Contributed Paper

Estimating Extinction Risk with Metapopulation Models of Large-Scale Fragmentation

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Abstract: *Habitat loss is the principal threat to species. How much habitat remains—and how quickly it is shrinking—are implicitly included in the way the International Union for Conservation of Nature determines a species' risk of extinction. Many endangered species have habitats that are also fragmented to different extents. Thus, ideally, fragmentation should be quantified in a standard way in risk assessments. Although 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 link fragmentation to extinction risk, but standard models work only at small scales. Counterintuitively, these models predict that a species in a large, contiguous habitat will fare worse than one in 2 tiny patches. This occurs because although the species in the large, contiguous habitat has a low probability of extinction, recolonization cannot occur if there are no other patches to provide colonists for a rescue effect. For 4 ecologically comparable bird species of the North Central American highland forests, we devised metapopulation models with area-weighted self-colonization terms; this reflected repopulation of a patch from a remnant of individuals that survived an adverse event. Use of this term gives extra weight to a patch in its own rescue effect. Species assigned least risk status were comparable in long-term extinction risk with those ranked as threatened. This finding suggests that fragmentation has had a substantial negative effect on them that is not accounted for in their Red List category.*

Keywords: forest loss, habitat fragmentation, metapopulation, range occupancy

Estimación del Riesgo de Extinción Mediante Modelos Metapoblacionales de Fragmentación a Gran Escala

Resumen: *La pérdida de hábitat es la principal amenaza para las especies. La cantidad de hábitat remanente—y la rapidez con que se pierde—están incluidas implícitamente en la forma en que la Unión Internacional para la Conservación de la Naturaleza determina el riesgo de extinción de una especie. Muchas especies en peligro tienen hábitats que también están fragmentados en diferentes grados. Por lo tanto, ideal-mente, la fragmentación debe ser cuantificada de manera estándar en las evaluaciones de riesgo. Aunque el mapeo de la fragmentación a partir de imágenes de satélite es fácil, son escasas las técnicas eficientes para relacionar mapas del hábitat remanente con el riesgo de extinción. Las métricas puramente espaciales de la ecología del paisaje son difíciles de interpretar y no abordan la extinción directamente. Los modelos metapoblacionales espacialmente explícitos relacionan la fragmentación con el riesgo de extinción, pero los modelos estándar solo funcionan en escalas pequeñas. Contraintuitivamente, estos modelos predicen que una especie en un hábitat extenso y contiguo tendrá menos éxito que en dos fragmentos pequeños. Esto ocurre porque aunque la especie en el hábitat extenso y contiguo tiene una baja probabilidad de extinción, la recolonización no puede ocurrir si no hay otros fragmentos que proporciones colonizadores para un efecto de rescate. Para 4 especies de aves ecológicamente comparables de los bosques de Centro América diseñamos modelos metapoblacionales con términos de autocolonización con ponderación de área; esto reflejó la*

repoblación de un fragmento con un remanente de individuos que sobrevivieron a un evento adverso. El uso de este término da peso adicional a un fragmento en su propio efecto de rescate. Las especies asignadas con menor riesgo fueron comparables en el riesgo de extinción a largo plazo con aquellas clasificadas como amenazadas. Este hallazgo sugiere que la fragmentación tiene un efecto negativo sustancial sobre esas especies que no esta considerado en su categoría de la lista roja.

Palabras Clave: fragmentación de hábitat, metapoblación, pérdida de bosques, rango de ocupación

Introduction

Habitat destruction is the greatest threat to species' survival (Pimm et al. 1995; Sala et al. 2000). It decreases habitat extent and fragments habitat, and remaining habitat patches are often small and isolated (Bierregaard et al. 1992; Andrén 1994; Debinski & Holt 2000). Not surprisingly, habitat extent and loss are important criteria in the International Union for Conservation of Nature's (IUCN) determination of a species' risk of extinction through criteria A (relating to population size) and B (relating to geographic range). In both A and B sets of criteria, recent habitat loss is just one criterion for inferring small population size or declining population trends, but justifications described by BirdLife International show that habitat is by far the most frequently invoked criterion. This likely occurs because the relation between habitat loss and extinction risk is well understood and because habitats are easier to assess than populations.

Until recently, the IUCN presented species ranges as continuous and with smooth edges—the kind of extent of occurrence (EOO) that field guides display. Previously, Harris and Pimm (2008) showed that after categorizing these types of range maps by known elevation limits and by broad habitat characteristics, extents of suitable habitat (Beresford et al. 2011; Buchanan et al. 2011) are often much smaller, especially for species in mountains, than those delineated by IUCN. BirdLife International conducts risk assessments for birds and continually updates them on their website (http://www.birdlife.org). Currently some, but not all, of their range maps are based in part on elevation.

