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Methods and models for identifying thresholds of habitat loss

Deyi Yin, Shawn J. Leroux and Fangliang He

D. Yin and F. He (fhe@ualberta.ca), SYSU-Alberta Joint Lab for Biodiversity Conservation, State Key Laboratory of Biocontrol and School of Life Sciences, Sun Yat-sen Univ., Guangzhou, P. R. China. FH also at: Dept of Renewable Resources, Univ. of Alberta, Edmonton, Alberta, Canada. – S. J. Leroux, Dept of Biology, Memorial Univ. of Newfoundland, St John's, Newfoundland Canada.

There is mounting evidence that many taxa respond in non-linear ways to perturbation (i.e. deviations from a natural trajectory brought on by an external agent), and many statistical, physical and ecological methods have been developed to detect the critical points or thresholds of perturbation. The majority of these methods define thresholds as the perturbation points causing abrupt ecological response, but in reality most species or ecosystems do not show a break point response but more gradual transitional change to perturbation. We develop a new method which delineates thresholds as a region in which the slope of the relationship between ecological response (y) and perturbation (x; e.g. habitat loss) is larger than 1: $|dy/dx| \geq 1$, where both x- and y-axes are scaled to (0, 1) range. The lower end of threshold zones so defined is of particular ecological interest because it is the smallest x that may trigger impending catastrophic response to a small change in x. We derived two landscape models (edge length and the number of patches of species distribution) and two biodiversity models (endemics–area relationship and half-population curve) to test this method. We applied our zonal thresholding method to these four models fit to empirical data of two forest plots to detect thresholds of species distribution to habitat loss. The two landscape metric models predict that no species could tolerate more than 40% of habitat loss and these thresholds can be much lower for relatively rare species with occupancy < 0.4 and for aggregated habitat loss compared to random habitat loss. The half-population model leads to a similar threshold level of 40% habitat loss. Overall, we suggest the maximum permissible habitat loss threshold to be between 0–40%, depending on the pre-disturbed occupancy (or abundance) of a species. This habitat loss threshold falls within the otherwise wide range of thresholds calculated from conventional methods. Our study contributes novel methods and models to quantify the effect of habitat loss on species distribution and diversity in landscapes with potential for conservation applications.

Picking a leaf off a plant is unlikely to have any effect on the plant. How about two leaves? Or continuously picking off leaves till all the leaves are gone? Obviously, no plant can afford to lose all of its leaves, but is there a tipping point at which a plant can no longer afford to lose leaves? Similarly, is there a threshold by which a species can no longer afford to lose its habitat? There is growing theoretical and empirical evidence demonstrating ecological thresholds – an abrupt change in ecological phenomena (Muradian 2001, Groffman et al. 2006) and the mechanisms underlying such changes (Lande 1987, Bascompte and Solé 1996, Pan et al. 2000, Huggett 2005, Radford et al. 2005, Andersen et al. 2009, Burdon et al. 2013). For example, Pan et al. (2000) report abrupt changes in the phosphorus-limited Everglades ecosystem in the United States where, at a certain phosphorus concentration level (11 ug l^{-1}), a small change in phosphorus concentration leads to the collapse of the macroinvertebrate assemblage. Similarly, Radford et al. (2005) show evidence for a threshold response in species richness of woodland-dependent birds to habitat cover in Victoria, Australia. Despite the growing evidence for ecological thresholds, species populations or assemblages may not always show a sudden response to change in their environment and if they do show a response the shapes of these responses can be quite different (Swift and Hannon 2010, Toms and Villard 2015). How to detect such thresholds or sensitive zones has been a challenging problem but is critically important to ecosystem management (Svancara et al. 2005, Ficetola and Denoël 2009, Suding and Hobbs 2009, Rondinini and Chiozza 2010, Samhouri et al. 2010, Swift and Hannon 2010, Matthews et al. 2014).

Habitat destruction, resulting from human activities and environmental changes, has been recognized as one of the chief culprits of biodiversity loss and change over time (Foley et al. 2005, Jager et al. 2006). It is therefore not surprising that much of the research on ecological thresholds has focused on investigating threshold responses of biodiversity to habitat loss and fragmentation (Andrén 1994, Bascompte and Solé 1996, Fahrig 2003, Swift and Hannon 2010, Richmond et al. 2015). For example, Richmond et al. (2015) report evidence of abrupt declines in forest bird species richness in Ontario, Canada with 4–45% of coniferous, deciduous or mixed wood forest cover remaining. Following an initial loss of species after habitat destruction, the extirpation process of local populations is accelerated by the compounding effect of habitat loss and fragmentation

(Bascompte and Solé 1996, Fahrig 2003, Swift and Hannon 2010) which may eventually push the ecosystem to an alternative state (Scheffer et al. 2001). Methods to identify possible ecological thresholds are critical for designing robust habitat preservation and restoration plans to avoid or mitigate undesirable alternative ecosystem states (Fahrig 2001, Suding and Hobbs 2009).

A survey of the literature reveals that typical threshold relationships between habitat amount and environmental variables fall into three types according to their shapes (Fig. 1). The first type (type I), for simplicity, is characterized as a V-shaped (or Λ) threshold composed of two straight lines with different slopes (Fig. 1a) although in reality few ecological responses would show an abrupt breakpoint but a continuous (narrow) transitional zone (Fig. 1a). For instance, the probability of occurrence of spotted salamander and wood frog in vernal pools in eastern Massachusetts, USA respond to forest cover with a Λ-shaped threshold (Homan et al. 2004). The second type (type II) is an S-shaped threshold, which is an asymptotic curve with a region of rapidly accelerating change in the slope (Fig. 1b). For example, several herb and fern species show S-shaped responses to the change in habitat amount and two levels of fragmentation in Spain (Rueda et al. 2015). The third type (type III) is a monotonically increasing or decreasing curve without an abrupt transition but a fast changing zone (Fig. 1c). For example, the species extinction curve caused by the loss of habitat is characterized by this type of threshold as species loss is initially slow but accelerates as habitat loss continues (He and Hubbell 2011).

There exist a large number of methods for identifying the different types of ecological thresholds (Table 1), including those based on statistical inference (Chiu 2002, Toms and Lesperance 2003, Qian et al. 2003), methods that are introduced from physics (Gardner et al. 1987, Stauffer and Aharony 1994, Solé et al. 2004) and ecological methods (Lande 1987, Bascompte and Solé 1996, Hill and Caswell 1999, Parker and MacNally 2002, Homan et al. 2004, Radford et al. 2005). All of these methods can, in principle, be applied to detect ecological thresholds in a diversity of ecological responses from population dynamics (e.g. survival, dispersal success, growth rate), to community metrics (e.g. species richness), to landscape metrics (e.g. number of patches, size of the largest patch) of species distribution.

While ecological thresholds are usually defined as 'points or zones of abrupt change in relationships' (Huggett 2005, Toms and Villard 2015), the identification of thresholds varies from different types of response curves. For V-shaped thresholds, the point at which the two lines join is commonly defined as the threshold and several statistical methods have been developed to identify V-shaped thresholds, for example, bent-cable regression (Chiu 2002), a nonparametric method based on the reduction of deviance (Qian et al. 2003), and piecewise regression (Toms and Lesperance 2003). Despite that point thresholds are easy to quantify, rarely do ecological responses have true point thresholds and even the V-shaped threshold is just a convenient approximation of a more general zonal threshold as shown in Fig. 1a. Zonal thresholds are particularly conspicuous for S-shaped (Fig. 1b) or monotonic response curves (Fig. 1c).

