

IDEA AND PERSPECTIVE

Species–area relationships and extinctions caused by habitat loss and fragmentation

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Abstract

The species–area relationship (SAR) has been used to predict the numbers of species going extinct due to habitat loss, but other researchers have maintained that SARs overestimate extinctions and instead one should use the endemics–area relationship (EAR) to predict extinctions. Here, we employ spatially explicit simulations of large numbers of species in spatially heterogeneous landscapes to investigate SARs and extinctions in a dynamic context. The EAR gives the number of species going extinct immediately after habitat loss, but typically many other species have unviable populations in the remaining habitat and go extinct soon afterwards. We conclude that the EAR underestimates extinctions due to habitat loss, the continental SAR (with slope ~ 0.1 or somewhat less) gives a good approximation of short-term extinctions, while the island SAR calculated for discrete fragments of habitat (with slope ~ 0.25) predicts the long-term extinctions. However, when the remaining area of land-covering habitat such as forest is roughly less than 20% of the total landscape and the habitat is highly fragmented, all current SARs underestimate extinction rate. We show how the ‘fragmentation effect’ can be incorporated into a predictive SAR model. When the remaining habitat is highly fragmented, an effective way to combat the fragmentation effect is to aggregate habitat fragments into clusters rather than to place them randomly across the landscape.

Keywords

Endemics–area relationship, extinction, extinction debt, extinction threshold, habitat fragmentation, meta-population capacity, species–area relationship.

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INTRODUCTION

The species–area relationship (SAR) is a fundamental empirical generalisation in ecology (Rosenzweig 1995; Lomolino 2000; Blackburn & Gaston 2003) and the *prima facie* reason for predicting declining biodiversity with on-going massive habitat conversion by humans (Millennium Ecosystem Assessment 2005). MacArthur & Wilson’s (1963, 1967) theory of island biogeography was the first dynamic model to predict the SAR, followed by many other models (Ricklefs & Bermingham 2004; Kadmon & Allouche 2007; Rosindell & Cornell 2007, 2009; Whittaker *et al.* 2008). Given that very different models predict SARs, it is clear that just demonstrating a SAR for a particular system does not tell much about the mechanisms that have generated it. Nonetheless, it is widely agreed that the two main ecological processes that contribute to SARs are increasing habitat heterogeneity with increasing area, which allows a larger number of species with dissimilar ecological requirements to co-occur within larger areas (though see Allouche *et al.* 2012); and increasing probability of population survival with increasing population size and hence with increasing area, given that, other things being equal, larger areas tend to support larger populations (Hanski & Gyllenberg 1997).

SARs are most commonly described by the power-law $S = cA^z$ (Arrhenius 1921; Rosenzweig 1995), where S is the number of species, A is the area of the habitat, and c and z are two parameters. In log–log space, the value of z gives the slope of the increasing number of species with increasing area. Starting with the pioneering study by Connor & McCoy (1979), researchers have attempted to

relate the value of z to environmental and ecological variables, but with only limited success (Matter *et al.* 2002; Ovaskainen & Hanski 2003; Drakare *et al.* 2006; Tjorve & Tjorve 2008). One generalisation to emerge is that, across a large range of spatial scales, the SAR exhibits three phases: a relatively steep slope for very small areas, which harbour only small numbers of individuals per species; a shallower slope for intermediate (regional) scales; and again a steep slope for very large scales, in the extreme covering several continents, which tend to have different sets of species (Rosenzweig 1995; Hubbell 2001). Most analyses, including the present one, are concerned with the regional scale, typically ranging from roughly 1 to 10^6 km².

Power-law SARs have been used to predict extinctions of species due to reduced area of habitat (Whitmore & Sayer 1992; May *et al.* 1995; Brooks & Balmford 1996; Cowlshaw 1999; Ney-Nifle & Mangel 2000; Pimm & Raven 2000; Brooks *et al.* 2002; Brook *et al.* 2003; Pereira & Daily 2006; Pimm *et al.* 2006; Hanski *et al.* 2007). If the original habitat area A is reduced to A_{new} , the fraction of species that is predicted to remain following habitat loss is given by

$$S_{new}/S = (A_{new}/A)^z. \quad (1)$$

In other words, if $A_{new} = xA$, where x is the fraction of remaining habitat, fraction x^z of the original species will survive – the rest go extinct. Note that eqn 1 assumes that the power-law SAR applies both before and after habitat loss with the same value of z , which raises the question as to when, following habitat loss, the new species number S_{new} should be recorded, immediately after habitat loss or following any transient dynamics. We return to this question below.

Recently, He & Hubbell (2011) have argued that eqn 1 always overestimates extinctions, because the area required to remove the last individual of a species from a landscape, corresponding to extinction, is typically much larger than the area needed to encounter the first individual, on which basis SAR is constructed. To demonstrate their claim, He & Hubbell (2011) fitted to empirical data the power-law SAR as well as the following equation:

$$S_{\text{loss}}/S = 1 - (1 - a/A)^{\zeta}, \quad (2)$$

where a is the area destroyed and S_{loss} is the number of endemic species to area a , that is, species that only occurred within a and which were hence immediately lost when a was destroyed. He & Hubbell (2011) call eqn 2 the endemics–area relationship (EAR), which is however confusing, because eqn 2 does not describe the increase in the number of endemic species with area, given by $S_{\text{loss}} = ca^{\zeta}$ (Harte & Kinzig 1997; Kinzig & Harte 2000). Considering the slope values, ζ in eqn 2 is typically equal or less than ζ in the power-law SAR, whereas ζ in the power-law EAR, $S_{\text{loss}} = ca^{\zeta}$, is greater than ζ in the corresponding SAR (Harte & Kinzig 1997; Kinzig & Harte 2000). Equation 2 may be rewritten as