In producing more realistic range maps, one quickly uncovers how fragmented they are. Fragmentation especially threatens tropical forest species because unbroken canopies become tiny, isolated fragments that often include only a fraction of the original forest (Bierregaard & Lovejoy 1989; Turner 1996; Ferraz et al. 2003). Although the increased risk of extirpation for species in isolated small fragments is fairly well understood (e.g., Ferraz et al. 2003; Laurance et al. 2011), species can persist in fragmented landscapes if dispersal between patches is sufficient (Levins 1969, 1970). However, navigating between isolated patches can have high cost (Bonte et al. 2012), even for birds, which are relatively mobile (Bélisle et al. 2001).

Accurate assessments of extinction threat under habitat loss requires one to evaluate a species' remaining habitat distribution and the effects of this distribution on extinction risk in a practical and consistent way. The IUCN's current 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 (severely 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. Here, we 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 (McGarigal et al. 2002) calculates a variety of statistics related to spatial patterns. More recent approaches borrow from graph theory (Saura & Torné 2009) or circuit theory (McRae et al. 2008). These approaches are essentially nonbiological, can sometimes be difficult to interpret, and provide no direct assessment of extinction risk. At the other extreme, large-scale, spatially explicit implementations of models of population dynamics allow for a great degree of realism but are complex and often require many parameters. Our goal was to devise a metric that can be applied in a wide range of real-world circumstances that is based on readily 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 extents because analyses generally address equilibrium occupancy or some derived measure of the long-term behavior of a highly fragmented system of small patches (Hanski & Ovaskainen 2000; Hanski 2001). Such metrics can 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 nonzero 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 available evidence.

We overcome this behavior by modifying the standard SEM to include self-colonization. By this, we mean a patch is rescued by a small number of individuals that survived whatever catastrophe affected the population in 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 nonintuitive behavior of occupancy-based models when they are applied at large scales. With range data of 4 forest bird species endemic to the highlands of North Central America, we used metapopulation capacity (Hanski & Ovaskainen 2000) and extrapolated persistence time (defined below) to quantify fragmentation and consequent extinction risk for these species in a network of habitat patches before and after recent forest loss.

Methods

Metapopulation Models

Hanski's (1994) SEM model followed Levins' model (1969, 1970) except that there is a separate expression for each patch,

$$\frac{dp_i}{dt} = col_i(1 - p_i) - ext_i p_i, \tag{1}$$

where dp_i/dt is the change in population over time, p_i is the occupancy rate of patch i, col_i is colonization rate, and ext_i is extinction rate. Hanski also incorporated concepts from island biogeography (MacArthur & Wilson 1963, 1967), whereby area and connectivity functions determine colonization and extinction rates (Hanski & Gyllenberg 1997; Hanski & Ovaskainen 2000).

In most formulations, ext_i is an inverse function of patch area,

$$ext_i = \frac{E}{A_i^x}, \tag{2}$$

where E and x are constants and A_i is the area of patch i. The x constant is typically set to 0.5 for many taxa, and this is supported for tropical forest birds by Ferraz et al. (2003). These authors also suggest a value of 0.07 for E.

The col_i is the sum of the incoming rates from all other occupied patches. These rates increase as the size of the colonizing patch increases and decline as interpatch distance increases according to a simple function,

$$col_i = C \sum_{j \neq i} f(D_{ij}) A_j p_j, \tag{3}$$

where C is a constant, A_j is the area of patch j, $f(D_{ij})$ is a function of the distance between patches i and j, and p_j is the occupancy rate of patch j (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 the distance between them. We considered this distance value (D_{ij}) the minimum distance between patch edges, rather than centroid-to-centroid distances (e.g., Ovaskainen & Hanski 2003).

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 $e^{-\alpha D_{ij}}$, in which $1/\alpha$ is the average interpatch survival distance. This function implies vanishingly small survival at long distances. This contradicts the evidence that although most birds make short movements most of the time, they can travel long distances when necessary (Van Houtan et al. 2007; Hansbauer et al. 2008). Thus, we used a heavy-tailed log-sech function that Van Houtan et al. (2007) proposed for bird movements from habitat fragments in the Amazon. This is a probability distribution of movement distances, not a survival rate function, so we converted it into one by integrating over distances from D_{ij} to infinity,

$$f(D_{ij}) = \int_{D_{ij}}^{\infty} \frac{2/(\pi br)}{(r/\alpha)^{1/b} + (r/\alpha)^{-1/b}} \, dr$$

$$= \frac{2 \arctan\left[(\alpha/D_{ij})^{1/b}\right]}{\pi} \quad D_{ij} \geq 0, \tag{4}$$

where $D_{ij} \geq 0$, α and b (or α and β, where β is the tail function and $b = 1/(\beta - 1)$) are parameters of the log-sech function, and r is the distance moved. Van Houtan et al. (2007) published a range of fitted parameter values within which the best fit across a variety of species in fragmented forest is obtained with $\alpha = 317$ and $\beta = 1.77$. This is conservative as a survival rate because the birds in their study were not dead at the time their final position was measured.