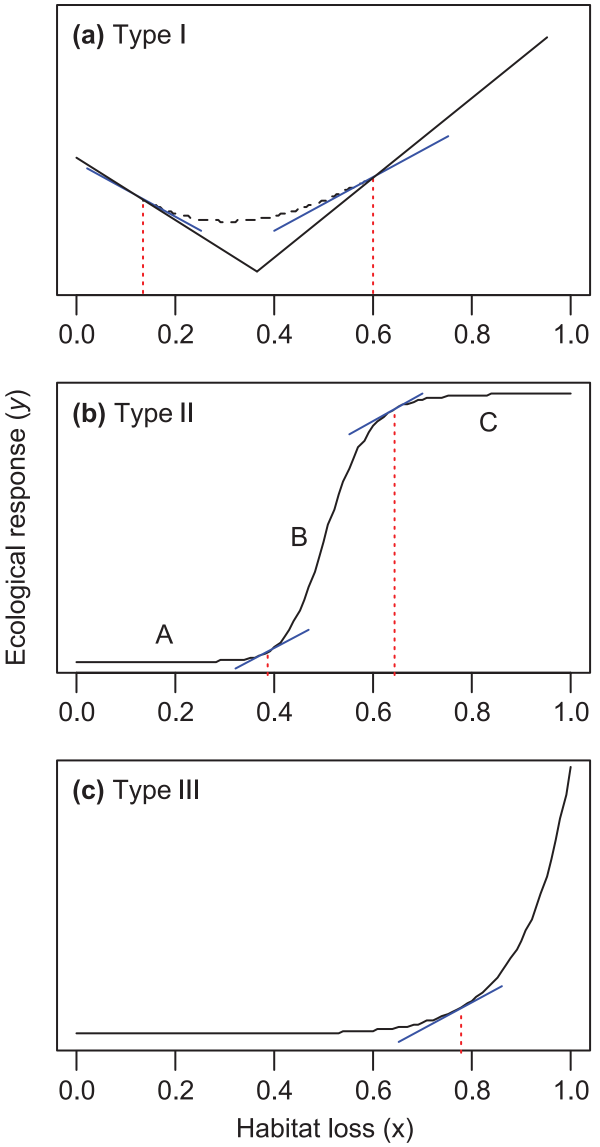

Figure 1. Three types of responses of ecological variables to the loss of habitat. The first type is V-shaped composed of two straight lines with different slopes (a). The second type is S-shaped which is asymptotic curve with a region of rapid change in the slope (b). The last type is a monotonically increasing curve without an abrupt transition but a fast changing zone (c). Red dashed lines indicate the x values at which $|dy/dx| = 1$. The blue lines indicate the slope of $|dy/dx| = 1$.

The identification of threshold zones is important as it may enable resource managers to define the minimum and maximum critical points where abrupt ecological changes occur. The minimum point of a threshold zone has particular applied interest because it identifies the first threshold of concern. In contrast, the maximum point of a threshold zone, similar to the conventional critical point of V-shaped thresholds, identifies a point where environmental perturbations have led to ecological changes that are not easily reversible. To identify the minimum (and maximum) threshold points, we first need to define threshold zones. The definition of threshold zones is a mathematically elusive question because most ecological

Table 1. A summary of tools for identifying ecological thresholds. The types of thresholds are in correspondence with those shown in Figure 1 and described in the main text (i.e. type I = V-shape, type II = S-shape and type III = monotonic curve).

Categories	Methods	Data requirement	Model outputs	Type of threshold	References
Statistical inference	Non-parametric model	observations of response variables along a perturbation gradient	model fit predicting an abrupt transition	type I, II, III	Qian et al. (2003)
	Piecewise regression model	observations of response variables along a perturbation gradient	model fit predicting an abrupt transition	type I	Toms and Lesperance (2003)
	Bent-cable regression model	observations of response variables along a perturbation gradient	model fit predicting a sharp or smooth transition	type I	Chiu (2002)
Physical methods	Percolation theory	occupancy (presence/absence) map of species	landscape connectivity, largest patch size or other related response variables	type II	With and Crist (1995)
	Self-organization process	simulated landscape occupancy of species	simulated generalized fractal dimensions	type I, II	Solé and Manrubia (1995)
Ecological approaches	Theoretical methods: Patch occupancy model	real or simulated occupancy (presence/absence) map of species	dynamics of meta-populations balanced by extinction and colonization	type III	Lande (1987)
	Simulation: cellular automaton	real or simulated occupancy (presence/absence) map of species	dynamics of populations based on pre-set of rules	type III	Bascompte and Solé (1996), Hill and Caswell (1999), With and King (1999b)
	Neutral landscape model	landscapes with two/multiple randomly distributed habitat types or hierarchical random landscapes	neutral landscape	type II	With (1997), With and King (1997)
	Empirical method	observations of response variables along a perturbation gradient	usually apply statistical methods above to detect thresholds	type I, II, III	Parker and MacNally (2002), Homan et al. (2004)

response curves are continuous functions of underlying change in habitat. Facing this difficulty, there have been some attempts to define thresholds for such continuous curves. For instance, Swift and Hannon (2010) suggested the midpoint of the curve around which the slope changes as thresholds for the S-shaped relationship, while Fahrig (2001) proposed a threshold at the point where the response variable starts to show an accelerating change. For many response curves (e.g. types I and III), however, a rigorously defined 'accelerating point' (i.e. inflexion point) does not actually exist. Thus, proven quantitative methods for defining critical threshold points and threshold zones are not yet available (Ficetola and Denoël 2009) but urgently needed because continuous responses are widespread in ecology.

In this study, our objectives are to model the effects of habitat loss on the distribution of species populations and species diversity. In particular, we first propose a method to define thresholds for continuous ecological variables that do not have abrupt responses to perturbations. We then present four metrics to model the effect of habitat loss on species distribution. They include two landscape metrics: edge length and the number of patches of species distribution and two biodiversity metrics: endemics–area relationship and half-population curve under scenarios of habitat loss for conservation concern. We finally apply our new thresholding method to the four models to detect habitat loss thresholds for two stem-mapped empirical forest data sets.

A new method for detecting ecological thresholds to habitat loss

Here, we propose a new method for detecting ecological thresholds that focuses on a *zone* of change in ecological relationships. Our method defines a threshold as a region in which the slope of the relationship between ecological response (y) and perturbation (x; e.g. habitat loss) is larger than 1: $|dy/dx| \geq 1$, where both x and y axes are scaled to (0, 1) range to standardize the effect of measurement units between x and y. The threshold so defined describes the degree of sensitivity of dependent variable y in response to the change in x. When slope < 1, the change in y is slower than the change in x, i.e. x does not trigger as much change in y, as illustrated by the region A or C of Fig. 1b. When x enters region B, y starts to change faster than that in x, triggering an accelerating change in y before slowing down again in region C (Fig. 1b) or till the entire landscape is destroyed (Fig. 1c). In the case of a V-shape curve (Fig. 1a), our method no longer considers the conventionally identified breakpoint as a threshold but the two points at which $dy/dx = 1$ and -1. Of these two thresholds which define a threshold zone, the lower threshold point is of particular ecological interest because it is the smallest x that may trigger impending catastrophic response to a small change in x. This lower threshold thus is a useful early warning sign and could serve as the first concern to action.

Habitat loss and fragmentation are two intimately related forms of habitat destruction. Although it is possible to separate their respective effects under some specific circumstances (Yaacobi et al. 2007), the effects of habitat loss and fragmentation in general are compounded and are not separable because losing habitat almost always accompanies fragmentation and vice versa (Bascompte and Solé 1996, Fahrig 2003, Swift and Hannon 2010, Haddad et al. 2017). Here we do not explicitly distinguish habitat loss and fragmentation but focus on the consequences of habitat loss by understanding that a change in habitat could lead to fragmentation.