$$(S - S_{\text{loss}})/S = (1 - a/A)^{\zeta} = (A_{\text{new}}/A)^{\zeta}, \quad (3)$$

which gives the fraction of species surviving habitat loss as a power of the fraction of remaining area. We hence call eqn 3 and the equivalent eqn 2 as the ‘remaining species–area relationship’, RAR, to avoid confusing it with EAR as defined by Harte & Kinzig (1997) (Table 1). Equation 3 describes the relationship between the number of remaining species and the remaining area immediately following habitat loss and the loss of endemic species. Noting that $S_{\text{new}} = S - S_{\text{loss}}$, eqns 1 and 3 are structurally equivalent, but because different data are used to estimate the value of ζ , the respective ζ values may be different. There is much confusion in the literature concerning the use of eqn 3; we describe our approach explicitly in the following section.

While constructing any SAR, two issues that deserve attention are the spatial configuration of the habitat and the way species are sampled. Concerning the spatial configuration, the primary distinction is between continuous vs. fragmented habitats. The latter are represented by true and habitat islands, which are also the natural units of sampling while constructing SARs. In the case of continuous habitat, researchers typically overlay a regular lattice over the landscape for sampling. For different sampling schemes, see Dengler (2009), Gotelli & Colwell (2001), Scheiner (2003) and Smith (2010). An important point to note is that all these sampling schemes involve subareas of the same landscape. In contrast, in conservation one typically asks about the capacity of different landscapes with more or less habitat to support viable populations and species (Simberloff & Abele 1976; Hanski & Ovaskainen 2000). To address

this question, one may construct a SAR with individual data points representing different landscapes with dissimilar amounts of habitat rather than subareas of the same landscape. Table 2 summarises our view about the different types of situations for which a SAR may be constructed. We recognise three types of data sampled within a single landscape (region): nested or non-nested clusters of lattice cells from a continuous landscape, discrete habitat fragments from a mainland-island setting (as originally studied by MacArthur & Wilson 1963, 1967) and discrete habitat fragments in a landscape without a mainland (the metapopulation setting). On the other hand, when different landscapes are the units of sampling, we distinguish between cases where the habitat occurs as a single block, which is implicitly assumed by the conventional SAR (the ‘one-fragment’ (OF-)SAR, Table 2), and cases where the habitat occurs in many discrete fragments (the ‘fragmented landscape’ (FL-)SAR). The slope of the SAR depends on how it is defined (Rosenzweig 1995; Ulrich & Buszko 2004; Tjorve & Turner 2009), and hence, the definition affects any predictions concerning the survival of species in the face of habitat loss. In particular, applications of power-law SARs to predict extinctions are often based on the slope value 0.25, which stems from MacArthur & Wilson’s (1967) original work and a large number of subsequent empirical studies analysing variation in the number of species on true islands (Connor & McCoy 1979; Rosenzweig 1995). This slope value does not necessarily apply to the other settings in Table 2, especially not to continental SARs as has been known for a long time (MacArthur & Wilson’s 1967; Brown 1971).

To return to the task of predicting extinctions due to habitat loss, we reiterate that eqn 3 and EARs (Harte & Kinzig 1997; Kinzig & Harte 2000) by definition describe the number of species going extinct immediately following complete loss of habitat in the area occupied by the endemic species. In conservation, we are concerned not only with these immediate extinctions but also with subsequent extinctions due to the remaining habitat being insufficient to support, in the long-term, viable populations of other (non-endemic) species. Second, predictions about extinctions based on SAR, RAR and EAR are focused on the pooled amount of habitat that is lost across the region, while they ignore possible consequences of habitat fragmentation. Arguably, this is a major shortcoming when the total amount of remaining habitat is small or relatively small and fragmentation becomes severe (Hanski 2005). Third, most models that have been constructed to derive SAR, RAR and EAR ignore spatial correlation in habitat type and differences in species ecological requirements (e.g. Kinzig & Harte’s 2000 derivation of EAR from SAR, Hubbell’s 2001 neutral model, He & Hubbell’s 2011 sampling models and Storch *et al.*’s 2012 model of range placement; but see Sizing & Storch 2004). Fourth, SAR, RAR and EAR are typically not derived from dynamic models, which is a shortcoming

Table 1 Different types of species–area and endemics–area relationships. Here, S is the number of species that occur within area A , and c and ζ are two parameters; S_{loss} is the number of species that are confined to area a , which is a part of the total area A ; and $A_{\text{new}} = A - a$. Note that the formulas can be rewritten without parameter c as in eqns 1 and 3.

Acronym	Formula	Description
SAR	$S = cA^{\zeta}$	<i>Species–area relationship</i> gives the number of species occurring in area A . The power-law SAR given here is the most commonly used functional form; SAR may be calculated for different spatial scales and for communities with different spatial population dynamics (Table 2)
EAR	$S_{\text{loss}} = ca^{\zeta}$	<i>Endemics–area relationship</i> gives the number of species confined to area a that is a part of the total area A
RAR	$S - S_{\text{loss}} = c(A_{\text{new}}/A)^{\zeta}$	<i>Remaining species–area relationship</i> gives the fraction of species that have populations outside the area a , that is, within $A - a$

Table 2 Five different types of SARs calculated with different kind of data.