The colonization component 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 km^2) in the direction of every other patch in the system. It is not the rate at which they arrive in a patch, which is affected by $f(D_{ij})$. However, only one of our proposed metrics includes C in its formulation. In that case, we chose $C = 0.000012$ (except when testing the effect of varying C). This value means that a medium-sized patch of 100 km^2 provides 0.0012 colonizing individuals per other patch per year (or 0.0001 individuals per month). In a hypothetical 100-patch system of occupied patches of a similar size and with no dispersal mortality, this yields a colonization rate to a single empty patch of 0.12 individuals, which translates into an 11.3% probability of an empty patch being colonized by at least one individual within a year. For a thousand patches, the probability is approximately 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 Eq. 1). This makes sense if one defines colonization conventionally as between-patch movement. We defined 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 plausible that threats will drive a population to low numbers. Given time, survivors would likely repopulate the patch from within. This phenomenon is represented in the standard SEM via an extinction rate term that gets smaller as patches get larger. However, in such a model the patch continuously plays its role as an exporter of colonists to other patches, at a high rate if the patch is large. If threats have driven the population to low levels, emigration 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 reoccupy the now empty remainder of the patch than to leave it. Alternatively, if one considers the patch population to be functionally extinct, then there is a period before recolonization (whether from within or without) when it is not exporting colonists. The dependence of extinction rate on area still remains. Processes that render patch populations 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 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

Hanski and Ovaskainen (2000) introduced the concept of "metapopulation capacity" as a way of assessing the ability of a given, spatially explicit landscape to support a species. Calculating metapopulation capacity involves extracting the landscape components of the standard SEM (the extinction-area and colonization-distance functions) into a matrix **M** with terms,

$$m_{ij} = \begin{cases} f(D_{ij})A_j A_i^x & j \neq i \\ 0 & j = i \end{cases} \quad (5)$$

and summarizing them as a single value λ_M, the leading eigenvalue of **M**. They showed that a landscape can support a species in the long term as a metapopulation when $\lambda_M > E/C$. Henceforth, we refer to metapopulation capacity as λ. The units of λ can be thought of as Levins' patch equivalents, that is, the number of patches in a Levins-type (i.e., nonspatial) 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 Hanski and Ovaskainen (2000) pointed out, λ is useful because one can calculate it even when one

does not know the value of *E* and *C*, as is the case for most species (patch-leaving rates are particularly hard to estimate). Without values for these variables, one can use λ to compare landscape quality. One might compare different landscapes for the same species (e.g., original and current extent of suitable habitat). Or, one might compare different species expected to have similar extinction sensitivities and dispersal characteristics, on the basis of their ecology. So λ is a candidate metric of fragmentation, but it still rates single patches, no matter how large, as having zero long-term capacity. Even systems with a few large patches have a lower capacity than more fragmented systems 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. As for λ, λ_{self} combines overall area and fragmentation. To better assess fragmentation as a process independent of habitat loss, we used $\Lambda_{self} = \lambda_{self}/\sum_i A_i$, the metapopulation capacity per unit area, or metapopulation density. This parallels the IUCN's listing guidelines that embrace similarly independent criteria (Mace et al. 2008).

Metrics of Fragmentation When *C* and *E* are Known

If one knows the rate constants *C* and E, then one has other options for evaluating landscapes. One of these is a modification of metapopulation capacity. Because the criterion of species' persistence is $\lambda_M > E/C$, the metric $\lambda_M C/E$ describes capacity relative to the minimum required. A habitat restoration goal could be something like achieving at least 2 times the minimum metapopulation capacity.

