 1/(\beta - 1)$] are parameters of the log-sech function. They published a range of fitted parameter values, with the best fit across a variety of species in fragmented forest being obtained with $a = 317$ and $\beta = 1.77$ [190]. (Note that this is conservative as a survival rate, because the birds in that study had not died at the time when their final position was measured.)

Finally, C is the most challenging parameter to estimate. It is the rate at which colonists leave a patch of 1 unit of area (in our case, 1 km²) in the direction of each other patch in the system. (It is not the rate at which they arrive, which is modified by $f(D_{ij})$.) Note, however, that only one of our proposed metrics includes C in its

formulation. In that case we chose $C = 0.000012$ (except when testing the impact of varying C). This value means that a medium-sized patch of 100 km^2 sends out 0.0012 individuals per other patch per year (or 0.0001 per month). In a hypothetical 100-patch system of occupied patches of a similar size, and with no dispersal mortality, this would mean an incoming rate to a single empty patch of 0.12, which translates into an 11.3% chance of being colonized by at least one individual within a year. For a thousand patches, the chance would be $\sim 70\%$. The actual colonization rate, when patch occupancy and the dispersal (survival) function are taken into account, would be less than this.

Self-colonization

Normally models assume no colonization from a patch to itself (the $j \neq i$ in equation 1). This makes sense if one defines colonization conventionally as between-patch movement. We define colonization more broadly as a process that ‘refills’ patches. For many kinds of threat (e.g., predators, disease), there is minimal likelihood that the entire population in a large patch will succumb. It is quite plausible that threats will drive it to low numbers. Given time, survivors would likely re-populate the patch from within. One could consider this a non-extinction, in which case it is represented already in the standard SEM via an extinction rate term that gets smaller as patches get larger. Note, however, that in such a model the patch continuously plays its role as an exporter of colonists to other patches, and at a high rate if the patch is large. If threats have driven the population to low levels, this is unrealistic. There are few individuals to disperse in the first place, and if between-patch dispersal is positively density-dependent (as it often is) those individuals are more likely to re-occupy the now empty remainder of the patch than to leave it. Alternatively, if we consider the patch population to have gone *functionally* extinct, then there is a period before re-colonization (whether from within or without) when it is not exporting colonists. Of course the extinction rate dependence on area should still remain. Processes that render patch populations either actually or functionally extinct will still occur less frequently in large patches.

Thus, we modified our metapopulation models to eliminate the exclusion of patches

from their own colonization term. In the model as normally given, this means that the colonization function will evaluate with $f(D_{ij}) = 1$ when $i = j$. A potential additional modification, which we did not explore here, is to reduce the A_j term in the self-colonization case to a fraction of the patch’s area, to represent the depleted number of individuals.

Metrics of fragmentation when C and E are unknown

The concept of *metapopulation capacity* was introduced as a way of assessing the ability of a given, spatially-explicit landscape to support a species [77]. Calculating metapopulation capacity involves extracting the landscape components of the standard SEM (the extinction-area and colonization-distance functions) into a matrix \mathbf{M} with terms

$$m_{ij} = \begin{cases} f(D_{ij}) A_j A_i^x & j \neq i \\ 0 & j = i \end{cases} \quad (2.5)$$

and summarizing them as a single value $\lambda_{\mathbf{M}}$, the leading eigenvalue of \mathbf{M} . They showed that a landscape can support a species in the long term as a metapopulation when $\lambda_{\mathbf{M}} > E/C$. Henceforth, we refer to metapopulation capacity simply as λ . The units of λ can be thought of as “Levins patch equivalents” — the number of patches in a Levins-type (i.e., non-spatial) metapopulation, with the same values for C and E , that would yield the same extinction threshold. Thus λ is somewhat analogous to effective population size, and might have been called “effective metapopulation size”!

As previously pointed out [77], λ is useful because we can calculate it even when we do not know E and C — as is the case for most species (patch leaving rates are particularly hard to estimate). In their absence, we can use λ to *compare* landscape quality. We might compare different landscapes for the same species (e.g., original and current extent of suitable habitat). Or we might compare different species that we expect, based on their ecology, to have similar extinction sensitivity and dispersal characteristics. So λ is certainly a candidate metric of fragmentation, but suffers the problem of rating single patches, no matter how large, as having zero long-term capacity. Even systems of a few large patches have a calculated capacity less than more fragmented versions of the same total area. This makes no ecological sense.

In the model with self-colonization, $m_{ij} = A_j A_i^x$ (rather than zero) even when $i = j$. We call metapopulation capacity with self-colonization λ_{self} . Henceforth, all references to metapopulation-based measures refer to the self-colonization version unless otherwise stated. Like λ , λ_{self} is a measure that combines overall area as well as fragmentation. To better assess fragmentation as a process independent of habitat loss, we also propose the use of $\Lambda_{\text{self}} = \lambda_{\text{self}} / \sum_i A_i$, the metapopulation capacity per unit area, or metapopulation *density*. This parallels the Red List listing guidelines that embrace similarly independent criteria [108].

Metrics of fragmentation when C and E are known

If we know the rate constants C and E , then we have other options for evaluating landscapes. One of these is a modification of metapopulation capacity. As the criterion of species' persistence is $\lambda_{\mathbf{M}} > E/C$, the metric $\lambda_{\mathbf{M}} C/E$ describes capacity relative to the minimum required. A habitat restoration goal could be something like “at least two times the minimum metapopulation capacity.”

Perhaps the most traditional way to rate landscapes is to calculate *equilibrium* patch occupancy (\hat{p}_i) values, and develop a metric that summarizes these — such as the total area, or fraction of total area, occupied at equilibrium.

A third metric considers transient dynamics following fragmentation. Full initial occupancy is a reasonable assumption for habitat fragments recently formed from larger, contiguous patches, as there can be a considerable delay before species disappear [182, 30]. We therefore set $p_i = 1$ for all i . In the standard SEM (Eq. 1) this would remove colonization considerations (and therefore the spatial distribution of patches) because there would be no patches needing colonization. Patch areas alone would drive extinction, and thereby occupancy changes. To include patch connectivity via dispersal in this metric, we added a rescue effect, so that incoming colonizers reduce the extinction rate of currently occupied patches:

$$\delta_i = \text{Ext}_i \left(\frac{\text{Ext}_i}{\text{Col}_i + \text{Ext}_i} \right) \quad (2.6)$$

where Ext_i and Col_i are given by Eqs. (2) and (3) respectively. The rate of overall loss

of occupancy, or *contraction* rate Δ , is the sum of the patch-specific loss rates:

$$\Delta = \sum \delta_i \quad (2.7)$$

Incorporating a rescue effect (and, so, colonization processes) means that with the standard SEM, the problem of undervaluing small numbers of large patches also affects the contraction rate, though to a lesser degree. As with metapopulation capacity, adding self-colonization resolved this.

While Δ_{self} , the initial rate of decrease of patch occupancy from a fully-occupied habitat network, seems potentially informative, it can be hard to interpret. For example, a system of several large patches will have a low value of Δ_{self} , but the same system surrounded by a number of very small, distant patches will have a much higher value because even though there is more overall area, the small patches will quickly become unoccupied. To create a more intuitive metric, we calculated the area-weighted average of the patch loss rates $\Omega_{\text{self}} = \sum(\delta_i A_i) / \sum A_i$, which describes the proportional rate of loss of occupied area. Unlike metapopulation capacity, this measure increases with increasing fragmentation. To better compare the metrics we calculated the inverse, $\sum A_i / \sum(\delta_i A_i)$, which we call Ψ_{self} . We think of this as the initial time to lose occupancy of one unit of area, with the unit of time being the same as that used for the rate parameters (e.g., years). This metric is independent of overall area, so it is comparable to Λ_{self} , the metapopulation density.

Finally, multiplying Ψ_{self} by total area produces a metric, ψ_{self} that we interpret as the extrapolated persistence time — how long the entire patch system would remain occupied if the initial rate of occupied area loss continued in a linear fashion. This would not happen, but serves to convert the initial loss rate into a measure that includes area as well as fragmentation, and is therefore comparable with λ_{self} , the metapopulation capacity.

	Based on metapopulation capacity (patch equivalents)	Based on extrapolated persistence time (months, years, etc.)
Total system	λ_{self}	ψ_{self}
Per unit area	Λ_{self}	Ψ_{self}

Table 2.1: Four measures of range fragmentation; the subscript “self” refers to the inclusion of self-colonization, which eliminates the ‘few patches’ problem (see text).

Testing the metrics

Artificial fragmentation sequence

We took an image of a highly-fragmented forest landscape and repeatedly applied a cellular automaton growth function that enlarged every patch with randomly placed pixels on the perimeter. We iterated this process until all patches had coalesced into a single, large patch. When reversed, the sequence of iterations describes a fine-grained fragmentation sequence. We calculated the various fragmentation metrics for the sequence, with and without the self-colonization modification.

Forest bird habitat in Central America

There are numerous ways to rank species by extinction threat. One is based on current habitat distribution, without reference to the past. In that case, we can compare species with each other if they share similar dispersal abilities, which we may infer from a combination of ecology and morphology, or if we know their dispersal characteristics directly. Alternatively, we can compare species with their historical condition if it can be known or estimated. Our collaborators [81] assembled data covering four endemic bird areas (EBAs — [165]). For each location, they digitized the field guide range of every bird species and overlaid it with appropriate elevations and forest type. The intersection between layers estimated each species’ *original* extent of suitable habitat. They then classified satellite images to locate remaining forest and incorporated this

information with the other layers to estimate birds' *current* extent of suitable habitat. We use as exemplars the forest distributions for four species from one of these areas, the North Central America EBA, that Birdlife has assessed for extinction risk:

- Azure-rumped Tanager (*Tangara cabanisi*) is endangered (EN) because of its small and declining range. Highly social, it occupies the upper canopy of broadleaf evergreen forests between 1000 and 1700 m elevation. This was originally a relatively restricted range occurring mainly in valley bottoms. Coffee plantations have replaced much of the existing forest. The species may sometimes occur in edge and secondary habitats.
- Pink-headed Warbler (*Ergaticus versicolor*) is vulnerable (VU) because of its small and declining range. It resides in cloud forests above 2800 m and oak-alder-conifer above 2100 m, in Guatemala and Chiapas, Mexico. This habitat has become highly fragmented due to deforestation, with “intense human use” in the remainder of the habitat.
- Rufous-browed Wren (*Troglodytes rufociliatus*) is of least concern (LC) because it has a large range and occurs widely in moist montane forest between 1700 and 3200 m elevation, with high forest dependency and minimum altitude of 1250 m. The population may be anywhere from moderately small to large (poor 2009 data quality), but is thought to be in decline from ongoing habitat destruction and fragmentation.
- Rufous-collared Robin (*Turdus rufitorques*) is of least concern (LC) because it also has a very large range (Birdlife International 2010). It occurs in varied habitat from 1500 to 3300 m elevation with medium forest dependency. As with the Wren, population size may be moderately small to large and is thought to be in decline due to ongoing habitat destruction and degradation.

These species are all forest-dependent. They do vary somewhat in body size and in tolerance of secondary habitats, and therefore also presumably in dispersal ability, although the Red List does not always reflect the latest literature. In fact, assessed threat levels

appear to be unrelated to secondary habitat tolerance [80]. As these species' original and current forest habitat distributions provide good coverage of the range of possibilities, we analyze them here as if dispersal characteristics were the same for all the species (so that differences are due to spatial patterns only). Of course, assessed differences in dispersal could be incorporated by adjusting parameters accordingly.

2.4 Results

Artificial fragmentation sequence

We simulated a decline in forest area from 45,000 km² to 0 km², progressing from 1 to almost 500 fragments (Fig. A.1a). Vertical lines indicate when the habitat breaks up into 2, 3, 4 and 6 patches. The original metapopulation capacity metric λ (Fig. A.1b, dashed line) is zero when the landscape consists of one patch, as it receives no colonization from surrounding patches. At the first fragmentation event, into two patches, λ behaves paradoxically, increasing in value. It also increases at subsequent fragmentation events until there are six patches. It declines gradually in between these jumps due to area loss. Only after the creation of seven patches does λ decline more-or-less continuously. The naive implication is that initial fragmentation reduces extinction risk. λ_{self} (solid line) avoids this counterintuitive behavior. The single large patch has the highest metapopulation capacity and subsequent fragmentation causes the metric to decline. (As the patches become numerous, small and isolated, the two metrics converge on zero.)