Habitat loss models for the distribution of species populations and diversity

Ecologists have measured the response of many ecological variables to habitat loss (Bascompte and Solé 1996, Hill and Caswell 1999, With and King 1999a, 1999b, Fahrig 2001). These include variables describing population dynamics (e.g. survival, dispersal success, growth rate), landscape metrics of species distribution (e.g. number of patches and size of largest patch), and diversity indices (e.g. richness). Among the many landscape metrics, edge length which is the total amount of edge of a species' distribution and the number of patches which is the total number of disconnected patches are two of the most widely used metrics for describing the effect of fragmentation on species distribution in landscapes (Wang et al. 2014). These two metrics are relevent for population migration, predation and growth (Swift and Hannon 2010), especially for those species with low migration ability. For example, Zurita et al. (2012) show that edge effects influence habitat suitability of most of the 46 bird species surveyed in an Atlantic forest of Argentina and Paraguay. Likewise, the number of patches is a fundamental determinant of persistence probability for species living in metapopulations (Hanski 1999). The relationships between habitat loss and edge length or number of patches could provide significant information and guidelines for conservation management. As for diversity indices, it goes without saying the great importance of the effect of habitat loss on species extinction and endangerment concern (IUCN 2013). Models predicting the relationship between habitat loss and the rate of species extinctions or endangerment are of critical importance.

Landscape metrics for species distribution

Edge–length model

He and Hubbell (2003) developed models for edge length and the number of patches of a species distribution. These models relate these two metrics with key ecological variables such as abundance, spatial dispersion of a species and spatial scale. The edge length model of a species' distribution counts the total number of joins where occupied cells abut empty cells and has the form

$$L = 2\sqrt{a}\,Jp(1-p) \tag{1}$$

where a is the area of the grid cell of a landscape map where the species is distributed, J is the total number of neighboring joins (i.e. two neighboring cells that share a common edge) in the lattice and $J = 2J_xJ_y - J_x - J_y$, where J_x and J_y are the number of cells along the horizontal and vertical sides of a regular grid map, respectively, and p is the probability that a cell is occupied (i.e. the occupancy of the species in the landscape map).

It is straightforward to generalize the edge length given by Eq. (1) to consider habitat loss. By definition habitat loss refers to the loss of occupied sites (e.g. forested areas for trees). For those areas that are not occupied, changes would not make any difference to occupancy. Thus, we can simply replace p in Eq. (1) by $(1–x)p$, where x is habitat area lost, leading to an edge length model of habitat loss

$$L = 2\sqrt{a}\,J(1-x)p[1-(1-x)p] \tag{2}$$

where x is the proportion of destroyed habitats. This model defines the relationship between L and habitat loss x for a given occupancy p and cell size a. Their slope is: $dL/dx = 2\sqrt{a}\,Jp[2(1-x)p-1]$. We can also easily solve for x that maximizes edge length: $x_{\max} = 1-1/(2p)$. Substituting this $x_{\max}$ into Eq. (2), we obtain the maximum edge length of a species: $L_{\max} = \sqrt{a}\,J/2$. We now scale L in Eq. (2) to (0, 1) range by $L/L_{\max}$, denoted as λ_L:

$$\lambda_L = 4(1-x)p[1-(1-x)p] \tag{3}$$

This scaled edge length is illustrated in Fig. 2 for different p values. Its slope is $d\lambda_L/dx = 4p[2(1-x)p-1]$. To identify a threshold zone, we need to find x values where the slope is either larger than 1 or smaller than –1. These can be easily solved by setting $|d\lambda_L/dx| = 1$, resulting in lower $x_{\text{slope}} = 1-\frac{4p+1}{8p^2}$ and upper $x_{\text{slope}} = 1-\frac{4p-1}{8p^2}$. These critical slopes are also indicated in Fig. 2.

It is important to note that the $\lambda_L \sim x$ relationship (Eq. 3) and $L \sim x$ relationship (Eq. 2) have the same shape but at different scales. Eq. (3) is a general form that does not require knowledge about cell size (a) or specific shape of study landscapes (because parameter J disappears after scaled to (0, 1) range). The model applies as long as the occupancy of species in landscapes is known.

In landscape ecology, perimeter-area ratio is also used to quantify landscape fragmentation (Wang et al. 2014). This metric can be easily derived by dividing Eq. (3) by area $(1–x)p$, leading to $\lambda_{\text{perimeter-area}} = 4[1–(1–x)p]$. This metric linearly increases with habitat loss (x), showing no threshold. As such, we will not further analyze this metric.

The above edge length models are derived from the assumption of the independence of cell occupancy. For randomly distributed species, Eq. (3) describes perfectly the relationship between edge length (λ_L) and habitat loss (x) as shown in Fig. 2 (left column). For non-randomly distributed species, Eq. (3) still holds but takes a general form as:

$$\lambda_L = c(1-x)p[1-(1-x)p] \tag{4}$$

where c is a general parameter replacing value 4 in Eq. (3) and p here is not the observed occupancy of an empirical species but is an occupancy equivalent to its random distribution counterpart, i.e. the random p that would achieve the same amount of edge length as the aggregated p. Both c and p in Eq. (4) are obtained by fitting the model to observed edge length of empirical species. The estimated p from Eq. (4) is generally smaller than the observed p for aggregated species.