Type of SAR	Spatial unit of sampling	Remarks
Continental	Subareas of different sizes	Subareas of a continuous landscape delimited in one way or another
Mainland-island	Discrete habitat fragments	Habitat fragments receive migration from permanent mainland populations; this is the original mainland-island setting of the theory of island biogeography
Metapopulation	Discrete habitat fragments	No mainland, species occur as metapopulations in a network of habitat fragments
One-fragment (OF-SAR)	Landscape	Calculated for isolated habitat fragments (e.g. true and habitat islands) of different sizes with completely isolated populations
Fragmented landscape (FL-SAR)	Landscape	Calculated for replicate fragmented landscapes with differences in the total amount of habitat and the degree of fragmentation

at regional scales, where the occurrence of most species is dynamic and affected by dispersal.

Here, we aim at providing a perspective on the use of SAR and RAR in predicting extinctions by taking a computational approach: we construct a dynamic simulation model of the spatial dynamics of a large number of species to analyse and clarify habitat area-dependent extinctions. We develop a simple yet robustly realistic model, with the following key features. We ignore interspecific interactions but assume differences in the ecological traits of the species. We model stochastic patch occupancy dynamics (Hanski 1994; Moilanen 1999) on a lattice, assuming an exponential dispersal kernel (Ovaskainen & Hanski 2004) with a parameter specifying the average range of dispersal. The lattice cells are characterised by spatially variable habitat type, which is spatially correlated at a scale that can be adjusted with a parameter. The performance of a local population in a lattice cell is determined by the match between the species phenotype and habitat type. The model includes regional stochasticity, that is, spatially correlated environmental stochasticity, which leads to spatially correlated extinctions. We construct continental SARs, OF-SARs and RARs for the simulation results, with the aim of examining differences in their slopes. We then analyse transient dynamics following habitat loss, to contrast extinctions that occur immediately following habitat loss vs. further extinctions in the course of transient dynamics towards the new quasi-stationary state. Finally, we analyse the influence of habitat fragmentation vs. the influence of habitat loss on the number of surviving species. We conclude that contrary to He & Hubbell (2011), RARs always underestimate even short-term extinctions, because following habitat loss many non-endemic species go quickly extinct in the remaining habitat, where they do not have viable populations. However, and what is very important, conventional SARs produce large or even very large underestimates of the number of species going extinct in highly fragmented landscapes with a small total amount of remaining habitat. We modify the power-law SAR to account for the effect of fragmentation, and we make a simple recommendation that helps reduce the fragmentation effect in practical conservation.

THE MODEL AND ITS IMPLEMENTATION

In this section, we describe the computational model, while the mathematical definitions and further technical details are presented in the online supporting information.

Stochastic patch occupancy model

We use a spatially explicit stochastic patch occupancy model (SPOM). These models are well-established in spatial ecology and

metapopulation modelling (Moilanen 1999; Ovaskainen & Hanski 2004). In our case, the patch network is represented by a finite regular grid, in which each cell represents a discrete habitat patch. Each cell is associated with a value b , $0 \leq b \leq 1$, which determines habitat type. Habitat type is spatially autocorrelated but temporally constant as discussed in the next section. We simulate a large assemblage of independent species with dissimilar ecologies. Each species is characterised by five parameters. The first three parameters are familiar from spatially explicit metapopulation models (Hanski 2001): the colonisation (c) and extinction rate parameters (e), and the average dispersal distance ($1/\alpha$, where α is the parameter of the negative exponential dispersal kernel). The remaining two parameters define the mean phenotype (φ) and niche width (γ). Parameter b , which is a property of the landscape, together with φ and γ specify the quality q of a particular grid cell for the focal species as a Gaussian function $q = \exp\left(-\frac{(b-\varphi)^2}{2\gamma^2}\right)$. Habitat quality determines the fitness (performance) of the species in the respective grid cell as described below. Note that each species will perform best in grid cells in which its phenotype φ is close to the habitat type b .

The dynamics are modelled as a discrete-time Markov chain. The state of each species is described by a binary occupancy matrix of the same size as the landscape grid. If a species inhabits a particular grid cell, the corresponding element in the occupancy matrix has the value of one, otherwise the value is zero. Thus, the state space of the chain is given by all possible occupancy matrices of each species. We assume that the extinction probability in an occupied cell is given by $1 - \exp(-e/q)$, where q is the quality of the cell for the species. The probability of colonisation of a currently unoccupied cell is given by $1 - \exp(-cS)$, where S is the connectivity of the cell, summing up the contributions of nearby occupied cells to the colonisation probability of the focal cell. The contribution of a particular source cell depends on its distance from the focal cell but also on its quality q , on the assumption that populations in high-quality habitat patches send out more dispersers than populations in low-quality patches. Further details on connectivity are given in supporting information (section S1).

Heterogeneous habitat and regional stochasticity

We generate heterogeneous landscapes with a simple recursive quadtree division algorithm reminiscent of a previous algorithm used for generating regional stochasticity in SPOMs (Gu *et al.* 2002). We initialise the habitat matrix to be a zero square matrix. The algorithm proceeds recursively by dividing the grid into four equally sized squares until individual cells are reached. At every

recursion level, each of the squares is given a random value from the unit range, which is added to the habitat type value of all cells in the square. Furthermore, each level is assigned a weight that determines the spatial scale of spatial autocorrelation in habitat type. We assume that the weight for the randomly generated values at depth k is given by $w_k = W\omega^{-k}$, where ω is a parameter and W is a normalisation constant depending on the size of the landscape. The greater the value of ω , the greater the spatial scale of autocorrelation. See Fig. S1 in the supporting information for examples.