Perhaps the most traditional way to rate landscapes is to calculate equilibrium patch occupancy values and to develop a metric that summarizes these values, (e.g., 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 large, contiguous patches because there can be a considerable delay before species disappear (Tilman et al. 1994; Brooks et al. 1999; Hanski & Ovaskainen 2002). We therefore set $p_i = 1$ for all *i*. In the standard SEM (Eq. 1) this removes 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 reduced the extinction rate of currently occupied patches,

$$\delta_i = \text{ext}_i \frac{\text{ext}_i}{\text{col}_i + \text{ext}_i}, \qquad (6)$$

where ext_i and col_i are given in 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,

$$\Delta = \sum \delta_i. \qquad (7)$$

Incorporating a rescue effect (and thus colonization processes) means that with the standard SEM, the problem of undervaluing small numbers of large patches also affects the contraction rate, although to a lesser degree. As with metapopulation capacity, adding self-colonization resolved this. Although 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. Multiplying Ψ_{self} by total area produced a metric, ψ_{self} that we interpreted as the extrapolated persistence time (i.e., 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 and fragmentation and is therefore comparable to λ_{self}, the metapopulation capacity. These proposed fragmentation measures are summarized in Table 1.

Table 1. Four measures of range fragmentation developed for extinction-risk prioritization.[a]

	Metapopulation capacity (Levins patch equivalents)	*Extrapolated persistence time (months, years, etc.)*
Total system	λ_{self}	ψ_{self}
Per unit area	Λ_{self}	Ψ_{self}

[a]*The subscript self refers to the inclusion of self-colonization, which eliminates the few-patches problem (defined in text).*

Testing the Metrics

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. This simulation showed a decline in forest area from 45,000 km^2 to 0 km^2, progressing from 1 to almost 500 fragments (Fig. 1a). We iterated this process until all patches had coalesced into a single, large patch. When reversed, the sequence of iterations described a fine-grained fragmentation sequence. We calculated the various fragmentation metrics for the sequence with and without the self-colonization modification. Harris and Pimm (2008) assembled data on 4 endemic bird areas (EBAs) (Stattersfield et al. 1998) around the world. For each area, they digitized the field-guide range of every bird species and overlaid these ranges with appropriate elevations and forest type. The intersection between layers estimated the original extent of forest habitat for each species. They then classified satellite images to locate remaining forest and incorporated this information with the other layers to estimate the current extent of suitable bird habitat. We used, as examples of real ranges, the forest distributions for 4 species BirdLife International assessed for extinction risk in one of these areas, the North Central American highlands EBA.

Azure-rumped Tanager (*Tangara cabanisi*) is endangered (EN) because of its small and declining range. It occupies the upper canopy of broadleaf evergreen forests at 1000–1700 m elevation. Coffee plantations have replaced much of this type of forest, but the species sometimes occurs at forest edges and in secondary forests.

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. These forests have become highly fragmented due to deforestation and intense human use.

Rufous-browed Wren (*Troglodytes rufociliatus*) is of least concern (LC) because it has a large range and occurs widely in moist montane forests between 1700 and 3200 m elevation. The species is highly dependent on forest at a minimum elevation of 1250 m. Populations range from moderately small (15,000–20,000 mature individuals) to large (>20,000). It is thought to be in decline from ongoing habitat destruction and fragmentation.

Rufous-collared Robin (*Turdus rufitorques*) is of LC because it also has a very large range (BirdLife International 2010). It occurs in various types of forests at 1500–3300 m elevation. The species is moderately dependent on forest. As with the Wren, population size may be moderately small (>20,000–30,000 individuals) to large and is thought to be in decline due to ongoing habitat destruction and degradation.