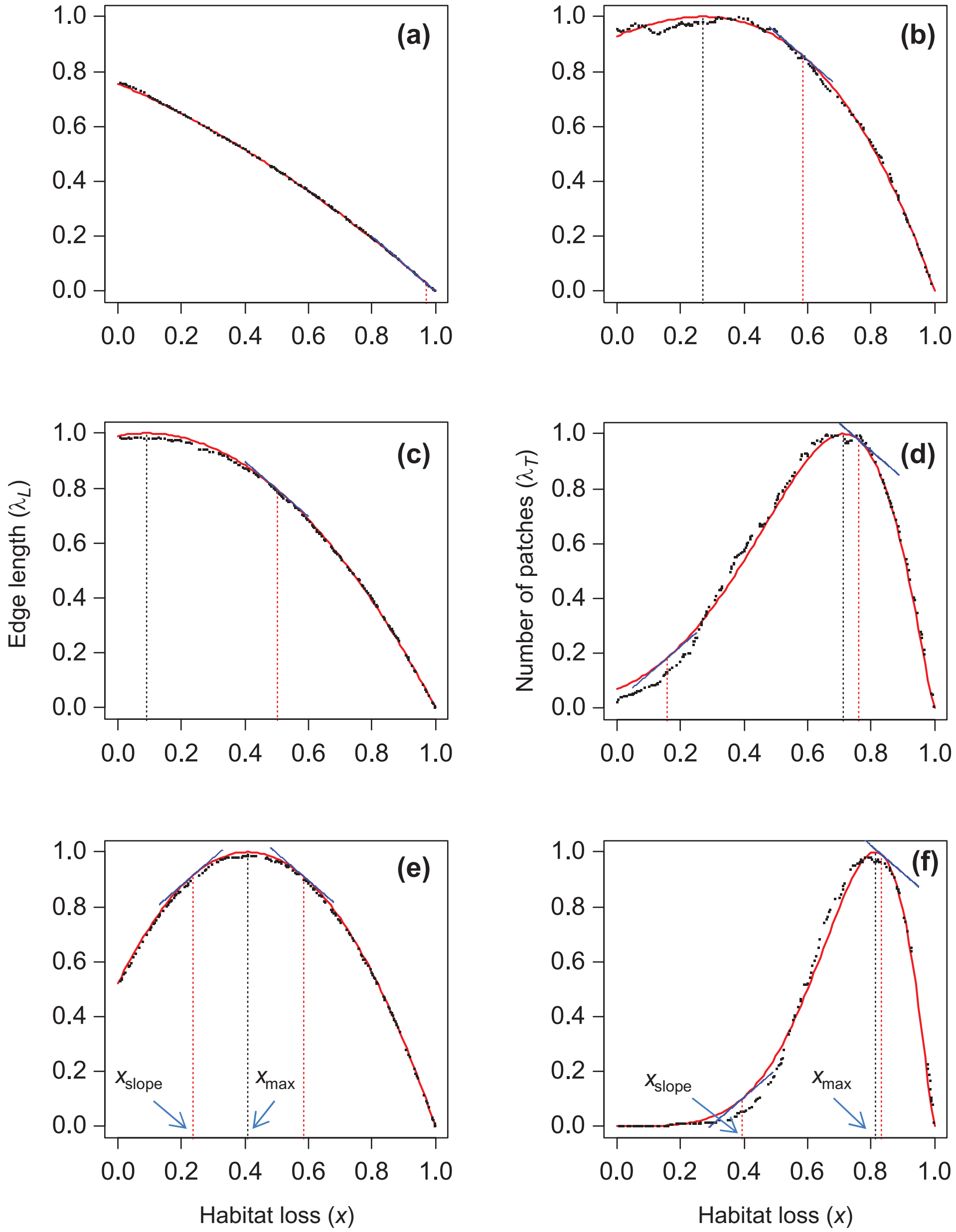

Figure 2. Relationships between edge length (left column, a, c, e) and number of patches (right column, b, d, f) and habitat loss (x), i.e. Eq. (3) and (6), for a simulated random distribution of species with occupancy $p = 0.25$ (a and b), 0.55 (c and d) and 0.85 (e and f). The black dots show the edge length or number of patches for each random distribution of species. The red solid lines are the relationships predicted from Eq. (3) (a, c, e) and fitted from Eq. (6) (b, d, f). The black dashed lines indicate the habitat loss x at which the maximum edge length (a, c, e) or patch number (b, d, f) is reached. Panel (a) indicates that edge length–habitat loss curves for species with low occupancy do not have a peak value. Red dashed lines indicate the x values at which $|dy/dx| = 1$ and blue lines show the slope of $|dy/dx| = 1$.

Number of patches model

We now turn to model the number of patches for species distributions in landscapes. A patch could be defined as a group of occupied cells which are connected side by side (circles in Fig. 3a). The relationship between the number of patches and probability of occupancy (p) has the form (He and Hubbell 2003)

$$T \propto p^m (1-p)^j \tag{5}$$

where m is the number of occupied cells for a patch, j is the number of occupied and empty joins for that patch.

We can easily generalize Eq. (5) to consider the effect of habitat loss by scaling T by its maximum (i.e. $\lambda_T = T/T_{\max}$), resulting in:

$$\lambda_T = \frac{(m+j)^{m+j}}{m^m j^j}[(1-x)p]^m[1-(1-x)p]^j \tag{6}$$

where x is the proportion of habitat loss, p is the occupancy of a given species, m and j have the same interpretations as in Eq. (5) but are numerically different because the loss of habitat would change their values. They are obtained by fitting the observed patch number and habitat loss of

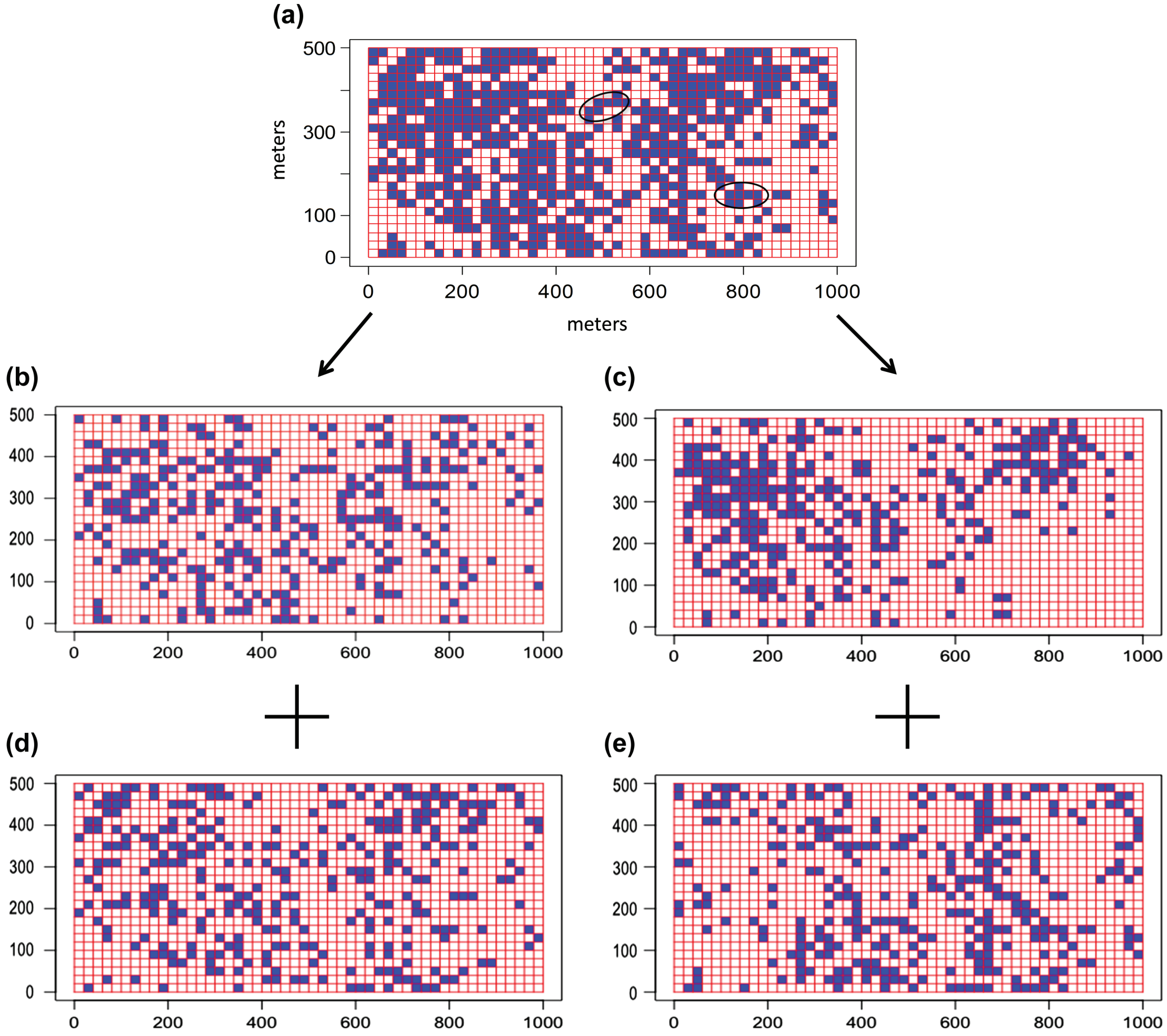

Figure 3. Illustration of habitat patches and the distribution of *Syzygium kwangtungense* (abundance = 1364) in Heishiding plot at 20 × 20 m grid size and two scenarios of habitat removal. (a) shows the original distribution of the species (occupancy = 0.5008) before habitat loss. (b) is the remained distribution after half of the occupancy (= 0.2504) being randomly removed and (d) is the distribution that is destroyed. (c) is the remained distribution after aggregated removal of half of the occupancy and (e) is the destroyed distribution. The circles in (a) illustrate two examples of patches.

empirical species. Eq. (6) describes well the relationships between patch number and habitat loss for both randomly distributed (Fig. 2) and empirical species (Results).