We included regional stochasticity, that is, spatially correlated environmental stochasticity (Hanski 1999) in the dynamics of each species, by generating during each time step spatially correlated coefficients affecting the habitat type of the grid cells. The algorithm for generating regional stochasticity is the same as the algorithm used to generate habitat type, with the difference that the random values are obtained from a truncated log-normal distribution. There is no temporal correlation, that is, the matrix is regenerated during each time step. Further details on regional stochasticity are given in section S2 of the supporting information.

Implementation

This section gives a high-level overview of the implementation of the simulations, while the technical details are given in the supporting information. Prior to the simulation, one needs to specify the parameters for generating the landscape, regional stochasticity and the pool of species. The landscape is specified by giving the dimensions of the grid and the scale of spatial autocorrelation in habitat type (ω). The set of species is characterised by assigning distributions for each species parameter as described in supporting information (see especially Table S1). In particular, the average phenotypes (φ) are selected from the unit range, meaning that the community includes all kinds of species in terms of their adaptation to the range of habitat types (b). Simulations were initiated with all grid cells occupied by all the species. As there is no colonisation from outside, the model is an absorbing Markov chain and eventually all species reach extinction as time $T \rightarrow \infty$. However, before extinction, a species may converge towards a positive quasi-stationary state – the metapopulation equilibrium. For the parameter combinations used in this study, the positive quasi-stationary state or extinction was typically reached within a few hundred time steps. All simulations were first run for a fixed number of time steps to ensure that most species had converged to their metapopulation equilibrium. Once this has happened, we can either analyse the system by computing various metrics, such as the SAR, perturb the system by assuming that some habitat is lost (habitat type set to a value resulting in zero fitness, q , in the cell) and so forth.

While the model is conceptually simple, in practice the simulation is computationally intensive due to large number of species (typically 500), large grids (typically either 512×512 or 256×256) and the many different parameter combinations that we wished to examine. We attempted to optimise many components of the simulator to attain reasonable running times. Most simulations were computed distributively on a high-performance computing cluster.

Computing SAR and RAR

Continental SARs (Table 1) and RARs are constructed by sampling contiguous areas with increasing size and recording the number of

species in each area (corresponding to type IIA SARs in Scheiner 2003). In the case of our simulation results, we divide the landscape into adjacent equally sized rectangles for all different sample scales a_0, a_1, \dots, a_k . For each rectangle of size a_p , we count the number of species and record the average number of species for areas of size a_p . We then use linear regression to fit the log–log transformed power-law SAR given by eqn 1 to these data. To construct the RAR, we divide the grid into subareas as in the computation of SAR, but instead of counting the number of species occurring in the area, we count the number S_{loss} of species endemic to the sample area a . The RAR is then fitted with linear regression to the log–log transformed eqn 3 using the fraction of remaining species $(S - S_{loss})/S$ and the fraction of remaining area $(1 - a/A)$ as data points.

The OF-SAR (Table 2) was fitted to the simulation results in the same manner as SAR using eqn 1, but with one important difference. Biologically, the difference between SAR and OF-SAR is that in the former, the populations inhabiting the focal subarea remain connected with populations in the rest of the grid, whereas in the latter, the rest of the grid is entirely unsuitable (removed in the simulation) and the focal subarea remains as an isolated habitat island. Thus, the OF-SAR was computed by considering each adjacent sample area as a distinct, isolated landscape and simulating these areas separately until the species reached the quasi-stationary state. Fitting of SAR, RAR and OF-SAR are further discussed in section S3 of the supporting information.

RAR, continental SAR and OF-SAR were calculated for 840 different parameter combinations (communities) assuming a grid of 512×512 cells and an initial number of 500 species. The parameter space was constructed by choosing either a fixed value or a range of values for each model parameter. If a range was specified, the actual parameter value for each species was chosen uniformly at random within the range. For example, the average dispersal distances $(1/\alpha)$ were picked from sets $\{1, \dots, 4\}$, $\{5, \dots, 8\}$ and $\{9, \dots, 12\}$. Thus, there were parameter combinations in which all species had on average short, intermediate or long dispersal distances, though there was also additional variation among the species in each community. All simulations were run for 500 time steps to ensure that the majority of species had reached the quasi-stationary state. To disregard implausible parameter combinations that produced very few viable species or mostly species that saturated the entire grid, we excluded parameter combinations that yielded < 50 species or > 450 species at the quasi-stationary state out of the 500 initial species. After excluding these species, there remained data from 460 simulations representing different parameter combinations. Details of the analysis and the parameter values are given in the online supporting information (section S4).

RESULTS

Species–area relationships

Figure 1 gives representative examples of RARs, SARs and OF-SARs in the simulations for 460 parameter combinations. Typically, RAR has the smallest and OF-SAR the steepest slope for a particular combination of parameters. The average values in the 460 simulations were 0.04 for RAR, 0.07 for SAR and 0.24 for OF-SAR (full statistics in Table S2). Examining the effects of parameter values shows that all slopes steepen with increasing extinction rate and