Without self-colonization, extrapolated persistence time (ψ) behaves better than λ — the metric always declines following fragmentation (Fig. A.1c, dashed line). The addition of self-colonization (ψ_{self}) simply increases the persistence time, more so when there are few fragments (solid line), and yields a trajectory very similar to that of λ_{self} . Both modified metrics capture the relative value of different landscapes in ways that intuitively fit our understanding of the ecological effects of fragmentation on species.

The per unit area versions of each metric, Λ_{self} and Ψ_{self} , also decline consistently, but the impact of fragmentation events accelerates later in the sequence (Figs. A.1d,

e). This occurs because these metrics place greater emphasis on fragmentation itself and less on overall area, and fragmentation events become more frequent as patches get smaller. These metrics are still not completely independent of area changes, however, as indicated by the negative slope even within the ranges where patch number is constant. Area appears in both the colonization and extinction rate terms. Dividing by area does not completely remove the dependence.

The effect of parameter choice

ψ_{self} and Ψ_{self} require values for C and E , which we do not know for most species and so must estimate roughly. To evaluate the effect of this uncertainty, we recalculated with C varying on a logarithmic scale from 10^{-5} to 10^{-2} and E from 10^{-5} to 10^0 . Unsurprisingly, the metrics showed strong changes in response to these constants (ψ_{self} is shown in Fig. A.2; Ψ_{self} behaves similarly). This could be problematic if it affects the ranking of different landscapes. However, on a log scale, the lines for different values of C and E are nearly parallel over the full range of fragmentation, indicating that the proportional change in landscape value is independent of both parameters. In that sense, ψ_{self} is similar to λ_{self} in that it provides a consistent relative ranking of landscapes.

Four species examples

Table 2.2 presents summary statistics for four species from the Central American Highlands. These birds likely share broadly similar dispersal abilities, but vary in habitat distribution and currently-assessed threat (Fig. A.3). For montane species like these, estimated remaining forest areas are dramatically smaller than the extent of occurrence [81], and for all these four species the estimated current forest area is less than the proposed threshold for endangerment of 11,000 km². Indeed the forested area for the least concern robin is smaller than that of that warbler, which Birdlife lists as vulnerable.

Including self-colonization has a large impact on these examples: unmodified metapopulation capacity (λ) ranges from <1% to 3.6% of λ_{self} for the original ranges, and from 3.2% to 7% for current ranges (Table 2.2).

Status of current habitat distributions

In terms of overall remaining forest area, the robin (least concern) has less than the vulnerable warbler. Metapopulation capacity (λ_{self}) actually follows the Red List decisions more closely, in that the non-endangered wren and robin have values notably larger than the other two species (Table 2.2). The inconsistency between the robin's area and λ_{self} rankings relative to the warbler stems from the existence of a single, contiguous patch in the north of its remaining range. This patch is larger than anything available to the warbler, even though the rest of the robin's range exists in tiny fragments. Metapopulation capacity reflects the long-term properties of a landscape, and so gives the existence of larger patches much weight (because small patches will be unoccupied most of the time).

Extrapolated persistence time ψ_{self} follows area: the robin again ranks worse than the warbler. This occurs because the very small fragments that make up most of its range, while assumed to contain the species initially, will lose them very quickly. The habitat of the warbler contains a number of moderately-sized patches where the species is likely to persist longer.

Comparison to estimated former distributions

Species whose ranges are naturally fragmented might have successful dispersal strategies, and so better tolerate anthropogenic fragmentation. When we compare the original and current estimated forest distributions, the reductions in metapopulation capacity and extrapolated persistence time for all species are greater than the reduction in area alone, reflecting the additional effect of fragmentation. Furthermore, the wren and robin, whose forest distributions originally had *greater* metapopulation capacity, retain a much smaller percentage ($< 1\%$) of that capacity (Table 2.2). Their original ranges were largely contiguous.

Extrapolated persistence time (ψ_{self}) tells a more complicated story. The robin has by far the smallest time in comparison to its original range value, whereas the other species' reductions are similar to each other. As before this result is attributable to the

distribution of patch sizes. The robin’s current range is almost entirely tiny fragments, whereas the other species either have relatively more, larger patches (wren), or their original ranges also had many small patches (tanager, warbler).

Two metrics measuring quality per unit area, Λ_{self} and Ψ_{self} , corroborate these conclusions. Current Λ_{self} is notably higher for the robin than any other species. This again reflects the strongly skewed distribution of patch sizes; of the very small area remaining, a relatively large proportion is in a single contiguous patch, so the capacity *per unit area* is particularly high. The persistence time per unit area, however, mirrors the overall persistence time. The robin is worse off than both the wren and warbler and so arguably the more threatened bird.

2.5 Discussion

Metapopulation capacity and extrapolated persistence time, when calculated with self-colonization, link widely available, detailed landscape data to species’ relative, and in some case absolute, extinction risk. Certainly, other factors contribute to the extinction risk of the example species we consider here. Nonetheless, since fragmentation strongly influences each listing, it is troubling that of five metrics — the four we propose, plus the estimate of remaining area [81] — three (area, ψ_{self} and Ψ_{self}) rank the least-concern robin between the endangered tanager and the vulnerable warbler (Table 2.2). Furthermore, when we make a comparison to the original ranges of these species, four out of five rank the robin as *most* at risk (only Λ_{self} does not). We are currently extending this analysis to a large number of species in a variety of locations, which will enable a more powerful comparison with Red List determinations.

Which metric is most appropriate will depend on the application. Are we concerned about what is happening shortly after fragmentation occurs — how fast species’ occupied ranges are contracting — or what will happen eventually, assuming that nothing is done to reverse the habitat loss? Many will choose metapopulation capacity, with its emphasis on long-term species support. Those who restore forest connectivity will choose otherwise. Such quantitative methods also assist in prioritizing conservation

strategies, and in their justification to policy-makers.

Estimating absolute risk does require knowledge about local extinction rates in isolated patches and species' dispersal tendencies and survival rates when moving between patches. The first of these relationships is fairly well known for many groups [49, 51, 156, 66, 170, 56, 19]. We are only just starting to understand how individuals move in complex landscapes [127] and what the risks are. Still, decisions about optimal landscape configuration must inevitably make some assumption about movement, often presented in terms of 'connectivity.'

Most spatial ecology models still assume largely passive, undirected dispersal. This leads to the strongly entrenched view that connectivity leads to high patch occupancy. That view may be wrong. [153] found that the disappearance of birds from small British islands consistent with risk-based active abandonment of *less*-isolated islands. [190], studying forest fragments in Brazil, found that bird species with wide-ranging tendencies in contiguous forest tended to disappear first from isolated patches, and make longer movements out of patches, again implying active abandonment. Both studies reverse the traditional view.

The data-derived log-sech dispersal kernel is an improvement on the traditional exponential decay survival function that tends to eliminate the possibility of long-distance dispersal citeVanHoutan2007. We need to know more. For example, we would like to divide the species into categories depending on dispersal ability. Alternatively, we could view landscapes in such a way that patches are considered 'connected' for inter-patch migration if they meet a certain dispersal threshold (see [90]). The threshold would vary for different taxa. A focused research agenda presents itself. Until we can make direct measurements of dispersal traits for all species of interest, we can link the data we do have to better known ecological traits (body size, trophic habit, etc.; see [82]) or to taxonomic identity, allowing extrapolation to suites of species.

A second question is whether we assess species relative to some absolute standard of fragmentation, relative to other similar species, or relative to their historical range as best understood. If the robin and wren, which likely once had large, relatively contiguous habitat distributions, are therefore poorly adapted to small fragments, they might

well have a greater extinction risk than the tanager and warbler. Conversely, one might make the case that if a particular species has survived on naturally fragmented habitat for a long time, it may be better adapted to withstand further anthropogenic losses. Unfortunately, there is little evidence for this, at least in birds [80]. A potential way to answer this question, which will be part of our next analysis, is to compare data on population decline with both absolute and historical-relative measures of fragmentation.

Finally, each of these landscape-level metrics is the sum of the contributions of the individual patches. We can therefore rank patches either by their own capacity (which includes their receipt of incoming colonists) or by their contribution to the overall landscape (which includes their provision of colonists to other patches). We can also create new patches, or enlarge or join existing ones, to identify the exact block, or corridor of land, to restore. Thus, our method can optimize plans to conserve or restore landscapes to produce the maximum capacity increase for either a targeted species or a complete assemblage.

	Azure- rumped Tanager	Pink- headed Warbler	Rufous- browed Wren	Rufous- collared Robin
Birdlife category	EN	VU	LC	LC
Birdlife EOO ^{a,b}	1700	17,100	98,500	61,100
Original area ^b	1578	10,720	24,584	19,253
Current area ^b	359.0	3192	7423	2887
% area remaining	22.8	29.8	30.2	15.0
Original λ	471	10,557	15,451	24,794
Current λ	21.7	317	942	316
Original λ_{self}	15,757	296,520	1,779,680	1,464,170
Current λ_{self}	398	4512	14,161	9907
% λ_{self} remaining	2.5	1.5	0.8	0.7
Original ψ_{self}	211,134	3,545,520	9,978,330	10,542,700
Current ψ_{self}	9383	187,754	517,024	105,723
% ψ_{self} remaining	4.4	5.3	5.2	1.0
Original Λ_{self}	10.0	27.7	72.4	76.0
Current Λ_{self}	1.11	1.41	1.91	3.43
% Λ_{self} remaining	11.1	5.1	2.6	4.5
Original Ψ_{self}	134	331	406	548
Current Ψ_{self}	26.1	58.8	69.7	36.6
% Ψ_{self} remaining	19.5	17.8	17.2	6.7

Table 2.2: Fragmentation statistics for four example species. ^a‘EOO’ stands for extent of occurrence. ^bAll extent and area values are in km².

Chapter 3

Quantitative analysis of forest fragmentation in the Atlantic Forest reveals many more threatened bird species than the current Red List

3.1 Summary

Habitat loss and attendant fragmentation threaten the existence of many species. Conserving these species requires a straightforward and objective method that quantifies how these factors affect their survival. Therefore, we compared a variety of metrics that assess habitat fragmentation in bird ranges, using the geographical ranges of 127 forest-endemic passerine birds inhabiting the Atlantic Forest of Brazil. A common, non-biological metric — cumulative area of size-ranked fragments within a species range — was misleading, as the least threatened species had the most habitat fragmentation. Instead, we recommend a modified version of metapopulation capacity. The metric links detailed spatial information (fragment sizes and spatial configuration) to birds' abilities to occupy and disperse across large areas (100,000+ km²). In the Atlantic Forest, metapopulation capacities were largely bimodal, in that most species' ranges had either low capacity (high risk of extinction) or high capacity (very small risk of extinction). This pattern persisted within taxonomically and ecologically homogenous groups, indicating that it is driven by fragmentation patterns and not differences in species' ecology. Worryingly, we found that of 58 species in the low metapopulation capacity cluster, 28 (nearly half) are not considered threatened by the IUCN. We propose that, compared to examining habitat area alone, assessing the effect of fragmentation will separate species more clearly into distinct risk categories.

3.2 Introduction

Assessing a species' risk of extinction is a core activity for conservation science. It is important to identify the species that need protection and how to provide it. Moreover, individual species' assessments provide the elements to set priorities for areas that may differ greatly in how many threatened species they contain. The International Union for Conservation of Nature (IUCN) assesses threat for species globally. IUCN's scheme groups species deemed Threatened into three main classes: Critically Endangered (CR), Endangered (E), Vulnerable (V) and two Non-Threatened classes: Near-Threatened (NT) and Least Concerned (LC). It relies on well-defined criteria. For the terrestrial species we consider here, two factors dominate: some measure of declining population numbers — most often assessed indirectly by continuing habitat loss — and a small geographical range. For birds, IUCN delegates the task to BirdLife International, which in turn recruits thousands of individuals to contribute to species' assessments. Our experiences in that assessment process motivate our seeking more consistent measures of risk that employ readily available data to refine geographical ranges.

To date, we have used elevation and land-cover data to trim the range maps BirdLife International provides to produce more realistic ones. In doing so, we observed that some ranges are very much smaller than previously thought and some are massively fragmented. We now seek to move this aspect of species' assessments towards a more consistent, quantitative framework, which until recently has been hard to implement broadly. In this paper, we compare a number of methods of quantifying habitat fragmentation. Our worrying conclusion is that we find important discrepancies that suggest some species are likely more threatened than currently expected.

Habitat loss harms species [140], and threatens many more [28, 29]. The species IUCN deems Threatened are overwhelmingly those with currently small geographical ranges [111]. Indeed, range size is built into the criteria and is sufficient, if not necessary to give Threatened status. It is essential to estimate range size appropriately. The need is particularly acute for species in montane areas, where the ranges that fall within known elevational limits may be very much smaller than those shown by IUCN maps.