Biodiversity metrics for species distribution

Endemics–area relationship

The loss of habitat could drive local species to instantaneous extinction. This process is modeled by the endemics–area relationship (EAR) (Harte and Kinzig 1997, He and Hubbell 2011). Here we use this relationship to quantify thresholds of habitat loss where extinctions are most prevalent. A general EAR model can be derived from the probability of finding the n^{th} nearest individual of a species from a random location in a landscape. This probability is given by a cumulative binomial distribution (Eberhardt 1967):

$$F_n(a) = \sum_{i=n}^{N}\left[\binom{N}{i}\left(\frac{a}{A}\right)^{i}\left(1-\frac{a}{A}\right)^{N-i}\right] \qquad (7)$$

where N is the abundance of the species in a landscape, A is the total area of the landscape, and a is the searching (sampling) area required to encounter the n^{th} nearest individual. Equivalently, if a is considered as the area destroyed, Eq. (7) is the probability that n of N individuals of the species is lost with the loss of a habitat.

The EAR model can be easily derived from the above probability by setting $n = N$ (i.e. the area a required to encounter the last individual, the N^{th}). This endemic probability is: $F_N(a) = \left(\frac{a}{A}\right)^{N}$. Summing this probability across species leads to the EAR (He and Hubbell 2011): $s(a) = \sum_{i=1}^{S}\left(\frac{a}{A}\right)^{N_i}$, where S is the total number of species in the extent of the landscape A. The scaled EAR (i.e. the relative EAR) is

$$\lambda_{\text{EAR}}(x) = \frac{1}{S}\sum_{i=1}^{S} x^{N_i} \qquad (8)$$

where N_i is the abundance of the i^{th} species in A and $x = a/A$. The slope of this EAR is: $\dfrac{d\lambda_{\text{EAR}}}{dx} = \dfrac{1}{S}\sum_{i=1}^{S} N_i x^{N_i - 1}$

Half-population curve

Similarly, we can derive an EAR model for losing half of a population for each of the S species, i.e. the probability for losing half of abundance of a species. We are interested in deriving a half-population EAR because the IUCN red list criteria consider species that have lost more than 50% of their original abundance as 'Endangered' (IUCN 2013). Consequently, identifying the half-population EAR as a function of habitat loss has considerable conservation value. Directly from Eq. (7), this half population probability is $F_{N/2}(a) = \sum_{j=[N/2]}^{N}\left[\binom{N}{j}\left(\frac{a}{A}\right)^{j}\left(1-\frac{a}{A}\right)^{N-j}\right]$ $= 1 - \sum_{j=0}^{[N/2]-1}\left[\binom{N}{j}\left(\frac{a}{A}\right)^{j}\left(1-\frac{a}{A}\right)^{N-j}\right]$, where $[N/2]$ denotes the smallest integer larger than $N/2$. This probability describes that half of the N individuals of a species are contained in the area a (i.e. those that are lost if a is destroyed) and half are still at large (those that remain). Summing this probability across all species S, we obtain a scaled (relative) half-population EAR model:

$$\lambda_{N/2}(x) = 1 - \frac{1}{S}\sum_{i=1}^{S}\sum_{j=0}^{[N/2]-1}\binom{N_i}{j}x^{j}(1-x)^{N_i - j} \qquad (9)$$

The slope of this half-population EAR is:

$$\frac{d\lambda_{N/2}}{dx} = \frac{1}{S(1-x)x}\sum_{i=1}^{S}\sum_{j=0}^{[N/2]-1}(xN_i - j)\binom{N_i}{j}x^{j}(1-x)^{N_i - j}$$

Although the above EAR models are derived from randomly distributed species, He and Hubbell (2011) proved (see their Supplementary Information E) that the EAR models are invariant to spatial aggregation and the above Eq. (8) and (9) are general EAR models applicable to any empirical system. However, it is useful to note a key difference between these two EAR models. $\lambda_{\text{EAR}}(x)$ describes the global loss of species (i.e. extinction from the study landscape A) due to habitat destruction, while $\lambda_{N/2}(x)$ describes the local loss of species (i.e. extirpation from local areas within the landscape A).

Applying the habitat loss models and our thresholding method

Data

We fit the above four models (Eq. 4, 6, 8, 9) to two empirical data sets and apply our method of detecting ecological threshold zones to each model. The four models allow us to predict minimum habitat loss levels (i.e. habitat loss that does not lead to large changes in species distribution). These two empirical data sets are the distribution and abundance of tree/shrub species in two study plots from the CTFS-ForestGEO network (<www.forestgeo.si.edu/>) that mapped the location of every stem of each species in respective plots. The first plot describes the distributions of 213 tree/shrub species with 213 969 stems (with diameter at breast height ≥ 1 cm) in a 50 ha (1000 × 500 m) subtropical evergreen broadleaved forest in Heishiding Nature Reserve (HSD) in southern China (Yin and He 2014). The second plot describes the distribution of 302 tree/shrub species with 243 541 stems in a 50 ha lowland tropical forest located in Barro Colorado Island (BCI), Panama (Condit et al. 2000). For each plot, the spatial location of each individual stem and the abundance of each species are known.

Model fit and habitat loss scenarios

To fit Eq. (4) and (6) to the empirical data, we generated a 1000 × 500 m map with grid cell size of 20 × 20 m for each species (e.g. Fig. 3a). To assess the effect of habitat loss on the landscape and biodiversity metrics, we implemented two scenarios of habitat loss. The first scenario assumes random removal of habitat (e.g. Fig. 3b, 3d). The second describes aggregated removal of habitat (e.g. Fig. 3c, 3e), which begins with randomly selecting 5 occupied cells as removal centers. The preset rules of aggregated removal are: 1) we only considered removing cells that are less than or equal to 60 m from a removal center; 2) occupied cells within the 60 m circle have the removal probability $p = e^{-\eta \times dist}$ according to their distance from the removal center, where η controls the intensity of habitat removal. The probability decreases with the distance from the removal center. In this study, we used $\eta = 0.25$ to assess the effect of aggregated habitat loss on landscape and biodiversity metrics. Our results are qualitatively robust to variations in η values and distribution map cell sizes (e.g. 10 × 10 m and 50 × 50 m).

For the landscape metrics Eq. (4) and (6), habitat reduction, i.e. x, varies from $x = 0$ (intact habitat) to 1 (all habitat is destroyed) by 0.01 step increments. At each x level, we measured edge length and the number of patches. Equations (4) and (6) were then fitted to the observed edge length and number of patches for the random and aggregated removal scenarios, respectively.

For the biodiversity metrics (Eq. 8, 9), we also varied habitat destruction from $x = 0$ to 1 and then counted the number of species going extinct (Eq. 8) or losing half of population size (Eq. 9) following habitat loss.

Determining habitat loss thresholds

Identifying maximum permissible habitat loss, which is of great conservation concern, is an important goal but something challenging to determine in practice. Our zonal threshold method offers a way to determine maximum permissible habitat loss (i.e. the lower x_{slope}; Fig. 2) and we apply this method to the four species distribution models to identify habitat loss thresholds for the HSD and BCI species distribution. For comparison, we also identify the conventional peak breakpoint habitat loss ($x_{\max}$; see Fig. 2) whenever $x_{\max}$ exists ($x_{\max}$ only exists for type I response curve, not type II and III).

Results

We fit the two landscape metrics (Eq. 4, 6) to each of the 213 HSD and 302 BCI plot species for the two habitat removal scenarios. As example, Fig. 4–5 present the modeled results for three species from the HSD plot under random and aggregated habitat loss. For each species, we identify four thresholds: 1) lower x_{slope} for edge-length threshold, 2) $x_{\max}$ for edge-length threshold, 3) lower x_{slope} for number of patches threshold, and 4) $x_{\max}$ for number of patches threshold (Fig. 6). As it is clear from the above analytical results, thresholds of a species are dependent on occupancy and spatial distribution of each species and also on the metric (edge length or number of patches) that is used. For the edge length model and randomly distributed species with occupancy < 0.5, our analytical result shows that the peak threshold $x_{\max}$ $\left(x_{\max} = 1 - \frac{1}{2p}\right)$ and low x_{slope} threshold $\left(x_{\mathrm{slope}} = 1 - \frac{4p+1}{8p^2}\right)$ do not exist. For empirical species, this is true for the low x_{slope} threshold (Fig. 6a) but not true for $x_{\max}$, i.e. $x_{\max}$ can exist even when occupancy < 0.5 (Fig. 6b).