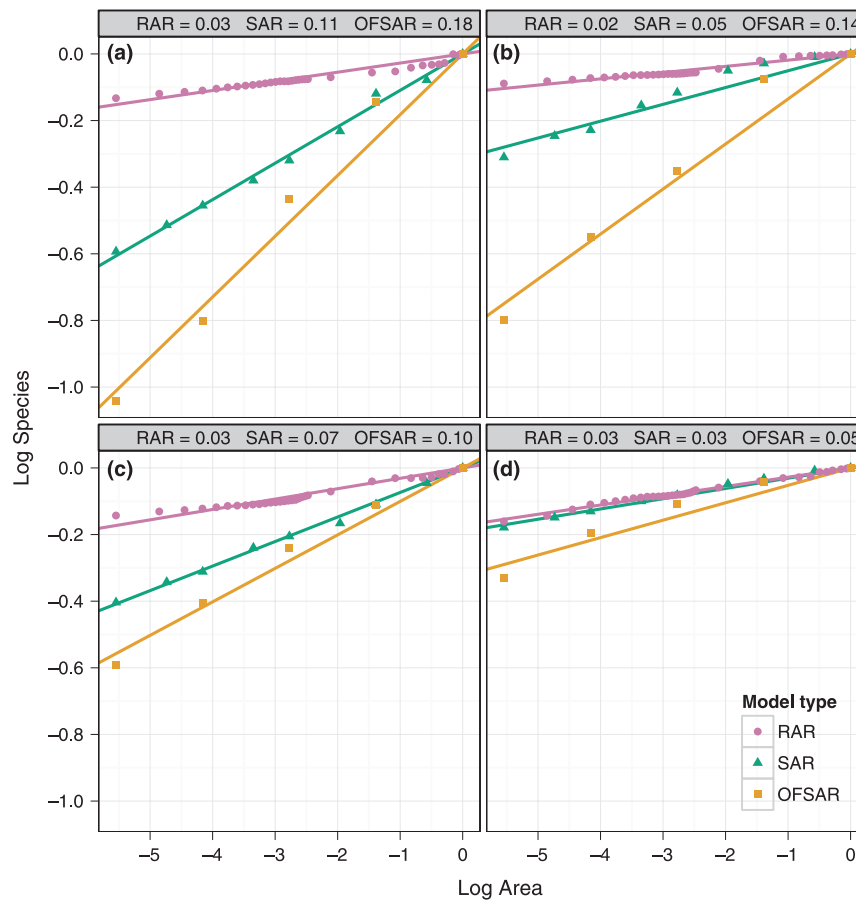


Figure 1 Four examples of remaining species–area relationship (RAR), species–area relationship (SAR) and one-fragment (OF)-SAR constructed for simulated data from a 512×512 grid with the following (average) parameter values: (a) $\omega = 2$, $\epsilon = 0.125$, $e = 0.025$, $1/\alpha = 6.5$; (b) $\omega = 1.5$, $\epsilon = 0.375$, $e = 0.025$, $1/\alpha = 10.5$; (c), $\omega = 1$, $\epsilon = 1.75$, $e = 0.175$, $1/\alpha = 2.5$; and (d) $\omega = 0.5$, $\epsilon = 1.75$, $e = 0.225$, $1/\alpha = 2.5$. All cases have $\gamma = 0.1$. Note that the scale of spatial autocorrelation in habitat type decreases from (a) to (d), though there are also other differences in parameter values. For details of parameter values, see the online supporting information.

decreasing colonisation rate (Table S3). This is consistent with an inverse relationship between the slope value and the total number of species in the community in the quasi-stationary state (Fig. S7), as the number of species increases with colonisation rates and decreases with increasing extinction rates. Thus, species-rich communities with many widely distributed (common) species have shallower slopes than species-poor communities.

Increasing dispersal distances decrease the slope of SAR but steepen the slope of OF-SAR (Table S3). In the former, long dispersal distances help maintain species across the landscape, whereas in OF-SAR, long dispersal distances lead to elevated emigration losses from isolated habitat fragments and thereby to increased extinction rate in small fragments. In the OF-SAR plots, the initial nonlinear phase extends to larger areas when more species disperse beyond the boundaries of the isolated habitat fragments (Fig. S8). Increasing niche width decreases the slope values (Table S3), but this effect was substantial only for parameter combinations that generated species-rich communities.

The spatial scale of autocorrelation in habitat type has an important effect on the slopes of RAR, SAR and OF-SAR: the slopes are steeper when the spatial scale of autocorrelation is greater (Fig. 2). This effect was weaker in parameter combinations that produced species-poor communities (less than 300 species in the quasi-stationary state).

Note that the slopes of SAR and RAR are on average equal when there is no spatial autocorrelation in habitat type (Fig. 2). In contrast, when there is long-range correlation in habitat type, the slope of SAR is about twice the slope of RAR (Fig. 2).

Transient dynamics following habitat loss

We next examined the dynamics of species number following sudden habitat loss. It is clear that immediately following the loss of habitat, the first species to go extinct are the ones whose entire populations resided within the lost area. In the course of time, however, further species may go extinct, namely species whose long-term viability was compromised by the elimination of the populations directly affected by habitat loss.