Habitat fragmentation compounds this problem [156, 59, 54]. Habitat fragmentation and its relevance towards extinction [45, 99, 98, 54, 82] has been studied exhaustively in birds [61, 142, 14, 78, 195, 128, 15, 53, 116, 4, 167, 66, 83, 185, 62, 170, 43, 56, 6, 19, 168, 55, 169]. The problem is well understood theoretically: as population size increases, the risk of stochastic extinction drops precipitously. Empirical data for birds on real islands and forest islands surrounded by agricultural land readily confirm the theory [142, 141, 56, 153]. Thus, two species with identical range sizes will differ sharply in risk if one range is composed of continuous habitat, while for the other it exists in tiny fragments. For example, using species curves to approximate bird extinction from forest fragments, one study [56] recommended that individual forest fragments be a minimum of 10 km² for long-term within-patch survival.

To simplify, ours is a three-step process:

1. Existing IUCN criteria use what we can think of as “field guide ranges” — technically Extent of Occupancy estimates. These are maps with generally smooth boundaries, and do not factor in realistic habitat requirements except in general terms. Ranges are typically continuous, though there could be a few isolated populations. Employing these maps, IUCN sets a threshold of 20,000 km² below which a species is likely to be threatened, given assumed continuing loss of habitat or population.
2. Unsatisfied with how this applied to terrestrial bird species, [81] trimmed those ranges by elevation, broadly suitable habitat, and remaining forest. These maps showed inevitably smaller ranges that typically had convoluted boundaries. Those for montane species followed contour lines, for example, even in regions of intact forest. They suggested that a threshold of 11,000 km², below which a species is at particular risk, would ensure consistency in listing. In doing so, they added to the list of putatively Threatened species those that had very much smaller ranges than their Extent of Occupancy estimates.
3. For most species, these trimmed maps uncovered highly fragmented ranges. To

derive their threshold, [81] assumed that the fragmentation was broadly comparable across species. By inspection, that assumption is clearly invalid. Some species have ranges larger than 11,000 km², yet heavily fragmented. The IUCN acknowledges that fragmentation is a distinct problem for species, separate from the problem of small ranges alone [85]. It also has a history of updating criteria to be more consistently quantitative [109, 35, 108], especially Criterion E “quantitative analysis of extinction probability” [25]. Yet there is no accepted, standardized method that quantifies range fragmentation and links it to extinction threat for that species. Providing one is our objective.

Inevitably, both greater fragmentation and smaller habitat patches reduce the chance a species will survive. What requires further clarification is how we can quantify a fragmented range that directly relates to its quality as a species’ habitat. Area is a fundamental quantity to consider for conservation, yet between further anthropogenic destruction and climate change, fragmented landscapes are inevitably going to become more fragmented. A more comprehensive measure of fragmentation is therefore needed.

There have been many previous attempts to quantify fragmentation. The FRAGSTATS program exemplifies spatial-only metrics, and can produce area, edge, shape, and nearest neighbor metrics, among other things [117]. As an example of a spatial-only metric, we examine plots describing the cumulative amount of area of size-ranked fragments within a bird’s range. As we will describe below, this approach can be misleading. Moreover, such approaches do not relate directly to extinction risk.

METAPHOR is an example of discrete-time, stochastic individual-based model that simulates landscape effects on metapopulation persistence [192, 58, 57, 194, 193]. Relatedly, one can derive ecologically scaled landscape indices (ESLI) from landscapes that account for dispersal and carrying capacity [193, 194]. However, individual-based movement models typically require many parameters, describing both the landscape and the behavioral choices made by individuals, and many of them are likely to be poorly known and difficult to estimate.

Our method treads a middle ground by adapting basic metapopulation theory. Many studies have pioneered and employed metapopulation dynamics on butterflies,

mammals (like the American pika, *Ochotona princeps*), plants, and plant-herbivore-parasitoid communities (reviews in [74, 75]) to examine patterns of extinction and colonization. Despite their being highly informative, these approaches have generally not involved large spatial scales and, indeed have a critical failing in this regard. Our method addresses this deficit by a simple modification to the standard spatially explicit metapopulation model that allows it to describe species' abilities to occupy and disperse among fragments across a landscape covering a million square kilometers.

We employ a modified version of metapopulation capacity as the framework for quantifying fragmentation to inform threat assessments. Put simply, metapopulation capacity measures the long-term ability of a landscape to sustain a species. This metric incorporates information describing a species' ability to disperse, and the characteristics of fragmentation within its range: area, amount of fragmentation, fragment sizes and spatial configuration. In this regard, it forms a standardized approach to incorporate fragmentation in Criterion E. It also identifies potential errors in current threat assessments for birds in the Atlantic Forest, and by doing so demonstrates how threat assessments can be improved to generate greater consistency.

3.3 Methods

3.3.1 Range data

[81] collected field guide ranges, elevation, and forest ecotype data, and overlaid them to give historical range estimates. These were then further refined with satellite images of forest cover to produce current range estimates. Of their four study sites, we focus here on the Atlantic Forest of Brazil.

The Atlantic forest of southeastern Brazil is a biodiversity hotspot [126], with high levels of endemism, only 6-8% of forest remaining, and extensive fragmentation [44, 122, 148]. Birds with small ranges are often in areas where there are higher than expected numbers of threatened species. The Atlantic forest in particular stands out, with endemics being particularly threatened, unable to withstand the forest fragmentation [26, 63, 111, 149]. The study of this site is particularly important in quantifying

fragmentation effects for many bird species in peril because it is a prime example of an endemic bird area (EBA) and a site where both extreme fragmentation and many threatened bird species occur [111, 126]. Forest maps of this region, at a 1km^2 scale, form the basis of all the metrics described below.

3.3.2 Range size

This is the simplest metric, ignoring fragmentation completely, and the metric [81] used. The area estimates are usually much smaller than the ‘extent of occurrence’ area values cited in IUCN evaluations. (EOO is more similar to the ‘field-guide’ range.)

3.3.3 Forest fragment cumulative area distributions

One method of including fragmentation is to examine the distribution of sizes of isolated forest fragments. A standard technique plots the cumulative total area contained in patches below a certain area, against that area [17, 178, 24]. On a log-log scale, this plot is typically approximately linear over a very wide range of areas, and contains a number of pieces of useful information. The right-most point yields both the size of the largest fragment (its x value) and the total area of all the fragments (its y value). The slope describes the fraction of total area contained in progressively smaller fragments — the shallower the slope, the more the system is fragmented (but see Results). This metric takes no account of the spatial separation of patches.

3.3.4 Metapopulation-based metrics

Previously we took spatially explicit metapopulation models [72, 73, 74] as a starting point, and proposed two metrics of fragmentation. One is a simple modification of metapopulation capacity [77]. The modification is the addition of self-colonization, a biologically sensible addition to large patches. We obtain our modified metapopulation capacity (λ_{self}) by taking the leading eigenvalue of the matrix M with elements

$$m_{ij} = \begin{cases} f(D_{ij}) A_j A_i^x & j \neq i \\ 0 & j = i \end{cases} \quad (3.1)$$

where A_i is the area of the i patch, x is an exponent that scales extinction probability to area, and $f(D_{ij})$ is a dispersal function describing how arrival rate drops off with the distance D_{ij} between two patches. Here, D_{ij} is the minimum edge-to-edge distance between patches, and for $f(D_{ij})$ we used a survival-rate transformation of the log-sech dispersal kernel proposed [190] for forest birds in the Amazon.

The extrapolated persistence time metric arises from the transient behavior of recently fragmented systems. We assumed full occupancy of the landscape immediately after fragmentation (i.e. $p_i = 1$ for all i), and, using the full spatially explicit metapopulation model with a rescue effect (in which extinction rates are reduced by incoming colonizers), calculated the initial rate of decrease of occupied area. An inverse measure, the extrapolated persistence time (ψ_{self}), estimates how long the entire patch system would remain if the initial rate of decrease in occupied area loss continued linearly (as it is easier to compare with Λ_{self} because larger values are better). The two metrics, λ_{self} and ψ_{self} , give a long-term and short-term perspective on fragmentation respectively.

3.3.5 Threat status

We used a slightly more updated version of IUCN threat designations [16] than did [81]. Using the updated threats resulted in one species removed from our analysis for having only one 1 km² patch remaining in its range (*Philydor novaesi* – CR) and another for being extinct in the wild (*Mitu mitu* – EW), as well as three status changes.

3.4 Results

We calculated range area trimmed by elevation and forest cover, the cumulative area of fragments within a bird’s range, and the two metapopulation measures, for 127 passerine forest birds endemic to the Atlantic forest of Brazil. This area has the largest concentration of threatened bird species in the Americas [111].

3.4.1 Range area

Some 30 out of 127 passerine species fall below the proposed threshold describing extinction threat — 11,000 km² [81]. Of these birds, seven (23%) are not listed in the three classes that constitute “Threatened” (i.e. CR, EN, VU). Of particular concern are the three species that the IUCN lists as Least Concern: Serra Do Mar tyrant-manakin (*Neopelma chrysolophum*), minute hermit (*Phaethornis idaliae*), and white-bibbed antbird (*Myrmeciza loricata*).

3.4.2 Cumulative patch area plots

Though easy to understand, these plots (Fig. A.4) can seriously mislead. Certainly, the least-threatened species, shown in blue, have more total area and include one or more larger patches than more-threatened species, as expected. However, they also have shallower slopes, indicating a greater fraction of smaller patches making up the landscape. This would conventionally be interpreted as greater fragmentation, and in a sense that is correct. Species with larger overall range typically have a small number of larger patches, surrounded by a constellation of sometimes hundreds of smaller patches. These small patches raise the intercept and reduce the slope of the cumulative area plot. The smallest range species typically have only a very small number of patches, and the smallest are often not much smaller than the largest. In fact, for a fixed pixel size, there is a constraint on how fragmented a small-range species can appear. Some of this arises from data limitations — if we used a smaller pixel size, small-range species might seem more fragmented. (This would also be true of the large-range species.) More importantly, the cumulative-area plot does not account for the ecology of dispersed species.

The problem is that this spatial pattern fails to capture the ecological effects of fragmentation. Well-understood ecology tells us that most of the tiny patches will usually be unoccupied, and therefore contribute almost nothing to species’ persistence. The sizes and spatial relationships of the smaller number of large patches determine almost

all of the landscape’s ability to support that species. In any sensible metric, the existence of many small patches around some large patches should not make the situation seem worse than if the small patches were not present at all. Unfortunately, that is what the cumulative area plot does. Furthermore, it ignores patch spacing and configuration, two factors vitally important to dispersing organisms. Patch size cumulative distributions have been found elsewhere to be poor measures of forest fragmentation [197].

There is a second, practical problem with the cumulative area approach, given that landscape data typically come at a certain fixed resolution that determines the smallest possible size of a patch (one pixel). If the smallest range species occupy only a few pixels overall, then there is a constraint on how fragmented that range can appear because the largest patch cannot be much bigger than the smallest. (Were we to use a smaller pixel size, the small-range species might seem more fragmented, but the effect would hold true for large-range species, so it would not matter in a relative sense.)

We conclude that using habitat fragmentation to assess species threat requires us to incorporate ecology, in the form of species’ abilities to occupy and disperse between fragments.

3.4.3 Extinction risk metrics

We used histograms to present and compare alternative metrics for assessing extinction risk (Fig. A.5). Across passerines, the remaining range area shows a range of values (Fig. A.5A) and as expected, species listed as threatened are more often in the small-range categories. By comparison, values for metapopulation capacity (Fig. A.5B) are distinctly bimodal, as species cluster at either end of the metric’s range. Examination of the birds’ range maps reveals, unsurprisingly, that whether the range includes one or more large forest patches determines the difference between a high and low value for metapopulation capacity. This accords with ecological theory and data, in that metapopulation capacity takes a longer-term view of expected occupancy, and therefore patch area plays a more important role.

The 58 species in the smallest metapopulation capacity class include 31 (84%) of

the 37 IUCN Threatened species (those shaded green, orange, and red). They also include 28 species not threatened (shaded blue or grey), yet whose range fragmentation is apparently very similar. This is a potential omission rate of 48% — double that of the simple area analysis (Fig. A.5B).