The low x_{slope} thresholds are always smaller than the conventional $x_{\max}$ threshold (Fig. 2, 6). Also random habitat loss leads to higher low x_{slope} thresholds than does aggregated habitat loss (compare the black and red open dots versus the green and blue dots in Fig. 6a, c). The low x_{slope} thresholds in Fig. 6a and *c* (the *y*-axes) show that regardless of the occupancy of a species ~40% is the maximum habitat loss permissible by the metrics of edge length and number of patches, which means even the most abundant species (i.e. occupancy = 1) can tolerate at most 40% of the habitat loss without a sharp decline in edge length and number of patches of their distribution. However, it is important to note that for most species with low occupancies, the low x_{slope} are much smaller than this 40% threshold (Fig. 6a, c). Specifically, for those species with occupancies < 0.4, no habitat loss should be permitted, i.e. for small-range species (< 0.4), any habitat loss would inevitably increase the edge length and the number of patches of the species. This result suggests that, by the metrics of edge length and number of patches, the maximum permissible habitat destruction varies from 0 up to 40%, depending on the occupancy of the species of concern. This range of permissible habitat destruction could also approximately be derived from the empirical relationships, $y = 1 - a\exp(-bp)$, between low x_{slope} and occupancy as given in Fig. 6. Note that the upper x_{slope} for the edge length and patch number metrics (Eq. 4, 6) can

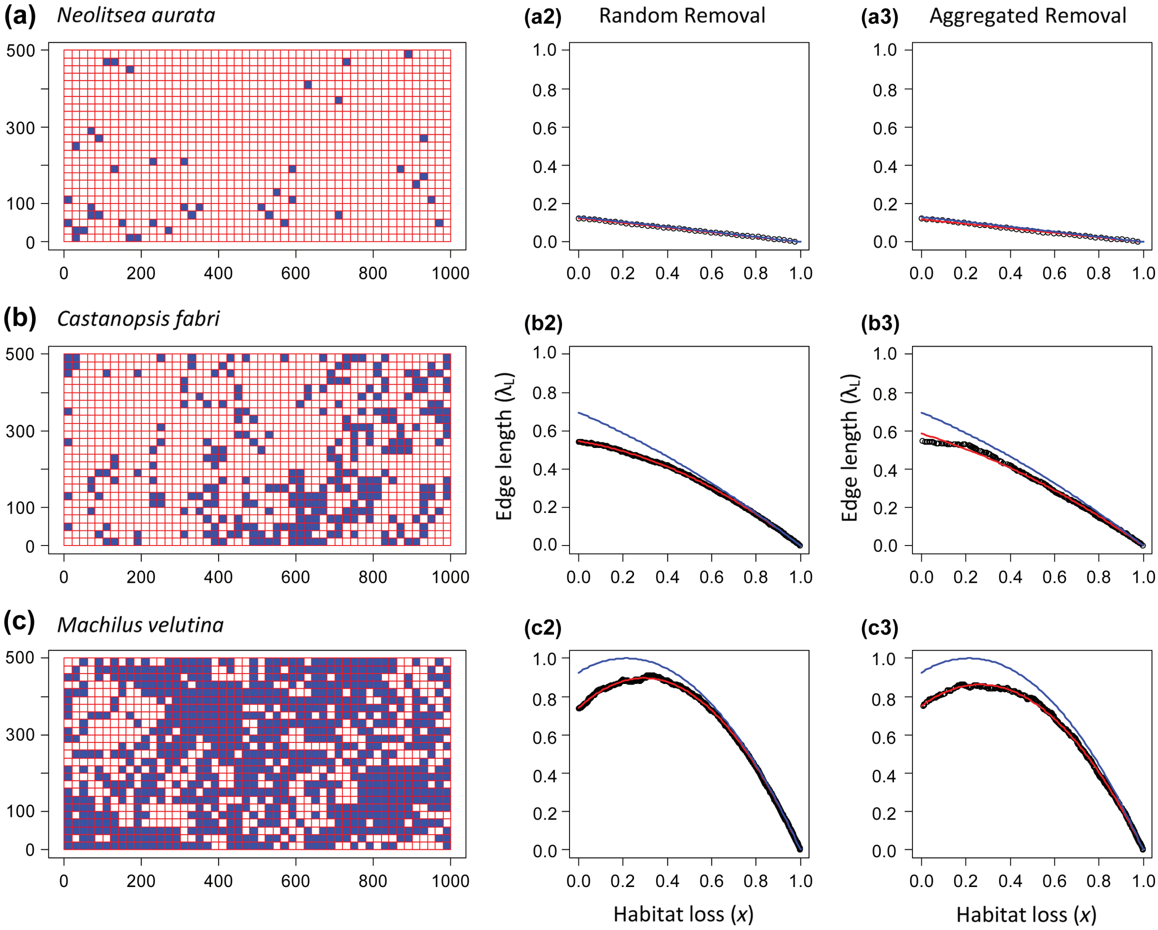

Figure 4. Relationships between habitat loss and edge length for *Neolitsea aurata*, *Castanopsis fabri* and *Machilus velutina* from the HSD plot. The left column shows the distributions of the three species at cell size = 20 × 20 m with abundances = 52, 506 and 2296, respectively. The middle and right columns represent the edge length–habitat loss relationships for random and aggregated habitat removal, respectively. The dots are the observed edge length at each habitat loss level. The red curves are the fitted Eq. (4). For comparison, the random edge length Eq. (3) is also shown (blue curves) that over-predicts the edge length of empirical species.