These species are all forest dependent. They vary somewhat in body size and in tolerance of secondary habitats and therefore also presumably in dispersal
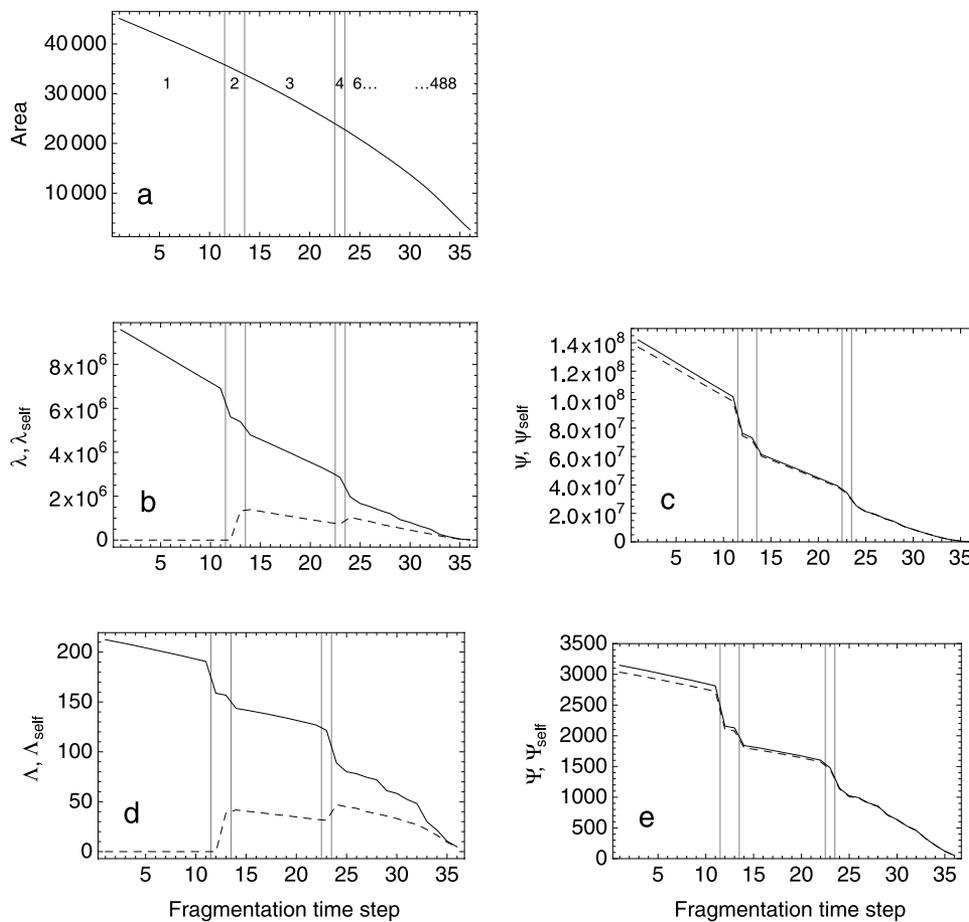
Figure 1. Changes in (a) area (numbers in body of graph, number of patches in the system at various time steps) and (b–e) measures of fragmentation as fragmentation increases in a simulation of habitat loss (vertical lines, early patch-splitting events). (b) Metapopulation capacity in its original form (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) Metapopulation capacity (the capacity of a landscape to support a species) and 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), respectively, but divided by area to better reflect fragmentation independent of area loss. For metrics that require colonization (C) and extinction (E) parameters, we used C = 0.000012 and E = 0.07 (see text).

ability, although their IUCN Red List categories do not always reflect the latest data in the literature. Because these species' original and current distributions in forest provide good coverage of the range of fragmentation possibilities, we considered their dispersal characteristics to be the same (so that differences are due to spatial patterns only). Differences in dispersal could be incorporated by adjusting parameters accordingly.

Results

Artificial Fragmentation Sequence

As forest area decreased, it broke up into 2, 3, 4, and 6 patches (Fig. 1). The original metapopulation capacity

metric λ (Fig. 1b) was zero when the landscape consisted of one patch because it received no colonization from surrounding patches. At the first fragmentation event (creation of 2 patches), λ behaved paradoxically and increased in value. It also increased in subsequent fragmentation events until there were 6 patches. It declined gradually in between these jumps due to area loss. Lambda declined relatively continuously after the creation of 7 patches. The naive implication is that initial fragmentation reduced extinction risk. Lambda$_{self}$ did not exhibit this counterintuitive behavior. The single large patch had the highest metapopulation capacity and subsequent fragmentation caused the metric to decline. As the patches became numerous, small, and isolated, values of the 2 metrics converged on zero.

Without self-colonization, extrapolated persistence time (ψ) always declined following fragmentation (Fig. 1c). The addition of self-colonization (ψ_{self}) increased persistence time, more so when there were few fragments and yielded a trajectory very similar to that of λ_{self}. Both modified metrics captured 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 Λ_{self} and Ψ_{self} also declined consistently, but the effect of fragmentation events accelerated later in the sequence (Figs. 1d and e). This occurred because these metrics placed greater emphasis on fragmentation itself and less on overall area. Fragmentation events became more frequent as patches got smaller. These metrics were not completely unaffected by area changes, however, as indicated by their negative slopes even within the ranges where patch number was constant. Area appeared in both the colonization and extinction rate terms. Dividing λ_{self} and ψ_{self} by area did not completely remove the dependence.