Perhaps the IUCN considers differences in secondary habitat tolerance or dispersal ability in making their rankings. Previously, we found that secondary habitat use did not affect rankings when compared to remaining area of primary habitat [80]. Moreover, if basic requirements (i.e., primary habitat) are inadequate, mobility of forest-dependent birds is unlikely to compensate [158]. Nevertheless, to evaluate these effects we separated out three groups of species by increasing taxonomic and ecological similarity. We reapplied our metapopulation capacity analysis separately for each group. Since fewer species are in each group, we present results with a slopegraph [184]. These slopegraphs compare the relative values of species' remaining ranges (the metric of [81]) and metapopulation capacities, with birds at greater extinction risk (smaller values) at the top and those at lesser risk (larger values) at the bottom (Fig. A.6).

“Understory specialists” (Fig. A.6A) included Conopophagidae, Dendrocolaptidae, Furnariidae, Rhinocryptidae, and Thamnophilidae. These species have similar body sizes and likely dispersal abilities. The bimodality of the metapopulation capacity metric remains clearly visible. The cluster of 30 low-capacity ranges at the top of this list includes fifteen species (50%) that the IUCN does not consider threatened. Eleven of these have smaller capacities than a species listed as Critically Endangered. These species are candidates for immediate reexamination.

The two other groups consisted of tyrant flycatchers (family Tyrannidae, Fig. A.6B) and antbirds (family Thamnophilidae, Fig. A.6C). These taxa are morphologically and ecologically homogenous. The bimodal distribution of extinction risk remains. Five and seven species in each taxon respectively occur in an obvious ‘low capacity’ cluster, yet are not ranked as threatened by the IUCN (omission rates of 45% and 39%). These results virtually eliminate the objection that the IUCN omissions stem from differences in secondary habitat tolerance or species dispersal abilities.

For the Tyrannidae, the high-risk species [16] include Brown-breasted Bamboo-tyrant (*Hemitriccus obsoletus*), Oustalet’s Tyrannulet (*Phylloscartes oustaleti*), Serra Do Mar Tyrannulet (*Phylloscartes difficilis*), Grey-capped Tyrannulet (*Phyllomyias griseocapilla*), and Sao Paulo Tyrannulet (*Phylloscartes paulistus*). All species except the Brown-breasted Bamboo-tyrant (LC) are Near Threatened due to suspected rapid declines from habitat loss. All except the Sao Paulo Tyrannulet have no quantified population size, and range in observational description from “uncommon” to “fairly common.” All species except the Grey-capped Tyrannulet (medium dependency) have high forest dependency. All share the habitat of subtropical/tropical moist forest, either lowland or montane.

For the Thamnophilidae, the overlooked species include Rufous-tailed Antbird (*Drymophila genei*), White-bibbed Antbird (*Myrmeciza loricata*), Rio de Janeiro Antbird (*Cercomacra brasiliana*), Rufous-backed Antwreio (*Dysithamnus xanthopterus*), Ochre-rumped Antbird (*Drymophila ochropyga*), Unicoloured Antwren (*Myrmotherula unicolor*), and Star-throated Antwren (*Myrmotherula gularis*). All species are Least Concern, since their numbers are suspected to be either stable or in decline, and any decline that might be happening is not rapid enough to warrant threatened status. All species except the Unicoloured Antwren have no quantified population size, and vary from “common” to “rare”. All species except the Rio de Janeiro Antbird (medium dependency) have high forest dependency. All live in some type of subtropical/tropical forest [16].

3.5 Discussion

Modified metapopulation capacity is an objective and consistent metric for assessing the effect of fragmentation on extinction risk. The incorporation of spatial information via a suitably modified metapopulation framework appears to simplify matters, at least for the species studied here. For a large sample of birds, most species fell into either a low capacity (high-risk) cluster or a high capacity (low-risk) cluster, and this bimodal pattern remained consistent within taxonomically and ecologically homogenous groups. Therefore, it was driven primarily by fragmentation patterns in the Atlantic Forest, and

not by differences between the varying natural histories of these species. The bimodality makes the process of including habitat fragmentation in overall threat assessments relatively simple and straightforward.

High metapopulation capacity is clearly linked to the existence of substantial patches of remaining habitat, in which large sub-populations will be expected to persist for long periods of time. There is, therefore, every reason to expect the patterns we describe to apply to other taxa and other regions.

Because metapopulation capacity is a relative measure [77], it will be most useful as a ‘peer group’ comparison, the way we have used it here. As the risk assessment process gets completed for more species, this type of comparison becomes straightforward. One can base peer groups on phylogeny/taxonomy, or any sensible combination of morphology and ecology (traits of which tend to follow phylogeny — [60]). Specific life history characteristics can make some groups, such as ant-followers [199], or ground nesters ([198], etc.), particularly vulnerable to extinction [101]. This is likely due in part to the influence of these characteristics on dispersal behavior.

It would be better, of course, if we had measured values of dispersal traits. Unfortunately, they remain unknown for most species. They are challenging to measure, requiring the tracking of many small and vagile animals in remote and inaccessible locations. Even when inferences can be made indirectly, such as from presence/absence snapshots from patch systems, or with repeated surveys [153, 41], the necessary data remain rare, and the parameters frequently uncertain. More generally, we need a better understanding of animal movements in complex landscapes, as straight-line distances are unlikely to be a good model of relative movement rates for many species. For now, correlations between known life history characteristics and dispersal traits may allow us to estimate values themselves, rather than just delineating peer groups.

Fortunately, some information can guide us. For example, dispersal distances of avian species correlate with body size and breeding territory size [171, 23]. Understory birds are thought less able dispersers in fragmented habitat, but this is an over-generalization [190, 68, 69, 113]. For instance, persisting species moved less in the Amazon forest than extinction-prone species in intact forest, but moved further after

fragmentation [190]. Some understory species showed no change in movement with the occurrence of fragmentation in the Atlantic forest, while others increased speed and the distances traveled [68]. Also in the Atlantic forest, one understory species increased its range to include matrix habitat, while another (an army ant follower) did so only at food source locations, and a third never ventured outside of intact forest [69].

Given the potential for improved understanding of dispersal, a key advantage of the metapopulation approach is that it is flexible and adaptable, allowing us to incorporate new data and even dispersal models as they become available. We recommend it as a framework to the IUCN and other organizations involved in species risk assessment. Now, we understand from our own experiences in species assessments that the process is already long and complex. That said, what the results of [81] and those herein suggest is a list of candidate species for which existing decisions of non-threatened status may be in serious error. We urge that such species be examined even more carefully before they are excluded from the lists of species for which we should have special concerns.

Chapter 4

Finding the best land for the most species

4.1 Summary

Available habitat in the world has grown increasingly fragmented, and continues to do so. This increases the importance of managing and protecting remaining suitable land. With the advances in satellite imagery, and the modelling capabilities of metapopulation theory, we are able to quantify fragmentation and make biologically-relevant estimates of patch value within large landscapes. An effective means of analyzing the fragmentation of complete species' ranges would greatly benefit conservation efforts. We tested two metrics, a modified version of metapopulation capacity and extrapolated persistence time, to quantify patch value for bird ranges in the Atlantic forest of Brazil. Both metrics give intuitive measures of the relative ability of fragmented habitats to support species across large scales. We determined the regions that contribute the most within this biodiversity hotspot for various subsets of species. Finally, we create maps ranking remaining 1km² forest 'pixels' based on their total contribution to the metapopulations of all the species whose potential ranges overlap at that point. We also prioritized forest 'pixels' for restoration by calculating where similarly-sized patches are separated by 1 km² for the most number of species, and then ranking these based on their impact on the combined metapopulation capacities of those species. By combining species' life history traits with these metapopulation measures, one can efficiently determine the most valuable patches within a fragmented habitat, depending on conservation goals.

4.2 Introduction

As the world becomes increasingly developed and human pressure increases, habitat fragmentation will only grow as a problem for all species [182]. This is especially problematic in the most species diverse regions [175, 164, 33]. The Atlantic forest of Brazil is one such site [44, 145, 122, 126, 148, 173] and fragmentation effects have been extensively documented for birds there [200, 26, 63, 31, 110, 115, 3, 149, 163, 114, 188, 69, 68, 20, 120, 8, 67, 70, 86, 21, 187]. As our geographical information technology improves, we become better able to determine realistic available habitat. Knowing the spatial environment allows us to estimate species' extinction risk better than ever before. Here we illustrate the uses of some metapopulation-based metrics in mapping habitat value and restoration potential for Atlantic forest bird species based on detailed maps of remaining forest.

One way of examining fragmented populations is through species distribution models. These types of models require a significant amount of input, however. On top of maps of the environment, one would require information as to habitat requirements, a model linking habitat to environmental variables, GIS to map predicted occurrence, and further data to validate the model. Thus, an extensive amount of data is necessary before one can model, and then it is only applicable to one or a few species. Furthermore, studies have found there to be no perfect model, and that in fact it is best to borrow from all models to get the best estimates [181, 133]. All of this adds to the level of information required for species predictions.

Instead, metapopulation theory provides us with one way of relating landscape information to actual occupancy estimates [73]. Metapopulation capacity is a spatially explicit model of habitat that leads to the estimation of long-term extinction risk [75]. We have previously adapted the metric to large landscapes, and here demonstrate how it can be applied for prioritization in preservation and restoration.

To determine the conservation value of a landscape, we first calculate the metapopulation capacity of said landscape. With these values in hand, we can then determine how to benefit a particular species by identifying the most valuable remaining habitat

patches in terms of their contribution to that capacity. We can also combine these value maps to estimate what area is most important to the most species. Finally, we assess the impact on total metapopulation capacity of adding 1 km² forested ‘pixels’ in obvious places (for example, where they join patches together).

4.3 Methods

Our collaborators collected range data and satellite imagery of ideal habitat for a large number of forest-dependent bird species in the Atlantic forest of Brazil, taking into account elevation and forest type [81]. They combined these data to produce maps of potential current range. Maps of historic forest distributions provided us with an estimate of the extent of each species’ original distribution. These ‘original’ maps can also identify where we might restore forest. Our range data was for 127 passerines, 10 non-passerines, and 37 near-passerines. Near-passerines are loosely defined as non-passerines that are most closely related to the passerines (perching birds) yet considered different enough in size, etc. to not qualify as a true passerine.

4.3.1 Modified metapopulation capacity

Our metric is founded in metapopulation theory, and in particular, metapopulation capacity. This measure for highly fragmented landscapes was previously developed [77], and connected landscape configuration to population predictions. The capacity value allowed for comparison of landscapes to determine optimal spatial conditions for overall metapopulation survival. To get the value of the whole landscape, [77] did so by first creating a matrix \mathbf{M} factoring in all landscape patch areas and the distances between them:

$$m_{ij} = \begin{cases} f(D_{ij}) A_j A_i^x & j \neq i \\ 0 & j = i \end{cases} \quad (4.1)$$

where $f(D_{ij}) = e^{-\alpha D_{ij}}$ represents the ‘migration survival’ function that gives the proportion of individuals leaving patch i that will make it to a patch j , D_{ij} distance units away. They then took the eigenvalue of this matrix to get the λ_M , or metapopulation

capacity. However, this metapopulation metric does not perform intuitively at the large scales of our assembled bird ranges, having been intended for smaller species in very small, highly fragmented habitat. For our patch scale of one to hundreds of thousands of square kilometers we allow patch self-colonization, essentially by setting the dispersal survival function to one:

$$m_{ij} = \begin{cases} f(D_{ij}) A_j A_i^x & j \neq i \\ A_j A_i^{0.5} & j = i \end{cases} \quad (4.2)$$

The dominant eigenvalue of the matrix above is λ_{self} , the modified metapopulation capacity metric. Additionally, we use a different dispersal function for $f(D_{ij})$ based on bird movements in Amazon forest fragments [190]. Their heavy-tailed function, which they called log-sech, was a probability distribution of movement distances that we convert into a survival rate function by integrating over distances from D_{ij} to ∞ .

4.3.2 Value maps

[134] provided an approximate method of calculating the value of a patch's contribution to overall metapopulation capacity after a large perturbation:

$$V_i^L \approx \lambda_M y_i x_i \quad (4.3)$$

where L represents when a large perturbation occurs (i.e., patch removal), and x_i and y_i are elements of x and y , the right and left leading eigenvectors of landscape matrix M. This allows assignment of patch value for any given species. Patch value applies to a complete patch, but one can assign 'pixel' values by dividing each patch value by its pixel area and assigning that value to each of the pixels in the patch. We then overlay the pixel value maps for various sets of species of interest and create a weighted sum map. This shows which areas provide the most combined value across all the species. The weights can be either uniform, or based on some measure of 'species importance.' Most obviously, importance can be based on severity of threat, from the current IUCN listing or from our own landscape-level metrics. Instead or in addition, importance might incorporate an external measure such as economic or social value.