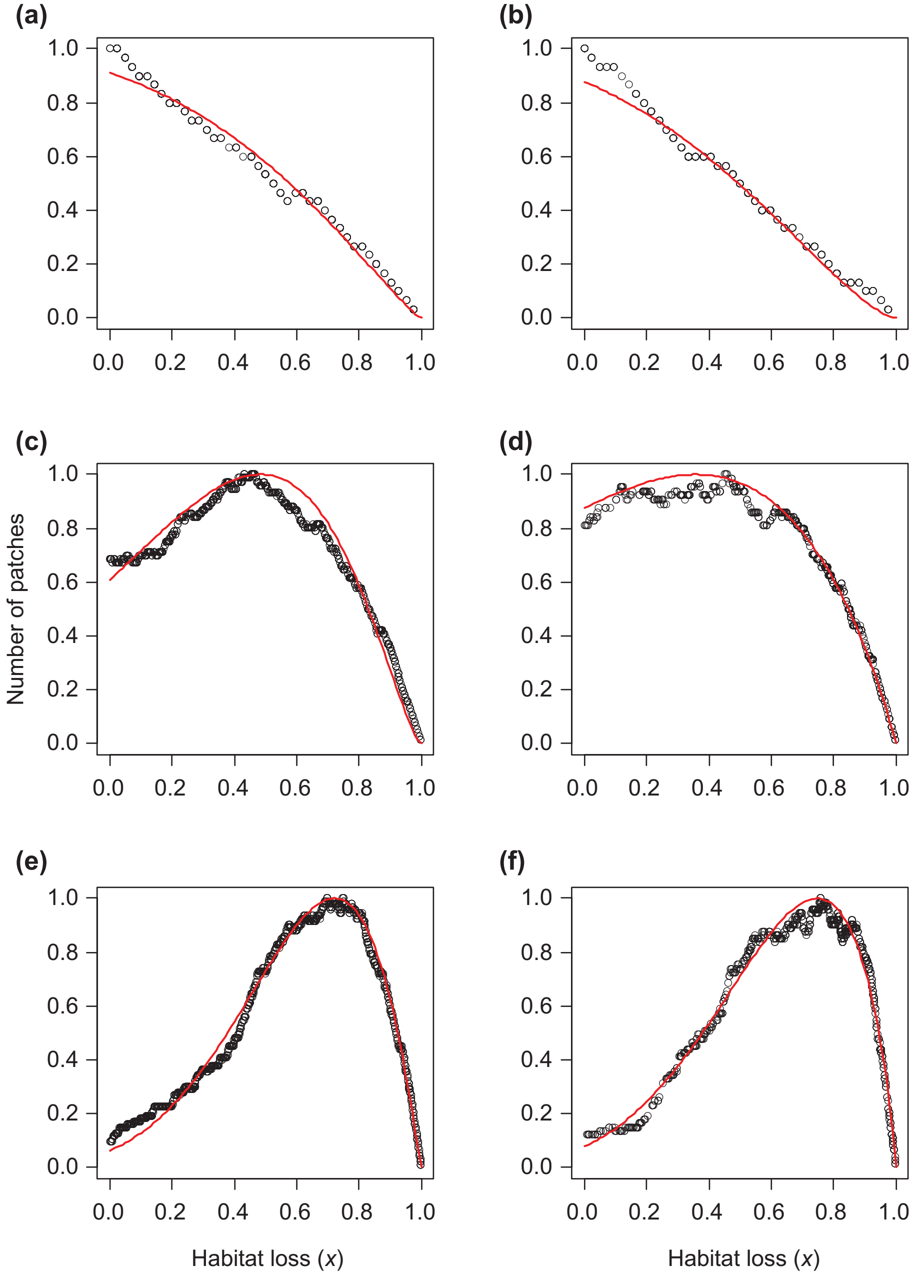

Figure 5. Relationships between habitat loss and the number of patches for the same three species shown in Fig. 4. The left column shows the relationships between habitat loss and patch number for random removal of habitat while right column is for aggregated habitat loss. The dots are the observed number of patches at each habitat loss level. The red curves are the fitted Eq. (6).

also be obtained for a species but there is no practical interest in the estimate for upper x_{slope} because it is larger than x_{max} in most cases.

The endemics–area curves and the half-population endemics–area curves are solely dependent on species abundance and are robust (invariant) to spatial distributions of species and different habitat removal patterns, as shown by the HSD and BCI species (Fig. 7). The EAR low x_{slope} thresholds are 0.932 and 0.913 for HSD and BCI plots, respectively, which are much larger than the half-population EAR thresholds. The low x_{slope} half-population thresholds are 0.423 and 0.397 for HSD and BCI plots, respectively. These thresholds coincidently agree with the low x_{slope} threshold as calculated from the landscape metrics of edge length and the number of patches. The upper x_{slope} does not exist for the EAR, while for the half-population they are 0.571 and 0.591 for HSD and BCI plots, respectively (Fig. 7).

Discussion

A large amount of evidence has shown that many species respond in non-linear ways to habitat loss and fragmentation (Ficetola and Denoël 2009, Swift and Hannon 2010). The most common methods for identifying non-linear changes in species–habitat relationships assume that true

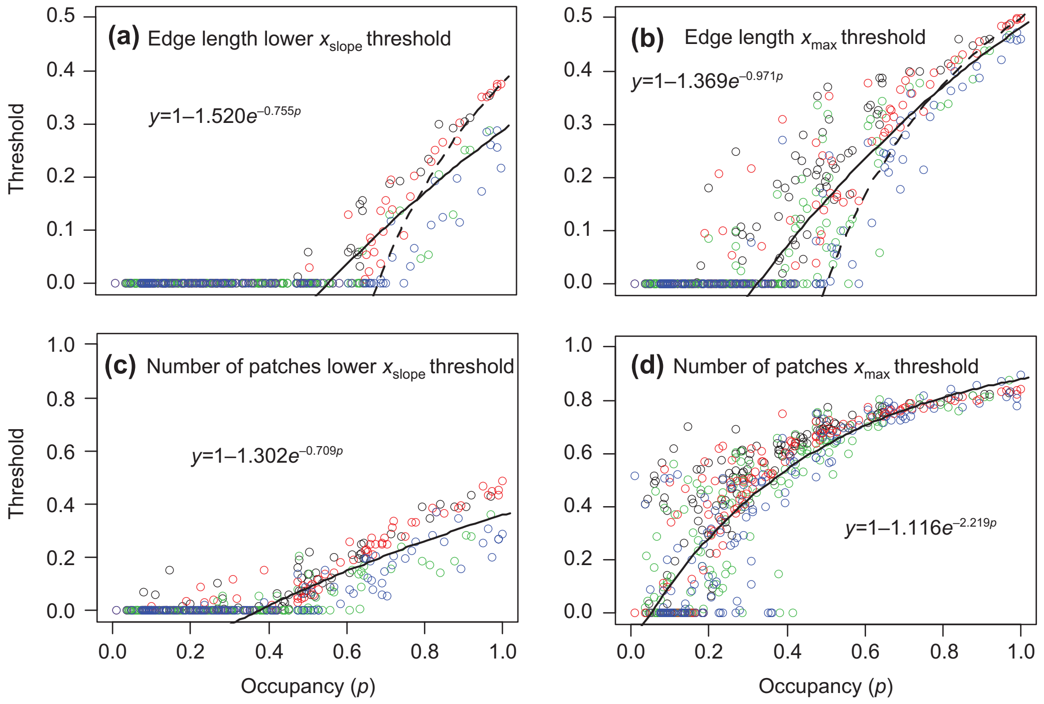

Figure 6. Habitat loss thresholds for edge length and number of patches for HSD and BCI species for both random and aggregated habitat loss (Fig. 3). (a) Lower slope thresholds for edge length, i.e. the lower x_{slope} at which edge length slope = 1 (Fig. 2) versus occupancy. The dashed curve is the theoretical threshold under random occupancy, i.e. $1-(4p+1)/(8p^2)$ (see text). (b) Peak thresholds for edge length, i.e. the x_{max} at which the edge length reaches maximum. The dashed curve is the theoretical threshold under random occupancy, i.e. $1-1/(2p)$. (c) Lower slope thresholds for number of patches. (d) Peak thresholds for number of patches. Black and green colors are the thresholds for HSD species for random and aggregated habitat loss, respectively. Red and blue colors are for BCI species for random and aggregated habitat loss, respectively. The solid curves are the fitted model $y = 1 - a\exp(-bp)$, to each threshold data.

point thresholds exist where the relationship switches from one state to another rapidly (Toms and Lesperance 2003, Homan et al. 2004, Ficetola and Denoël 2009). In reality, species–habitat relationships are most likely a continuous function, showing no point of abrupt change but a zone of change. As a result, the previous methods aiming to detect habitat thresholds are either of no use or the thresholds so detected do not reflect the real change important to the system of concern because ecologically sensitive changes often occur much earlier than the detected peak breakpoint indicates. However, few methods exist for defining and detecting such thresholds for continuous ecological response functions. In this study, we propose a method to identify habitat loss thresholds for the distribution and diversity of species in landscapes. In contrast to existing methods in the literature, we are not interested in the conventional breakpoint threshold but a smaller threshold indicating rapid changes in species distribution.