The transient dynamics were analysed by running the simulation until most species had converged towards their quasi-stationary state, then destroying habitat in a single step in time, after which the simulation was resumed until a new quasi-stationary state was reached. Based on the occurrence of the species in the landscape just prior to habitat loss, we calculated RAR, SAR and OF-SAR, and each of the three models was used to predict the number of extinctions following habitat loss (the horizontal lines in Fig. 3). Generally, the number of species decreased very rapidly, within a

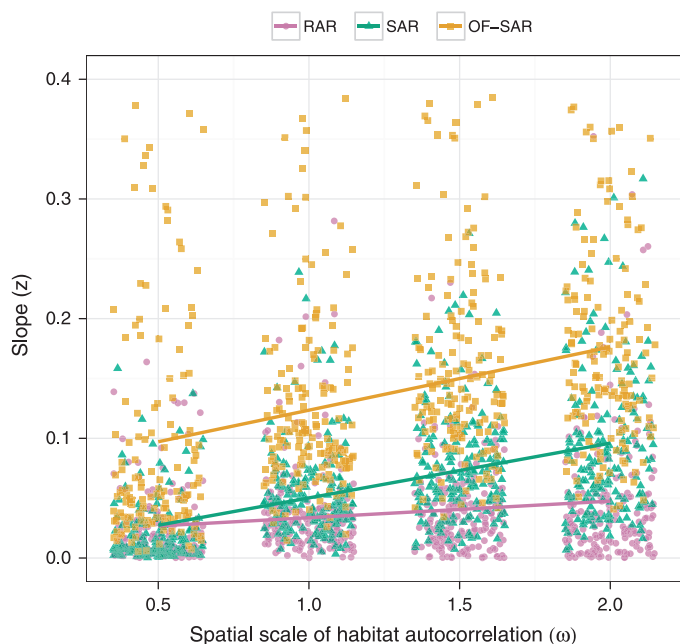


Figure 2 The slopes of RAR, SAR and OF-SAR for different parameter combinations plotted against ω , the scale of spatial autocorrelation in habitat type. A few slope values > 0.4 are not shown.

few generations only, below the level predicted by RAR and close to the level predicted by SAR, except in the case of landscapes with no or only limited spatial autocorrelation in habitat type, when RAR and SAR have similar slopes (Fig. 3). Subsequently, the number of species declined slowly towards the level predicted by OF-SAR, though for a long time the average number of surviving species in 100 replicate simulations remained between the predictions based on SAR and OF-SAR.

Habitat fragmentation leads to further extinctions

The different types of species-area relationships describe the association between the number of species in the community and the respective area of the habitat, but none of them takes the spatial configuration of the habitat explicitly into account. This question has great practical significance, because in reality increasing habitat loss is typically associated with increasing fragmentation of the remaining habitat.

We used the model to analyse the effects of habitat fragmentation on the number of surviving species as follows. As in previous simulations, we simulated a set of 500 species on randomly generated landscapes for different parameter combinations. We replicated all the simulations with and without regional stochasticity. After the species had reached the quasi-stationary state, a part of the habitat was destroyed at a single point in time, after which the simulation was resumed. The remaining habitat was distributed among non-adjacent small fragments rather than preserved as a single area as in the calculation of OF-SAR.

Figures 4a and b give examples of the relationship between the number of surviving species vs. the number of habitat fragments into which a given total amount of habitat is split. There are three major trends to notice. First, when the total amount of remaining habitat is large, roughly more than 20% of the entire landscape,

fragmentation makes no substantial difference. Second, when the total amount of remaining habitat is smaller, increasing fragmentation is highly detrimental to the survival of species when the degree of fragmentation exceeds a critical level, which is more than 16 fragments in the example in Fig. 4a. Third, when the spatial scale of autocorrelation in habitat type is short or relatively short ($\omega = 1$, Fig. 4a), the number of surviving species is highest when the habitat is least fragmented, but when the spatial scale of autocorrelation in habitat type is long ($\omega = 2$, Fig. 4b), more species survive if the given amount of habitat is split into several discrete fragments (8–32 fragments in Fig. 4b). This is due to different parts of the landscape having substantially different habitat types; hence, multiple reserves protect more species than a single reserve. Species parameters also influence the number of surviving species (Table S5). As expected, the number of species increases with colonisation rate and decreases with extinction rate; it decreases with increasing dispersal distances, which increases emigration from the habitat fragments; it increases with niche width; and it decreases with increasing regional stochasticity. The number of surviving species increases with the spatial scale of autocorrelation in habitat type.

To highlight the effect of habitat fragmentation on top of the effect of habitat loss on the number of surviving species, we have replotted in Fig. 5a in log-log space the result shown in Fig. 4b. The relationship is approximately linear when the amount of remaining habitat is more than ~15% of the total landscape area, but when less of the habitat remains, the degree of fragmentation makes an important difference. In other words, there is an interaction between the total amount of habitat and the degree of fragmentation: for more habitat, more fragmentation is possible without any additional ‘fragmentation effect’ on the number of surviving species. The reason is that for a given number of fragments, the average fragment size is larger the greater the total amount of habitat. In the example in Fig. 5a, the fragmentation effect starts to kick in when the size of individual fragments is 100–400 grid cells. What constitutes a small fragment naturally depends on the parameters of the species.

To construct a model for the SAR that would include the effect of habitat fragmentation, we added an extra term to the power-law SAR (Ilkka Hanski & Joel Rybicki unpublished).

$$S = cA^z e^{-b/\lambda_M}, \quad (4)$$

where b is a parameter and λ_M is the metapopulation capacity of the fragmented landscape (Hanski & Ovaskainen 2000). Metapopulation capacity is derived from single-species metapopulation theory: the smaller the value of λ_M , the greater the degree of fragmentation for a given total area A . In the case of equally large habitat fragments that are randomly distributed across the landscape, as in the simulations reported in Fig. 5a, and making plausible assumptions about the effects of habitat patch area on emigration and extinction rates (Hanski & Rybicki unpublished data.), λ_M is approximately proportional to A^3/n^2 , where n is the number of habitat fragments. The fraction of species surviving as a function of the fraction of remaining habitat area is then given by

$$S_{\text{new}}/S = (A_{\text{new}}/A)^z e^{-bn^2/A^3}. \quad (5)$$

Figure 5b shows the fit of this model to the simulated data in Fig. 5a. The effect of the number of habitat fragments into which the total habitat area is split, and which varies from 1 to 1000 in Fig. 5, is predicted well by eqn 5.