4.3.3 Extrapolated persistence time

We begin by taking the colonization and extinction components as defined by [77]:

$$\text{Ext}_i = \frac{E}{A_i^{0.5}} \quad (4.4)$$

$$\text{Col}_i = C \sum_{j \neq i} f(D_{ij}) A_j p_j \quad (4.5)$$

where E and C are extinction and colonization rate constants, respectively, A_i is the area of patch i , $f(D_{ij})$ is a function of the distance between patches i and j (see above), and p_j is the occupancy rate of patch j (as only an occupied patch can provide colonists). We then can combine these to estimate patch occupancy loss rate from a fully-occupied range ($p_j=1$) with a rescue effect, so:

$$\delta_i = \text{Ext}_i \left(\frac{\text{Ext}_i}{\text{Col}_i + \text{Ext}_i} \right) \quad (4.6)$$

To create an overall landscape metric that decreases as fragmentation increases, we take the inverse of the area-weighted average of the patch loss rates:

$$\Psi_{\text{self}} = \frac{\sum A_i}{\sum \delta_i A_i} \quad (4.7)$$

This can be thought of as the time to lose the entire landscape if the initial rate continued; we call this extrapolated persistence time. This allows us to expand the initial loss rate into a measure that includes area as well as fragmentation, and thus is comparable with metapopulation capacity.

4.3.4 Candidates for restoration

The Atlantic forest is currently 7-8% of its original area (1.5 million km²) and more than 80% of the fragments are < 0.5 km² [148]. It is far too time-consuming to evaluate the effect of reforesting each possible 1 km² square for every relevant species. Luckily, we do not have to. Preliminary studies showed that optimal pixels to restore are always those that are already attached to existing patches, and within that set, those that

connect the larger patches together are even better. We can therefore narrow down the candidates for restoration. To avoid the less helpful scenario of connecting a single pixel or very small patch to a larger patch, we calculate the ‘harmonic total’ of every set of connected patches. We define the harmonic total of a set of n areas, where a_i = area and n = the total number of patches considered, as n times the harmonic mean, or:

$$H = n \left(\frac{1}{\frac{\sum \frac{1}{a_i}}{n}} \right) \quad (4.8)$$

which can be simplified as

$$H = n^2 \left(\frac{1}{\sum \frac{1}{a_i}} \right) \quad (4.9)$$

The harmonic total weights connections between equal-area patches more strongly than those between unequal-area patches. For example, two 10 km² patches have a harmonic total of 20, whereas a 1 km² and 19 km² patch have a harmonic total of 3.8. As we will show, this weighting roughly reflects the degree of improvement associated with connecting the patches. Finally we add the totals for each candidate pixel across all the relevant species to create a final list of values per pixel. The top-ranked connecting pixels are those which we then go on to access in terms of their effect on species’ metapopulation capacities and other metrics.

4.3.5 Weighting species contributions

In all our analyses in which we add the effects across multiple species, there is the possibility of weighting the species unequally. One way is by current IUCN threat level, with more threatened species carrying more weight. Other methods that would give more weight to species that are likely at more risk are based on our own data, such as weighting by the reciprocal of each species’ total remaining range, or the reciprocal of its metapopulation capacity. For some analyses we examine the sensitivity of patch value assessment and restoration prioritization to these different weighting schemes.

4.4 Results

We illustrate priority mapping using our set of passerine species. The metapopulation-based metrics described here are just a few of the ways to assign value to patches. Elsewhere, we will examine a number of other possibilities whose relative suitability is based in part on what the management objectives for the region are.

4.4.1 Patch value

For comparison, we look at the ranges of two sample passerines (Fig. A.7), with both maps using a ‘heat’ color scale from blue (lowest value) through green (intermediate value) to red (highest value) based on patch value of λ_{self} . These two species are both considered to be Near Threatened, but with vastly different spatial range sizes and spatial layouts – the Rio de Janeiro Antbird is locally rare and known from only a few sites but has some tolerance for secondary habitat ((Fig. A.7B)), while the Blackish-blue Seedeater is wide-ranging but patchily distributed (Fig. A.7A) and also thought to be in rapid decline from habitat loss [16].

Next we compare the two patch-value metrics λ_{self} and ψ_{self} for one species, the Blackish-blue Seedeater (*Amaurospiza moesta*). As we previously saw, the ranking based on λ_{self} has a strong patch ranking — the red patch that is most important to the species stands out in stark contrast to the outlying purplish-blue colored patches that make up the rest of the species’ range. The most important patches are centrally located, but most of the weighting is based on area, on which λ_{self} in particular is strongly dependent (especially with the self-colonization modification). Unlike this, ψ_{self} values those small patches for their ability to receive colonists (Fig. A.8).

4.4.2 Combination maps

Considering the map of simple range overlap, or maximum species richness (Fig. A.9A), we see that the highest richness occurs in the center of the overall extent of the Atlantic forest region. This is likely, in part, an example of the mid-domain effect [42], given that the forest endemics we consider are largely constrained to this region, and so

statistically more likely to overlap in the center. Even so, forest pixels vary in richness in a gradual manner throughout the rest of the Atlantic forest region. When weighted by the inverse of total area, we see the emphasis concentrated more in the central region, indicating range-restricted species reside in those central locations (Fig. A.9B).

By comparison, the metapopulation capacity weighted map (Fig. A.9C), while showing the same central core area (as expected, given that we are combining overlapping range maps) is far more bimodal, with almost all regions that are not central having a negligible value compared to the center. This is because the core region consists of a number of large, barely-separated patches, and these spatial attributes amplify its already greater richness. The low values assigned to outlying patches reflect their typically smaller size and their separation from the largest patches in the core. We created a weighted sum of pixel-value maps based on the IUCN rankings as follows: Least Concern = 1, Near Threatened = 2, Vulnerable = 3, Endangered = 4, Critically Endangered = 5 (Fig. A.9D).

4.4.3 Restoration

The top candidate pixels for restoration, based on ‘combined harmonic total connected area’ (see Methods) can be found across complete sets of species. When we compare the combined harmonic total connected area maps with those based on which patches improve combined λ_{self} , we find that the same patches are chosen overall, but with occasional differences in exact ranking. This underscores the fact that prioritization will value the same patches, because they are fundamentally the most important in a given landscape. We see differences between the value of the combined harmonic total and the combined increase in the λ_{self} for all passerines (Fig. A.10). In particular, patches that are closer to the center of the forest are ranked higher with the increase in the λ_{self} map because of the extra valuation of the centrally located patch. There is a more gradual difference in combined harmonic total pixel values through the outer reaches of the forest landscape.

We note that for all passerines (Fig. A.10) and rare species (those below the 11,000 km² threshold [81] Fig. A.11), the candidate pixels are in completely different regions

of the Atlantic forest, reflecting the fact that the smallest-ranged species are generally concentrated in the northeast region. Those pixels also slightly vary in their relative weight between those with the greatest increase in metapopulation capacity and the increase in combined harmonic total connected area, but not as greatly as when looking at larger groups of species.

4.5 Discussion

Here we described an array of applications for targeting fragmentation from a conservation standpoint. We can locate the exact areas of habitat that are most beneficial for the most species. We can even pinpoint the precise km^2 that give the greatest benefit (to the most species) if they were restored. The framework is flexible enough to allow us to weight the species in a variety of ways: we can weight patches by the status assigned by the IUCN, so that more threatened species are prioritized; we can select species with small range area or low overall λ_{self} at the landscape level, below some set threshold; we can weight proportionally per area, by dividing by a species total range area, so that birds with the smallest ranges are given highest priority. There are a variety of ways one can weigh the metrics, depending on goals and interests.

The ‘back end’ process of habitat identification may also lead to improved range maps, with our basic approach of identifying forest eco-types and elevation ranges replaced by the output of, say, a species distribution model (e.g. GARP, BIOCLIM, GLM, GAM, MaxEnt, Boosted Regression Trees, Random Forests, etc.). Similarly, ‘forest/not forest’ satellite classifications may be improved to include other vegetation types, or even different forest compositions. Having a framework into which such data can be immediately placed can only boost efforts to get such collection projects funded.

Prioritization is key in targeting locations of the greatest importance for many different species. This has been done at different scales with different methods [126, 79, 86, 33]. Forest-endemic birds are most affected by forest cover [28, 3, 81], and was a main criterion for the species selected by [81] and used as our range data. This quantitative approach also highlights the question of how much to consider a species’

historical habitat. Birds with ranges that have been fragmented for a long time might be better adapted, but deforestation takes its toll nevertheless [31]. The large proportion of our species have remaining habitats that are a small fraction of the original estimated range. With our before and after fragmentation maps, historical fragmentation can be accounted for in our study, which combined with current range is much more reflective of species' survival [38].

We grouped our species into passerines, non-passerines, and near-passerines. Grouping together different species, although likely an oversimplification, nonetheless is a worthwhile attempt to break down a class (i.e. Aves) of extremely varied life history ecology and dispersal capabilities. However generalized grouping by order might be, more refined groups (e.g. by family) will improve the comparative quality of these analyses. It is important to understand that because metapopulation capacity is not based in absolute terms (e.g. quantified units), it is most beneficial as a relative measurement.

We have seen that the best 1 km² are not always the same for the same groups, and so it is important to determine what species are of interest. We can use other ecological traits to estimate species rarity; for example, frugivores and insectivores are known to be susceptible, due to variable food supply and/or being habitat specialists [63, 187]. Life characteristics can make species particularly vulnerable [101], such as with ant-followers [199] or ground nesters [198, 5, 91, 112, 94]. By examining groups of species with similar vulnerabilities, we can highlight particular species even within these groups that still stand out in vulnerability due to spatial considerations.

The framework is adaptable, allowing new information to be incorporated as it becomes available. Colonization and extinction rate parameters are generally not known for most species. The difficulty is more in estimating colonization, because it is harder to determine where actual absence within a patch was changed by true colonization. This would require knowing the absence and presence of all individuals in the metapopulation, to calculate true colonization of an empty patch (e.g. rescue effect). We can add extinction and dispersal rate information directly to the model, eventually allowing absolute, rather than relative, estimates of survival likelihood. More generally, straight-line distances are unlikely to be a good model of relative movement rates for

many species.

The greatest improvement to these metrics is a thorough understanding of dispersal, and with it the exact distribution of available habitat, is a critical factor determining species' survival [153]. Some work has been done in the Atlantic forest [7, 68, 69, 67, 70], and one study even suggests great potential for dispersal [113]. Some birds can navigate fragmented landscapes, or disperse over long distances [190], and can survive isolation once such distance is reached.

We can conserve forest more proactively than simply by preservation, by means of restoration of suitable habitat. All models can be improved with more data, and our estimates would be particularly improved with specifics regarding behavior and disturbance tolerance. Until then, accurate satellite imagery improves our habitat data considerably for our understanding of endangerment for conservation, and should be incorporated into management decisions accordingly [187].

Considering the rapid, alarming rate at which ecosystems around the world are deteriorating, measures such as these are not just important, but imperative. Understanding there is a necessity for conservation is no longer enough; we need to be able to prioritize specific regions for restoration quickly and efficiently. These techniques will make that possible and give us a powerful new tool in the effort to preserve Earth's environments and ecological diversity. Furthermore, the interaction of climate change and fragmentation [100] is a vital consideration, as climate change is both expected to have significant influence on future ranges, and can be better modelled with this metric.

Chapter 5

Conclusions

There are a number of factors that do not directly relate to spatial dynamics that impact extinction. Indirect effects, such as prey availability [136], hunting [137] and the illegal pet trade [46, 201, 65, 191, 146] are all additional pressures for species survivability. Habitat loss or degradation is the major threat to Brazilian birds (89.5%), followed by over-harvesting (35.5%), invasive alien species and pollution (14%), human disturbance and accidental mortality (9.5%), and other threats [114]. Habitat is indubitably the single most important determinant in species' extinction.

Numerous studies have examined the threat that fragmentation poses to different bird groups, including specifically in the Atlantic forest. Forest raptors, terrestrial insectivores, and large frugivores, as well as antbirds (Formicariidae, Thamnophilidae), cotingas, and, especially, icterids were very extinction-prone [147]. Understory birds such as antwrens are commonly found to be affected [115]. Other species found to be rarer in fragments [115] include: woodpeckers, furnariids, manakins [14]; antbirds, furnariids [88]; manakins, trogons, furnariids [39]. Insectivorous species were also sensitive to fragmentation, as has been shown by other studies in the Neotropics [200, 88, 167, 63]. Understory birds were limited not by insect prey availability, but by their own ability to disperse through deforested matrix [160]. Terrestrial and understory species, frugivores and granivores, and Atlantic forest endemics were found to be the most susceptible [149]. Undergrowth and forest-floor species were also less mobile between fragments [163]. Understory species were able to cross highway gaps and move within continuous Amazon forest, but were limited by large open spaces [96].