The Effect of Parameter Choice

Extrapolated persistence time and extrapolated persistence time per unit area (Λ_{self} and Ψ_{self}) required values for C and E, which we did not know for most species and so had to 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}. The metrics showed strong changes in response to these constants (Fig. 2). Extrapolated persistence time behaved similarly as when calculated per unit area. This could be problematic if it affects the ranking of different landscapes. However, on a log scale, the different values of C and E were nearly parallel over the full range of fragmentation, which indicates the proportional change in landscape value was independent of both parameters. In that sense, ψ_{self} was similar to λ_{self} in that it provided a consistent relative ranking of landscapes.
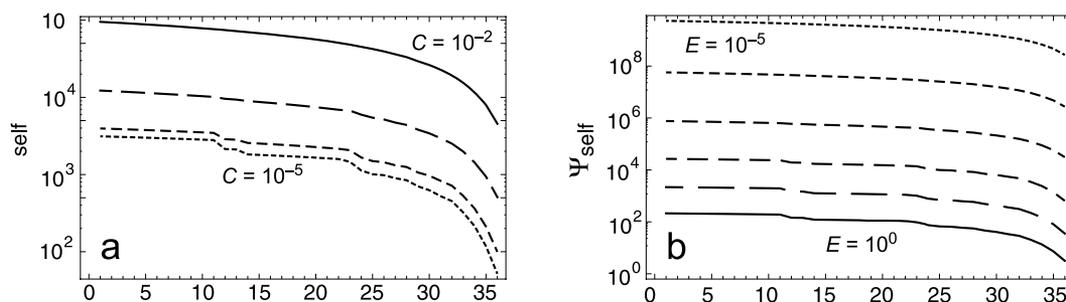
Four Species Examples

For all 4 species, the estimated current forest area was less than Harris and Pimm's (2008) proposed threshold for endangerment of 11,000 km^2, which differs from BirdLife International estimates that account for population fluctuations (Table 2). Including self-colonization had a large effect on species. Unmodified metapopulation capacity (λ) ranged from <1% to 3.6% of λ_{self} for the original ranges and from 3.2% to 7% for current ranges (Table 2). The Rufous-collared Robin is listed as of LC by the IUCN, even though its current range has the smallest extrapolated persistence time (ψ_{self}), smaller even than that of the VU or EN species (Table 2); this is due to its range being in small fragments. According to every metric we applied, its habitat has become much more fragmented over time than the habitat of the other 3 species.

Status of Current Habitat Distributions

The remaining forest habitat for the robin (LC) was less than that of the (VU) warbler (Figs. 3d and h). Metapopulation capacity (λ_{self}) conformed with the IUCN categorizations more closely in that the non-endangered wren and robin had values notably larger than the 2 endangered species (Table 2). The inconsistency between the robin's area and λ_{self} compared (by relative rank between the metrics and IUCN threat status) with that of 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 (Figs. 3d and h). Metapopulation capacity reflected the long-term properties of a landscape and thus gave the existence of larger patches greater weight (because small patches will be unoccupied most of the time).

Values for extrapolated persistence time ψ_{self} were similar relative to forest area. The robin had a lower persistence time than the warbler. This occurred because the very small fragments that made up most of