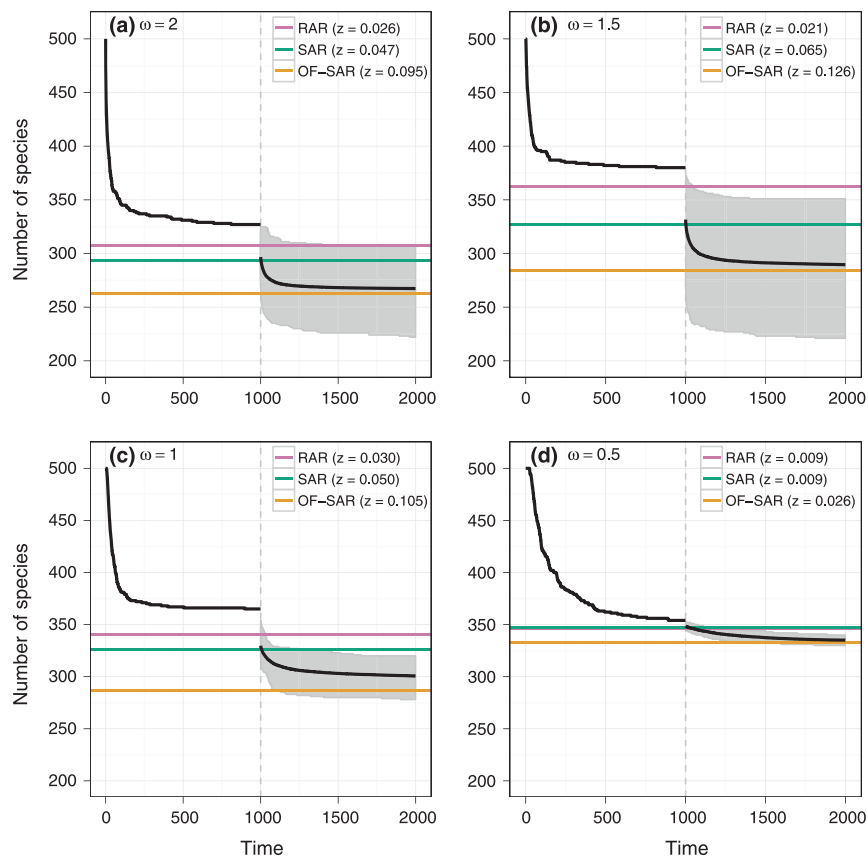


Figure 3 Transient dynamics following habitat loss. In each panel, the horizontal lines give the number of surviving species predicted by RAR, SAR and OF-SAR. The black line shows the number of extant species. After 1000 time steps (vertical dashed line), 90% of the habitat is destroyed leaving a single patch of 10% of total landscape area. Following habitat loss, the black line gives the mean for 100 simulations, while the grey ribbon highlights values that fall between 90% of the maximum and minimum values. For further explanation see the text.

Clustering of habitat fragments

In reality, habitat fragments are seldom randomly distributed across the landscape. To address non-random distributions, we applied two different patterns of fragmentation onto the landscape of total size A . In the first pattern representing maximal fragmentation, k habitat fragments cover a fraction r of the total landscape area. Each fragment is approximately of the same size, rA/k , and the fragments are randomly distributed throughout the landscape. In the second pattern representing clustered fragmentation, k_C clusters of fragments are randomly located throughout the landscape, with each cluster covering a fraction of r_C (cluster cover ratio) of the total landscape area. Within each cluster, there are k_L randomly located discrete fragments that cover r_L (local cover ratio) of the cluster. After habitat destruction, only the fraction of $r_C r_L$ of the total landscape area A remains covered by habitat. The idea here is that when $k = k_C k_L$ and $r = r_C r_L$, there are equally many habitat fragments of the same size both in the maximally fragmented and in the clustered pattern, but in the former pattern, the fragments are randomly distributed throughout the landscape, whereas in the clustered pattern they are aggregated. Figure S3 illustrates the different patterns. The clustered pattern reduces fragmentation locally, while the total habitat loss is the same in both cases.

The maximally fragmented and hence least clustered landscape has 640 habitat fragments of size A_f while the least fragmented

landscape has 20 large fragments, which can be interpreted as being 20 maximally tight clusters of 32 fragments of size A_f each (hence, in this case, $r_C = 1$). The intermediate cases have the same $k_C = 20$ clusters, each with $k_L = 32$ small fragments, but the fraction of the landscape area A covered by the clusters, r_C , and the fraction of the cluster area r_L covered by the small fragments varies as follows (r_C and r_L): 0.5 and 0.2; 0.33 and 0.3; and 0.2 and 0.5. In all cases $r_C r_L = 0.1$, and the degree of clustering increases from the first to the third case. Simulations were repeated for 720 combinations of model parameters to investigate the generality of the results (details in section S4 of the supporting information). We excluded from the analysis simulations in which less than 300 species of the original 500 remained at the quasi-stationary state prior to habitat loss. In these cases, habitat loss in the most fragmented landscape caused the extinction of most species regardless of parameter values (Fig. S9). The typical reason for the small number of species prior to habitat loss was low colonisation rates.