Even under selective logging, forest-dependent bird guilds such as terrestrial and understory insectivores are still susceptible [179, 2]. Four Atlantic forest-endemic species

identified as sensitive to logging were even included in our range data: Blue-bellied Parrot, Black-headed Berryeater, Russet-winged Spadebill, Eye-ringed Tody-tyrant [2]. Managing forest depletion is not an adequate solution; preservation or active restoration are the best choices for true conservation.

Minimum area requirements has been a standard approach in wildlife management. [56] found 10 km² to be the minimum patch size for understory birds (note: they had limited to no data collected for canopy and open field dwellers, such as falcons, woodpeckers, and parrots, so this holds strongest for birds that can be mist-netted.) But maximizing for area can result in even more extinctions, if other considerations, like habitat quality and population dynamics, are not accounted for [130]. It is necessary to look beyond just the minimal ‘extent of occurrence’.

Birds can move through the “inhospitable” matrix to varying degrees [78, 131, 6, 189, 67, 202, 113]. Such variation in movement ability has already been reported for birds in remaining southeastern Brazil forest, even within the categorization understory birds [7, 68, 69, 186, 67, 70, 113, 202, 187, 21]. Further integration of this dispersal knowledge needs to occur in spatial modeling, to ‘see’ as the birds see.

For example, corridors and “stepping stone” patches have been found to have value in connecting populations [110]. Birds moved more often between forest patches connected by forest corridors than between forest patches not connected by corridors [47, 3, 113]. Agroforest woodlots were used as stepping stones by other Atlantic Forest birds [186]. Even small “sink” patches can be of value to a metapopulation, by adding to the overall area and encouraging exchange between patches [57].

Currently there is no standardized measure of fragmentation effects for different species with biological significance [150]. This would be extremely beneficial to a risk classification system with incorporation of more key data. Although we note that the metrics described herein are intended for estimating relative extinction risk, such as comparing within or between species, we view this work as a step towards a comparative metric with broader applicability, for any large scale habitat and metapopulation of species. But the spatial aspect needs to be considered in relation to the organisms living there. [36] said it best: it is the understanding of the interaction of landscape structure

and dynamics with species dynamics that is crucial to achieving the ultimate goal of conservation, which is the persistence of biodiversity. Knowing how well these birds are able to cross such gaps will play an important role in determining the connectivity of their habitat landscapes.

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Appendix A

List of Figures

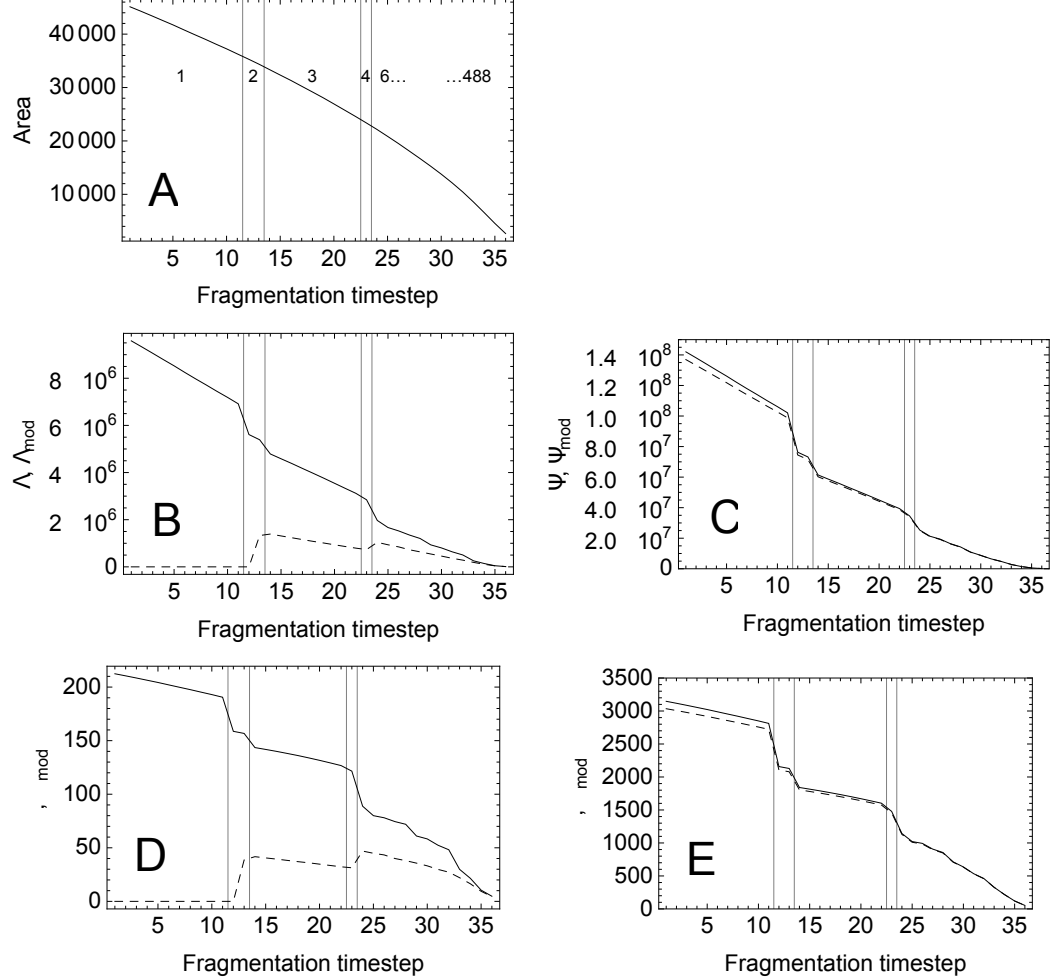


Figure A.1: Change in area A) and various fragmentation measures B-E) with increasing fragmentation in a habitat loss simulation. Vertical lines in all plots indicate early patch-splitting events; numbers in A) indicate the numbers of patches in the system at various timesteps. B) Metapopulation capacity, in its original form (λ , dashed line) and modified with self-colonization (λ_{self} , solid line). C) Extrapolated persistence time, without (ψ , dashed line) and with self-colonization (ψ_{self} , solid line). D) and E) as B) and C), but divided by area to better reflect fragmentation independent of area loss. For metrics that require colonization and extinction parameters, we used $C = 0.000012$ and $E = 0.07$ (see text).

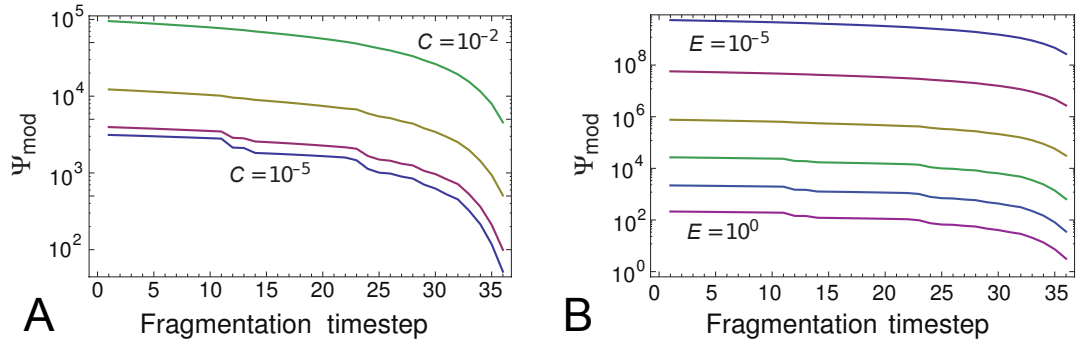


Figure A.2: Colonization A) and extinction B) rate parameters cause strong variation in Ψ_{self} , however, parallel lines on a log scale indicate a constant proportional change over the fragmentation series, no matter what the values of C and E .

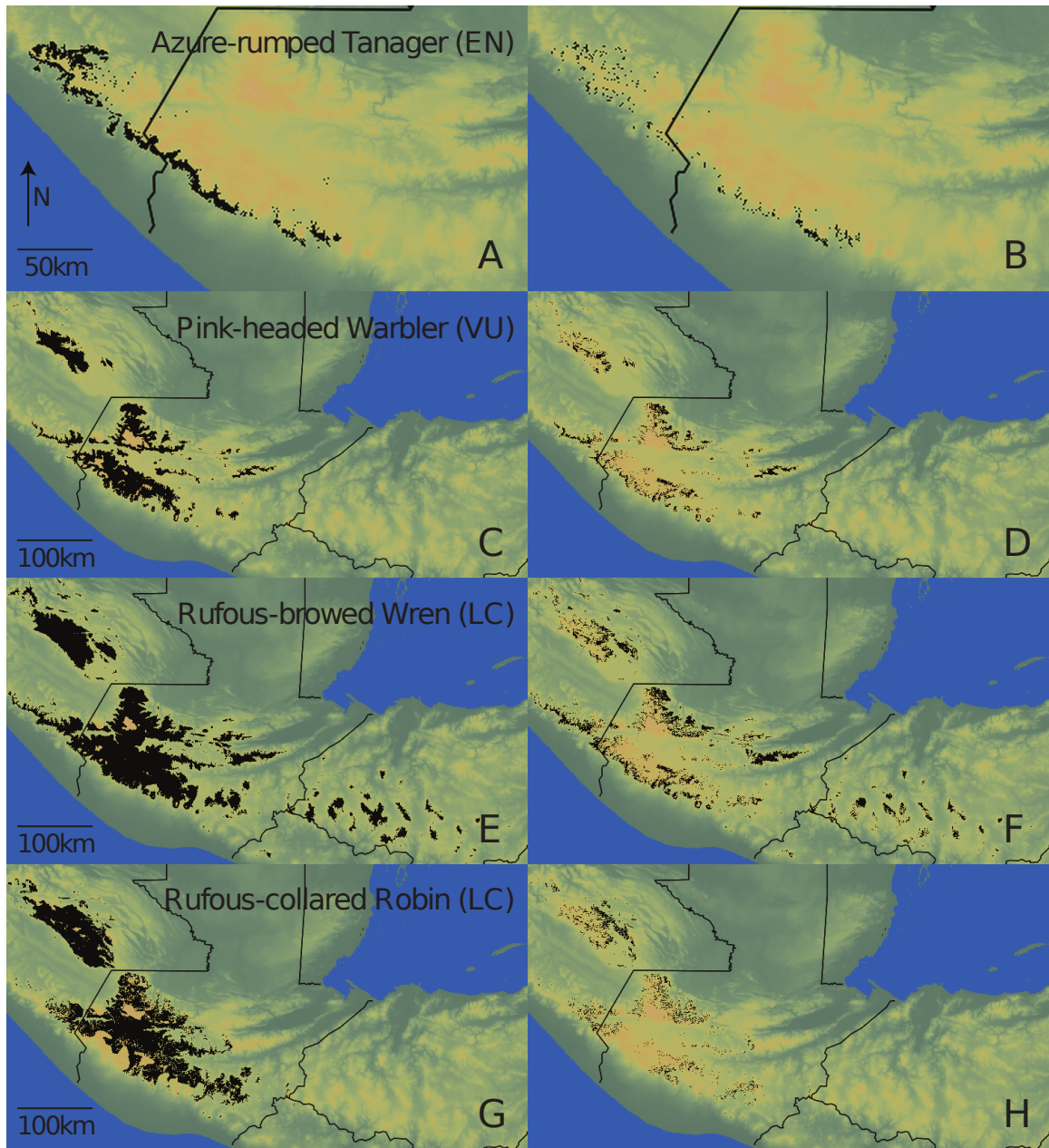


Figure A.3: Original (left) and current (right) habitat maps of four small-bodied species from the Central American Highlands. Pixels represent 1km^2 . The Rufous-collared Robin is listed as of least concern by the IUCN, even though its current range has the smallest extrapolated persistence time (ψ_{self}), even compared to the vulnerable or endangered species (Table 2), due to the many small fragments. According to every metric it has experienced much greater fragmentation over time, compared to its original range.