Figure 2. Proportional change of Ψ_{self} (initial time to lose occupancy of one unit of area, e.g., years) over the fragmentation series in rate of (a) colonization (log scale; solid line, $C = 10^{-2}$; line with long dashes, $C = 10^{-3}$; line with short dashes, $C = 10^{-4}$; dotted line, $C = 10^{-5}$) and (b) extinction (log scale; solid line, $E = 10^{0}$; line with long dashes, $E = 10^{-1}$; dotted line, $E = 10^{-5}$) parameters.
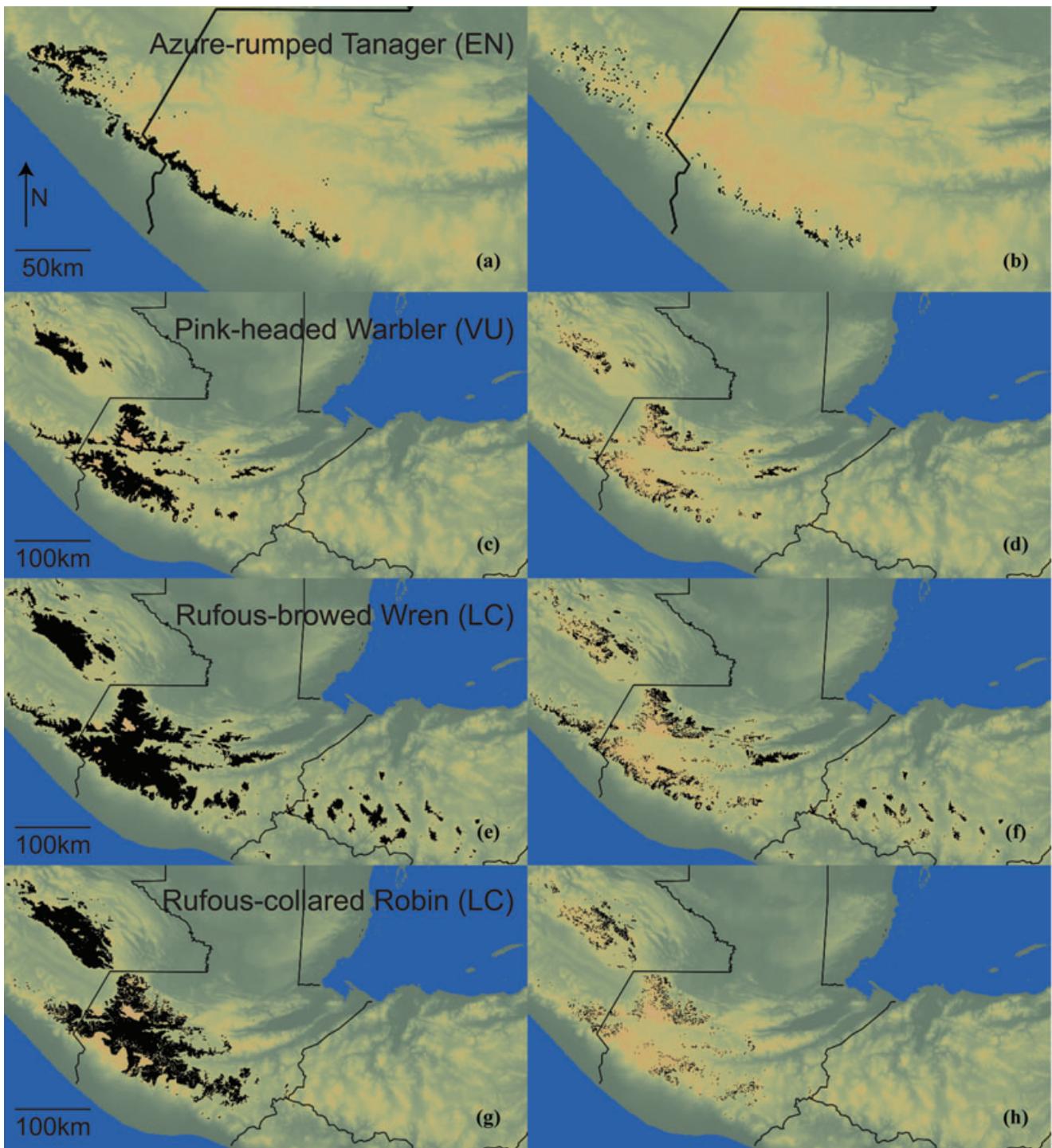
Figure 3. Maps of (a, c, e, and g) original and (b, d, f, and h) current habitat (black) of 4 small-bodied birds in the Central American Highlands (pixels, 1 km²; EN, endangered; VU, vulnerable; LC, least concern).

its range, although assumed to contain the species initially, would lose them very quickly. The habitat of the warbler contained a number of moderately sized patches where the species would be likely to persist longer (Fig. 3d).

Comparison with Estimated Former Distributions

When we compared the original and current estimated forest distributions, the reductions in metapopulation capacity and extrapolated persistence time for all species were greater than the reduction in area alone, which

Table 2. Fragmentation statistics for 4 example species.

	Azure-rumped Tanager	*Pink-headed Warbler*	*Rufous-browed Wren*	*Rufous-collared Robin*
BirdLife category	endangered	vulnerable	least concern	least concern
BirdLife extent of occurrence (km^2)	1700	17,100	98,500	61,100
Original area (km^2)	1578	10,720	24,584	19,253
Current area (km^2)	359.0	3192	7423	2887
Area remaining (%)	22.8	29.8	30.2	15.0
Original λ[a]	471	10,557	15,451	24,794
Current λ[a]	21.7	317	942	316
Original λ_{self}[a]	15,757	296,520	1,779,680	1,464,170
Current λ_{self}[a]	398	4512	14,161	9907
λ_{self} remaining (%)	2.5	1.5	0.8	0.7
Original ψ_{self} (years)	211,134	3,545,520	9,978,330	10,542,700
Current ψ_{self} (years)	9383	187,754	517,024	105,723
ψ_{self} remaining (%)	4.4	5.3	5.2	1.0
Original Λ_{self}[b]	10.0	27.7	72.4	76.0
Current Λ_{self}[b]	1.11	1.41	1.91	3.43
Λ_{self} remaining (%)	11.1	5.1	2.6	4.5
Original Ψ_{self} (years/km^2)	134	331	406	548
Current Ψ_{self} (years/km^2)	26.1	58.8	69.7	36.6
Ψ_{self} remaining (%)	19.5	17.8	17.2	6.7

[a]*Levins patch equivalents (see text).*
[b]*Levins patch equivalents/km^2.*

reflected the additional effect of fragmentation. Furthermore, the wren and robin, whose forest distributions originally had greater metapopulation capacity, retained a much smaller percentage (<1%) of that capacity (Table 2). Their original ranges were largely contiguous (Fig. 3).