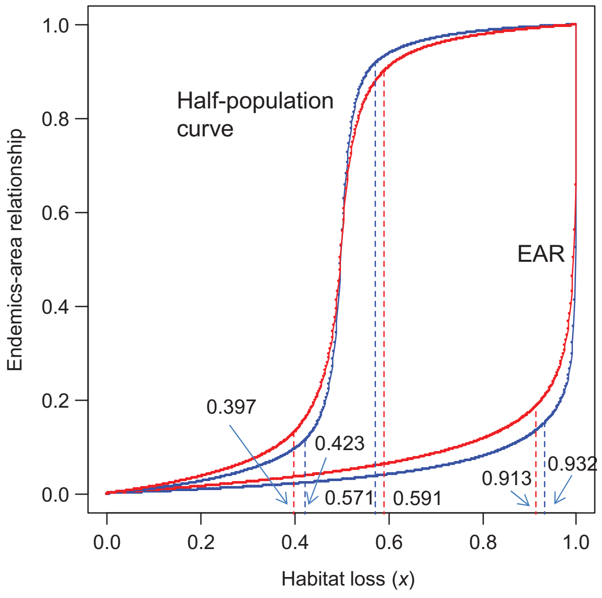

Figure 7. The endemics–area relationship (Eq. 8) and the half population curve (Eq. 9). The HSD curves are in blue color, while BCI curves are in red color. The dashed lines and the associated numbers indicate the slope threshold for each curve.

We approach this new thresholding method by the concept of threshold zones for species–habitat relationships. To evaluate the performance of our method, we developed four habitat loss models and fit them to empirical data from two forest permanent census plots. The results of our two landscape metric models show that edge length and number of patches for species with occupancy (distribution range) < 0.4 will decline significantly even with a small amount of habitat loss. Consequently, we recommend no habitat should be destroyed for species with low occupancy. The landscape metric models also show that the most widely distributed species could tolerate up to 40% of habitat loss before the rate of change in edge length and number of patches is greater than unity, depending on the occupancy of concerned species (Fig. 6). This 0–40% range is the maximum permissible habitat destruction to avoid creating significant landscape fragmentation, at least as measured by edge length and number of patches.

The landscape metrics are for describing edge length and number of patches for individual species. However, conservation decisions and landscape management are rarely made based on individual species but rather on assemblages of species or entire ecosystems. In this case, our half-population EAR models for the empirical HSD and BCI plot (Fig. 7) suggest that ~40% of habitat destruction is the maximum permissible habitat loss to avoid high rates of biodiversity loss. Together with the results of the edge length and patch number metrics, here we suggest 40% to be the maximum permissible habitat loss threshold for biodiversity conservation. We further argue there is no such thing as a minimum permissible habitat loss in landscape conservation and management as our results show that some species are sensitive to very low levels of habitat loss.

Our predictions for maximum permissible habitat loss are within the range (10–50%) of the majority of threshold values identified by the simulation studies reviewed in Swift and Hannon (2010). For example, Solé et al. (2004) report sudden biodiversity collapses at 10–40% habitat loss based on the analysis of a metapopulation model. Many empirical studies also have found ecological thresholds within the range identified by our study. For example, Desrochers et al. (2011) show that $>50\%$ habitat loss or conversion can lead to loss of bird species from regional assemblages in Ontario, Canada and van der Hoek et al. (2015) report bird extinction thresholds with 10–93% forest loss or conversion in northeastern United States. Although the identification of a single 'magic' (Matthews et al. 2014) threshold value may be attractive from a conservation perspective (Johnson 2013), threshold values often demonstrate considerable variability even within taxonomic groups and simple landscapes (reviewed by Swift and Hannon 2010). In this study, we found that occupancy and the pattern of habitat loss (i.e. random or aggregated) influenced our predictions of ecological thresholds. Specifically, our landscape metrics (i.e. edge-length and number of patches) predicted lower habitat loss thresholds (i.e. 0%) for relatively rare species (i.e. low occupancy) than relatively abundant species (Fig. 4–6) as well as lower habitat loss thresholds when habitat is lost at an aggregated compared to a random manner. Our biodiversity metrics (i.e. the endemics–area relationship and half-population curve) vary with occupancy but are invariant to spatial aggregation patterns (Fig. 7, He and Hubbell 2011).

In this study, we focus on the identification of early thresholds that may indicate rapid changes in species distributions or even extinctions. This approach is akin to the focus on early warning signals developed in the ecological dynamical systems literature (reviewed by Scheffer et al. 2009). From an applied perspective, early warning signals are valuable as they can inform resource management policies prior to undesirable changes. For example, thresholds at which logging intensity begins to seriously impact biodiversity are often used to set forest retention targets in tropical (Burivalova et al. 2014) and boreal forests (Craig and Macdonald 2009). Given the practical value of ecological thresholds, it is paramount that ecologists develop robust methods for defining thresholds (Swift and Hannon 2010, Johnson 2013). The key advantages of our approach are fourfold. First, we derive a quantitative method for identifying threshold zones. We argue that transition zones rather than points are the rule and not the exception in ecological thresholds, therefore an approach designed to identify zones is appropriate for most types of thresholds such as type II and III response curves where abrupt breakpoints do not exist (Fig. 1). Second, our method is simple in that it only requires one to measure the slope of the relationship between an ecological variable (e.g. species richness or other landscape metrics such as decayed connectivity) and a perturbation (e.g. habitat loss) and our method is general in that it may be applied to define threshold zones for any continuous ecological variable. Third, the more restrictive breakpoint thresholds (e.g. V-shape) will always occur within the zonal threshold defined by our proposed method. Finally, threshold zones are defined by lower and upper points, and the lower point provides a simple metric for early detection of ecological thresholds. Specifically, the lower point at which $|dy/dx| = 1$ is the point at which the ecological response variable (y, e.g. species richness) starts to change faster than the environmental variable (x, e.g. habitat loss) does. This lower point threshold is of particular ecological significance because it indicates a starting point signaling possible impending critical change in y. For example, in our analysis the lower threshold emerged at ~40% and at this point about 16% of species in HSD and BCI plots would have lost half of their populations (Fig. 7). In contrast, 90% of species would have lost half their populations if the upper zonal threshold (~60%) for the half-population EAR were considered (Fig. 7). Consequently, decision-making, which relies on the upper point thresholds or the conventional restrictive breakpoint thresholds (i.e. $x_{\max}$), may risk being too late for action. Therefore, the lower point of a zonal threshold should be used as an ecologically sensible threshold for conservation application. Overall, the new threshold zone method, paired with the novel habitat loss models we have derived, could be used for describing and understanding the effect of habitat loss on species diversity and distribution in landscapes.

Our study, however, is not without limitations. One key limitation is that our analyses do not specifically consider impacts of habitat fragmentation itself (not just habitat loss) on the identification of ecological thresholds. Although it is possible to analyze some aspects of fragmentation in our habitat loss models (e.g. by explicitly changing cell size or spatial patterns of habitat removal as in the above analyses), such analyses are not very useful by themselves without considering the loss of habitat, as empirical studies have demonstrated that habitat loss can interact synergistically with habitat fragmentation, particularly at high levels of habitat loss (Andrén 1994, Fahrig 2003). Our analysis also assumed a binary habitat/non-habitat definition of landscapes which is consistent with the dominant conceptual framework in fragmentation research (Brudvig et al. 2017). Growing empirical evidence, however, suggests that the quality of the intervening matrix impacts the fitness and response of species to habitat loss and fragmentation. For example, a meta-analysis by Prugh et al. (2008) shows that the negative effects of habitat area and isolation on species occupancy are reduced when the intervening matrix is higher quality (i.e. natural). Furthermore, although the three types of thresholds described in Fig. 1 are widespread, they are not exclusive (e.g. cusp catastrophe; Rose and Harmsen 1981). We do not suggest that the method developed in this study is applicable to all types of thresholds. Finally, our landscape metric and biodiversity models mainly focus on static scenarios of species distribution and therefore we have no inference on the impacts of habitat loss on population or community dynamics. Future developments of our method should investigate potential synergisms between habitat loss and fragmentation and the role of matrix quality for the delineation of ecological thresholds. Future work may also explore the relationship between characteristics of the full threshold zone – as identified using our method – and ecological responses, to address questions, for example, how the gradient or shape of the zone might impact recovery of species following habitat loss.

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