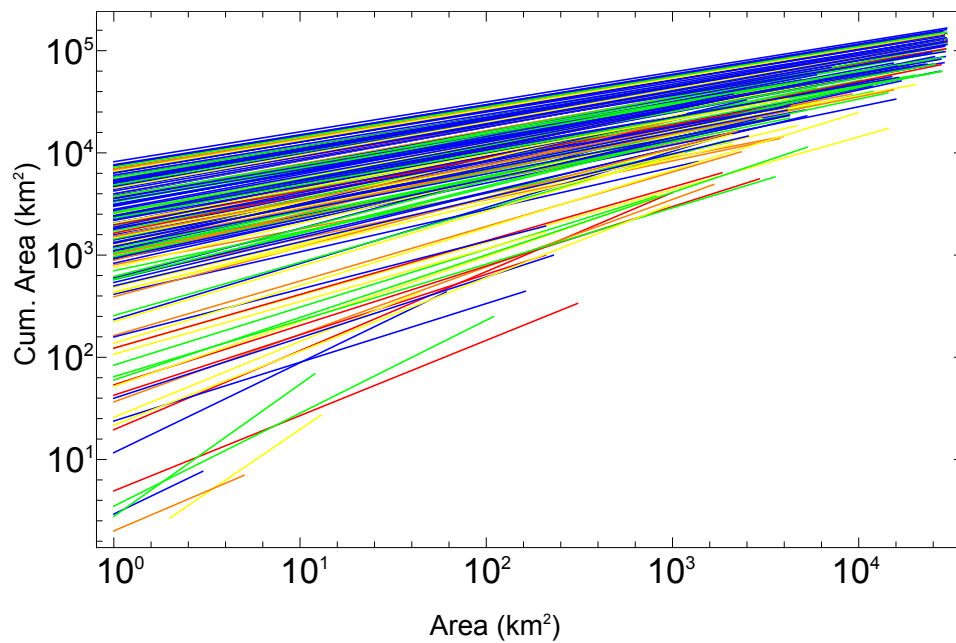


Figure A.4: Regression lines fitted to Atlantic forest bird range data on the logarithm of cumulative area in patches up to a given size, versus the logarithm of that size. (Figure does not show original data). Red, orange, yellow, green and blue indicate CR, EN, VU, NT and LC status, respectively. The LC species tend to be at the top of the graph and extend furthest to the right, reflecting larger overall ranges and having the largest patches in their landscapes, respectively. They also have smaller slopes, indicating greater fragmentation, if we took these results at face value (see text).

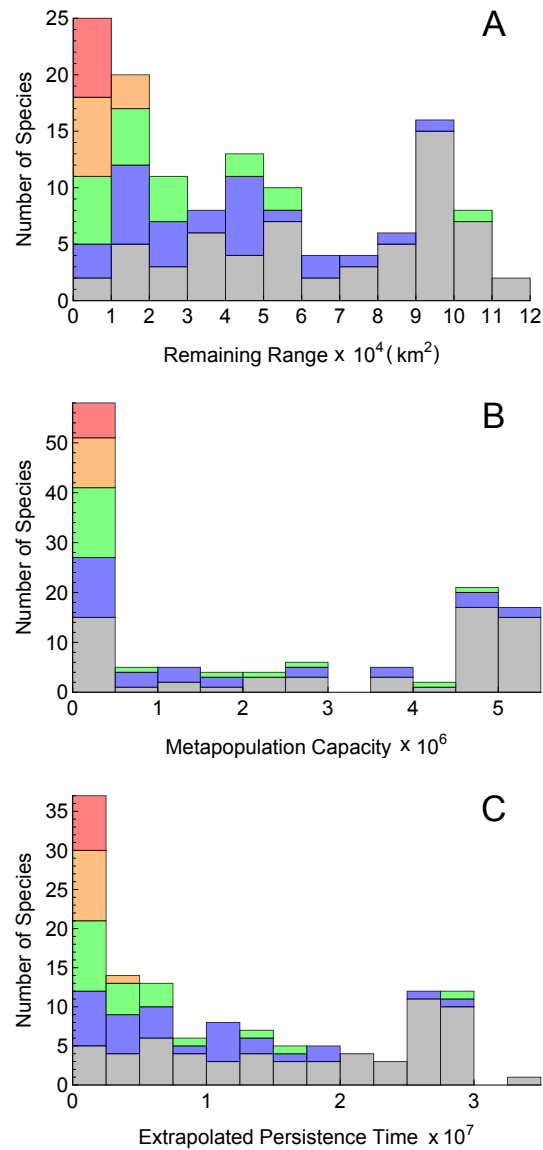


Figure A.5: Histograms of passerine species' fragmentation measures reveal differences between A) remaining range to the landscape values calculated with B) metapopulation capacity and C) extrapolated persistence time. Colors indicate their IUCN threat status. When compared to remaining range, extrapolated persistence time (weakly) and metapopulation capacity (strongly) tend to place most bird species at either end of their respective scales, indicating high or low risk.

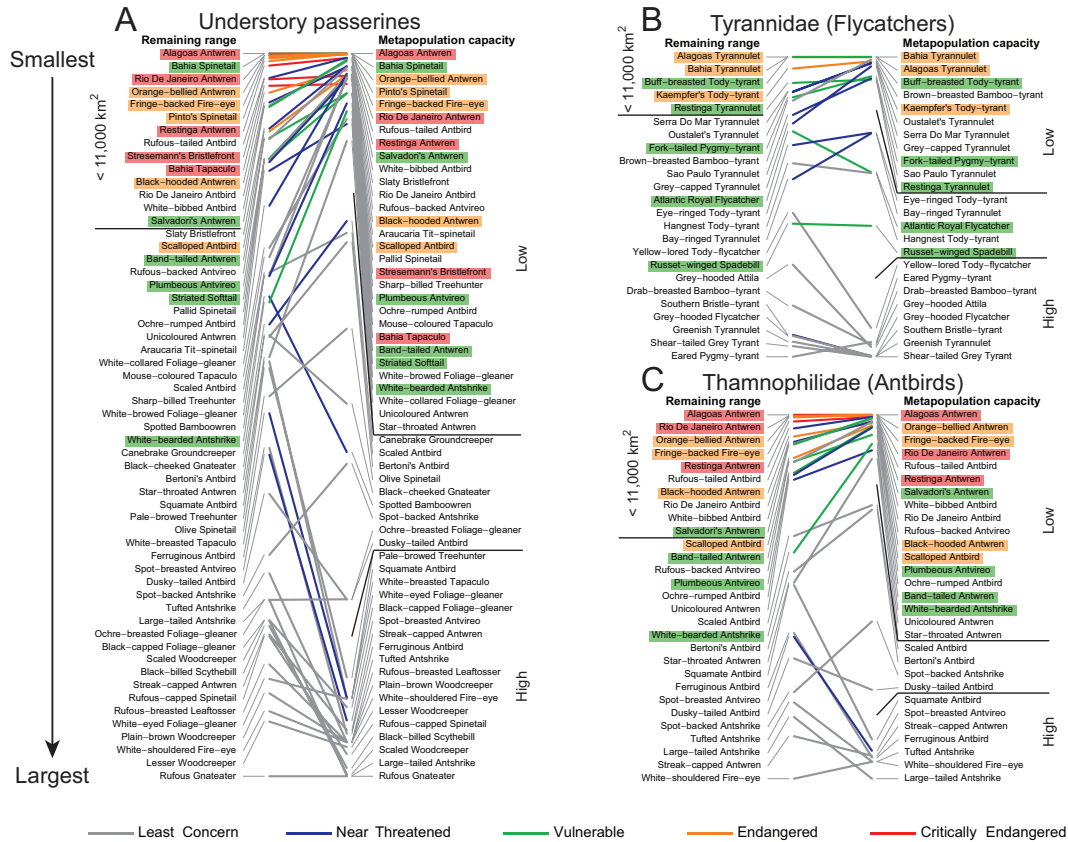


Figure A.6: Slopegraphs comparing the remaining range area and modified metapopulation capacity of three subsets of bird species in Brazil's Atlantic forest. The lists of species on either side rank them from smallest to largest in range size and metapopulation capacity, respectively. The center lines, scaled by actual respective values of area (left end) and metapopulation capacity (right end), and text background colors reflect IUCN status (see key — for text backgrounds, only species in the three threatened categories are colored). The thin gray lines point to each species' corresponding line. The metapopulation capacity values show strong bimodality in all three subsets, as indicated by the clustering of line end points at the top and bottom right side. While Critically Endangered, Endangered and Vulnerable species have generally small remaining range and low metapopulation capacity, many species with similar range characteristics are not listed as threatened.

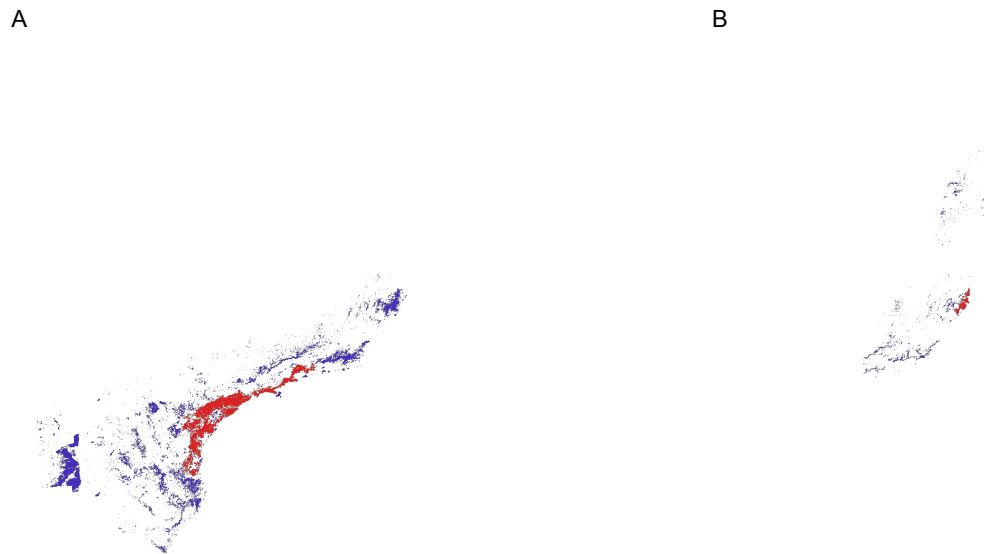


Figure A.7: The habitat patches of the near threatened Blackish-blue Seedeater (*Amaurospiza moesta*), which has an extensive range, and the near threatened Rio de Janeiro Antbird (*Cercomacra brasiliana*), which has a restricted range from the north-east region of the Atlantic forest. Patches are ranked by metapopulation capacity contribution (λ_{self}); patch value is represented by a linear color scale from blue through green and yellow to red. The maps show only shades of blue and a single red patch, indicating that the best remaining patch (the largest) is far more valuable than any of the others. More importantly, different species experience very distinct areas of highest importance, especially when looking at species with restricted ranges.

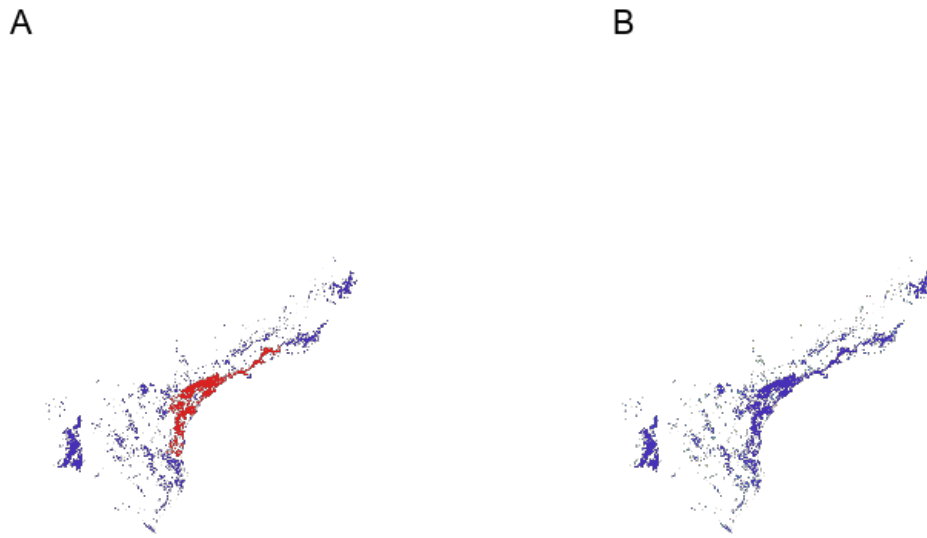


Figure A.8: This map compares the most valuable locations for the near threatened Blackish-blue Seedeater (*Amaurospiza moesta*) according to the two metrics. Warm colors highlight the most important fragment for the rest of the remaining range, the cool colors the least. A) Ranked by metapopulation capacity contribution (λ_{self}), which heavily favors patch area. B) Ranked by extrapolated persistence time (ψ_{self}), we see this metric places less emphasis on patch area and more on patch location (relative to other patches that provide colonists). ψ_{self} values those small outlying patches for their potential to receive colonists.