The robin had by far the smallest extrapolated persistence time (ψ_{self}) compared with its original range value, whereas the other species' reductions were similar to each other. This result was attributable to the distribution of patch sizes. The robin's current range was almost entirely in tiny fragments, whereas the other species either had relatively more, larger patches (wren) or their original ranges also had many small patches (tanager, warbler).

Values for Λ_{self} and Ψ_{self} corroborated these conclusions. Current Λ_{self} was notably higher for the robin than any other species. This again reflected the strongly skewed distribution of patch sizes. Of the very small area remaining, a relatively large proportion was in a single contiguous patch, so the capacity per unit area was particularly high. The persistence time per unit area, however, mirrored the overall persistence time. The robin has a more fragmented range than both the wren and warbler, given our assumption of equal dispersal ability, and so arguably was the more threatened species.

Discussion

Metapopulation capacity and extrapolated persistence time, when calculated with self-colonization, linked widely available, detailed landscape data to species' relative, and in some cases absolute, extinction risk. Other factors also contribute to the extinction risk of the species we considered here. Nonetheless, because fragmentation is an important determinant of a species' Red List category, it is troubling that of the 5 metrics—the 4 we propose and Harris and Pimm's (2008) estimate of remaining area—3 (area, ψ_{self}, and Ψ_{self}) ranked the robin, which is categorized as LC, between the EN tanager and the VU warbler (Table 2). Furthermore, on the basis of the original ranges of these species, 4 of the 5 metrics ranked the robin as most at risk (only Λ_{self} did 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 of extinction risk with species' IUCN categories.

Which metric is most appropriate will depend on the application. If one is concerned about what is happening shortly after fragmentation one would use ψ_{self}, but if one were concerned about what will happen over the long term, one would choose λ_{self}, assuming nothing is done to reverse habitat loss. Many will choose metapopulation capacity as a way to prioritize species and habitats because it emphasizes long-term species support (the ability of the landscape to support the species). Such quantitative methods can also help one prioritize conservation strategies and justify their use to policy makers.

Estimating absolute risk requires knowledge of local extinction rates in isolated patches and species' dispersal tendencies and survival rates when moving between patches. The first of these relations is fairly well known for many groups, and particularly birds (Stratford &

Stouffer 1999; Ferraz et al. 2003; Borgella & Gavin 2005, etc.). Researchers are just starting to understand how individuals move in complex landscapes (Nathan et al. 2008) and what the risks are. Still, decisions about optimal landscape configuration inevitably require some assumption about movement; often this movement is presented in terms of connectivity.

Most spatial ecology models are built on the assumption that dispersal is largely passive and undirected, and these models support the strongly entrenched view that connectivity leads to high patch occupancy. This view may be wrong. Russell et al. (2006) found that the disappearance of birds from small British islands is consistent with risk-based active abandonment of less-isolated islands. Van Houtan et al. (2007) found that birds with wide-ranging tendencies in contiguous Brazilian forest (i.e., good dispersers) tend to disappear first from isolated patches and make longer movements out of patches, which implies active abandonment. Results of both studies contradict the traditional view.

The data-derived log-sech dispersal kernel improves on the traditional exponential decay survival function that tends to eliminate the possibility of long-distance dispersal (Van Houtan et al. 2007). We need to do more. For example, if one were to divide the species into categories depending on dispersal ability, then one might be able to better assess specific species more accurately. Alternatively, one could view landscapes in such a way that patches are considered connected for interpatch migration if they meet a certain dispersal threshold (Keitt et al. 1997) that differs among taxonomic groups. Until direct measurements of species' dispersal traits can be made, current data could be linked to better-known ecological traits (e.g., body size, trophic habit) (Henle et al. 2004) or to taxonomic identity, which would allow extrapolation to suites of species.

A second question is whether one should assess species relative to some absolute standard of fragmentation, relative to other similar species, or relative to their historical range. If the robin and wren, which likely once had large, relatively contiguous habitat distributions, are poorly adapted to live in small fragments, then they might well have a greater extinction risk than the tanager and warbler. Conversely, 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 (Harris & Pimm 2004). A potential way to answer this question, which will be part of our next analysis, is to compare data on population decline with absolute and historically relative measures of fragmentation. Each of the landscape-level metrics we used was the sum of the contributions of the individual patches. Thus, we could rank patches either by their own capacity (which includes their receipt of incoming colonists) or by their contribution to the overall landscape (which in-

cludes their provision of colonists to other patches). One can also create new patches or enlarge or join existing patches to identify the exact block, or corridor of land, to restore. Thus, our method can be used to optimize plans to conserve or restore landscapes to produce the maximum capacity increase for either a targeted species or a complete assemblage.

Acknowledgments

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