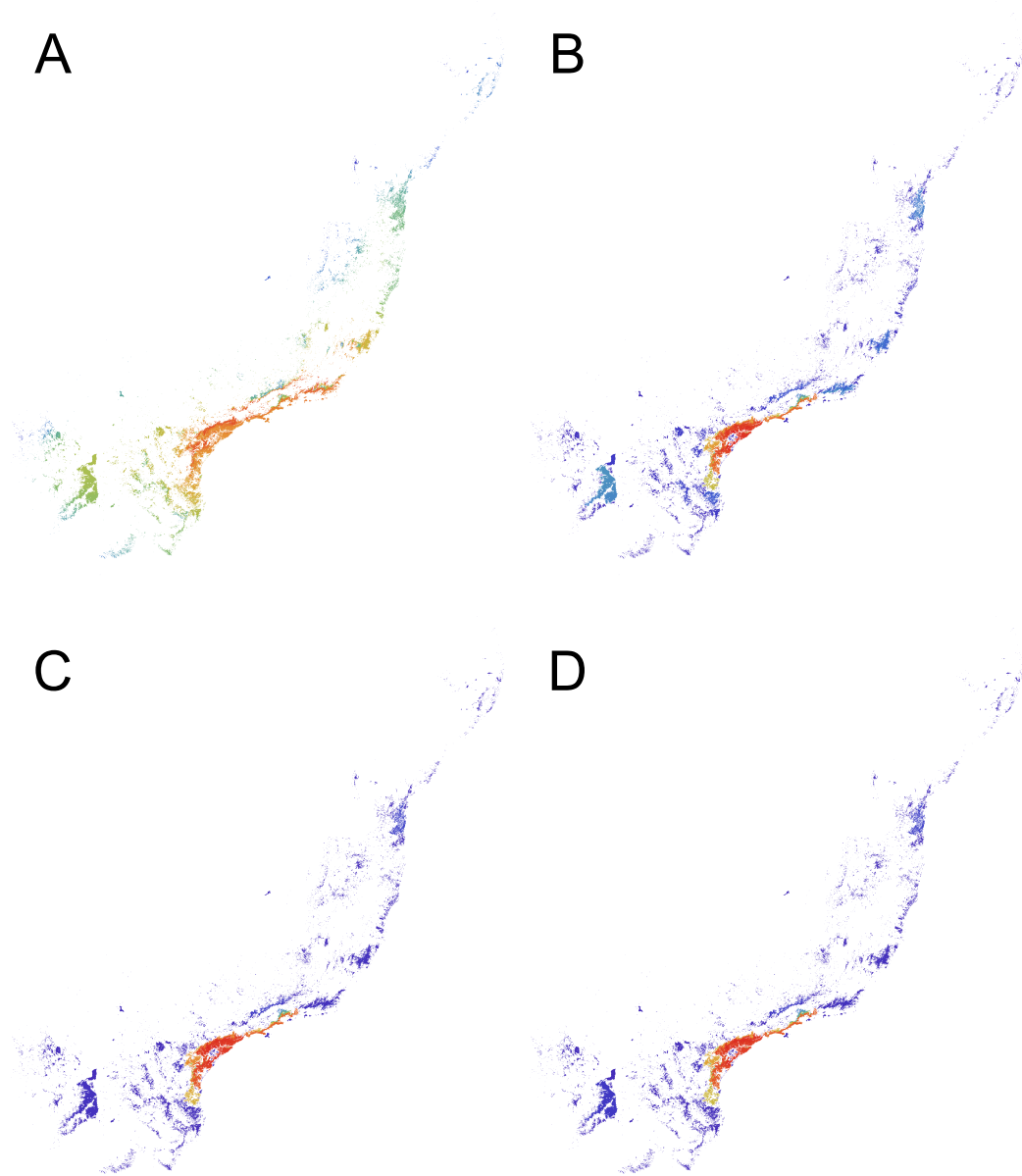


Figure A.9: Patch value is combined across all passerine species in our Atlantic forest dataset using different patch-level fragmentation metrics. All plots use a linear color scale from blue (lowest value) to red (highest value). A) Estimated passerine species richness. B) Species richness weighted by the inverse of total area. When weighting by the total range size for the species, we get a more graded weighting of the overlap in all species' ranges. Ranked by C) metapopulation capacity contribution (λ_{self}) per km^2 and D) λ_{self} weighted by IUCN Red List Category. Threatened species are weighted slightly less strongly in the central core area than when ranked only by λ_{self} .

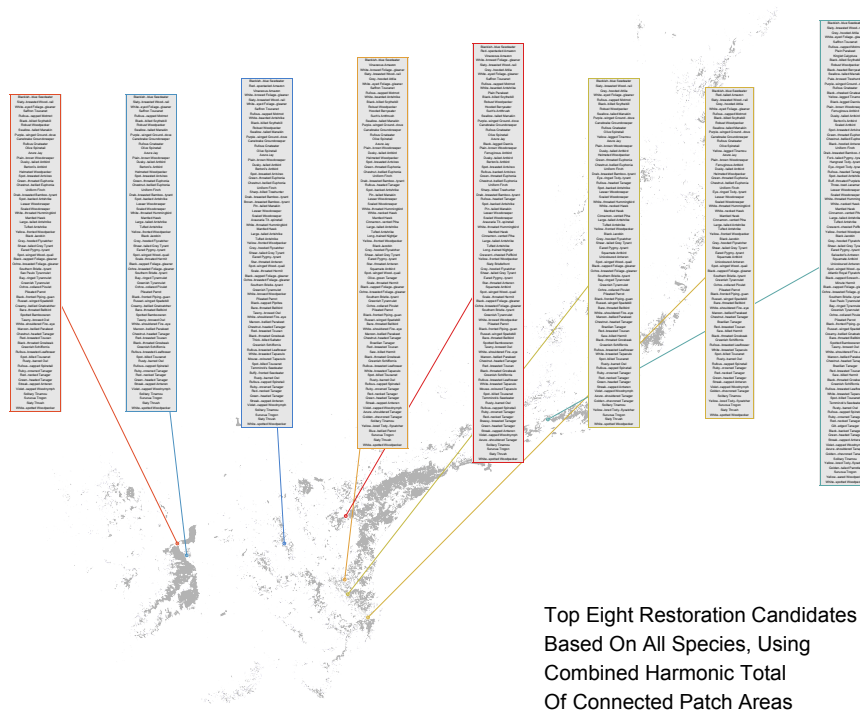
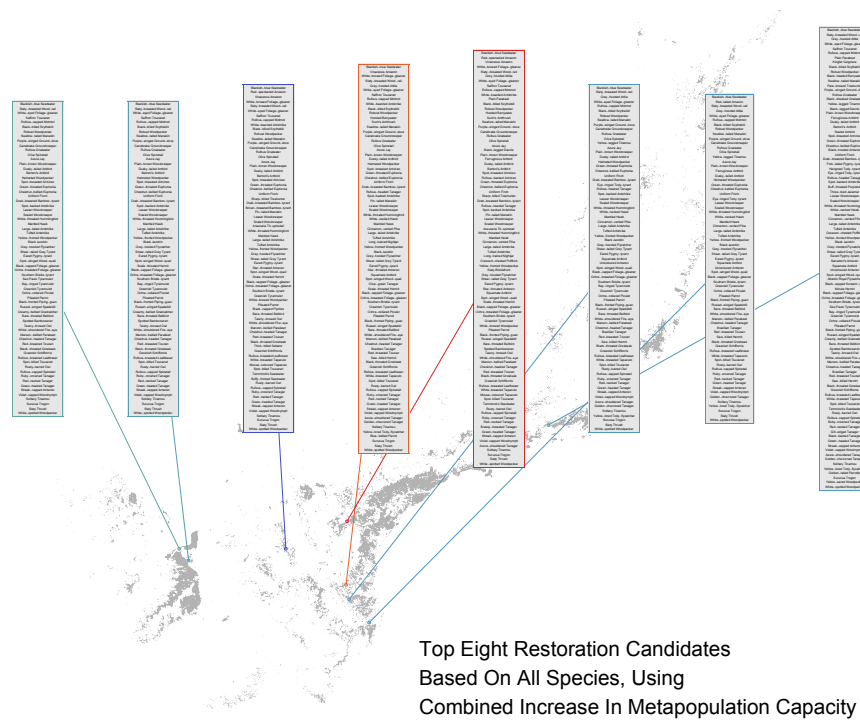


Figure A.10: Restoration prioritization based on improvement in A) metapopulation capacity and B) combined harmonic total of connected patch sizes. Boxed lists indicate the species for which patch connections would be made. As expected, selected pixels are those which connect the larger patches in each region.

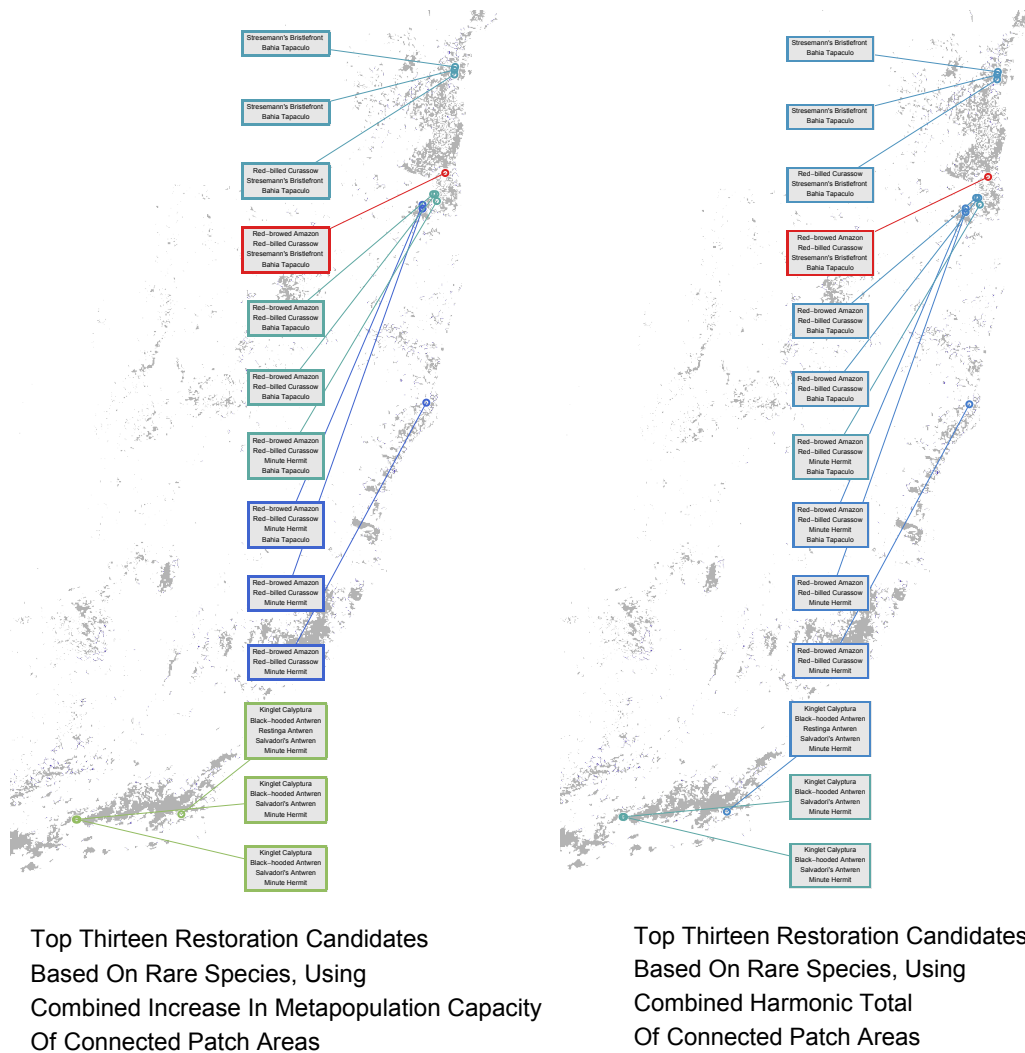


Figure A.11: Restoration prioritization based on improvement in A) metapopulation capacity and B) combined harmonic total of connected patch sizes for 'rare' species (those with ranges < 11,000 km²). Boxed lists indicate the species for which patch connections would be made.

Vita

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