The results demonstrate that increasing clustering of the k habitat fragments with the same pooled area strongly enhances the number of surviving species (Fig. 6). To examine how the positive effect of clustering depends on the traits of the species, we constructed regression models in which the number of surviving species in the clustered landscape was explained by the number of species surviving in the maximally fragmented landscape (as in Fig. 6) as well as by model parameters. Species persistence is enhanced by clustering

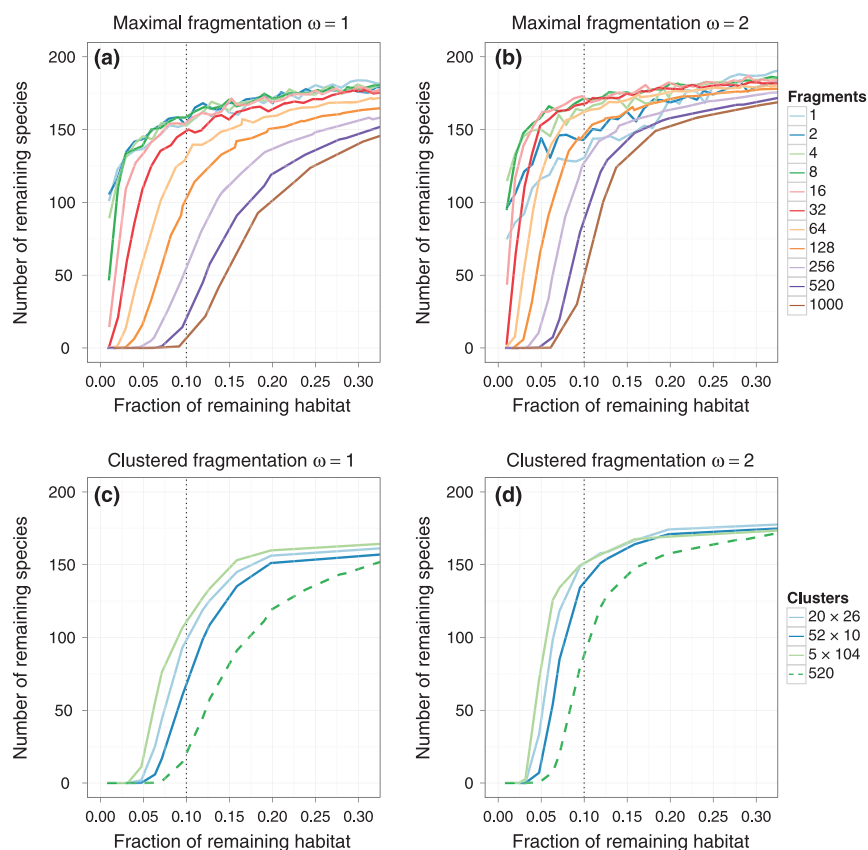


Figure 4 The effect of habitat fragmentation on species richness. The upper panels show the number of species surviving at quasi-stationary state against the fraction of remaining habitat out of the total landscape area. The habitat occurs either as a single fragment or is split into 2, 4, ..., 520, 1000 equally large fragments located randomly in the landscape. The scale of spatial autocorrelation in habitat type (ω) is either 1 (panel a) or 2 (b). The two lower panels show the results of clustering the habitat fragments in the case of 520 fragments (see the text). The broken line shows the corresponding result for randomly located 520 fragments (the same line as in the upper panels).

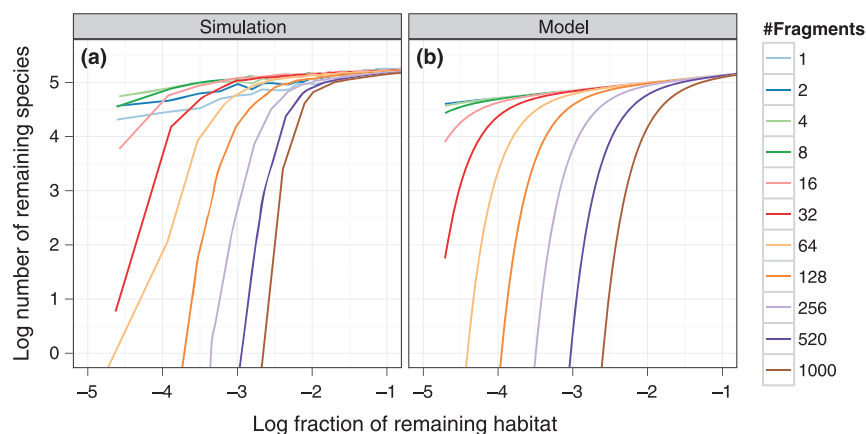


Figure 5 Panel (a) shows the same data as in Fig. 4b but plotted here in log–log space. Panel (b) shows the fit of eqn 5 to the simulated data in panel (a). Parameter values: $\alpha = 0.14$ and $b = 2.0 \times 10^{-9}$.

especially in communities in which species have high colonisation rates, have relatively short dispersal distances and have large niche widths (Tables S5 and S6). The persistence of species is enhanced by clustering of habitat fragments more in landscapes in which habitat quality is spatially autocorrelated over long than short distances. Regional stochasticity decreases the benefits of clustering (Tables S5 and S6), but the effect is relatively weak (Fig. S10) though we

assumed a realistically high level of spatial correlation in extinction rates (Fig. S2).

Finally, we studied how the number of clusters into which a fixed number of habitat fragments are aggregated affects the number of surviving species. In Figs. 4c and d, we compare the numbers of surviving species in landscapes with 520 habitat fragments aggregated into 5, 20 or 52 clusters with 104, 26 and 10 individual frag-

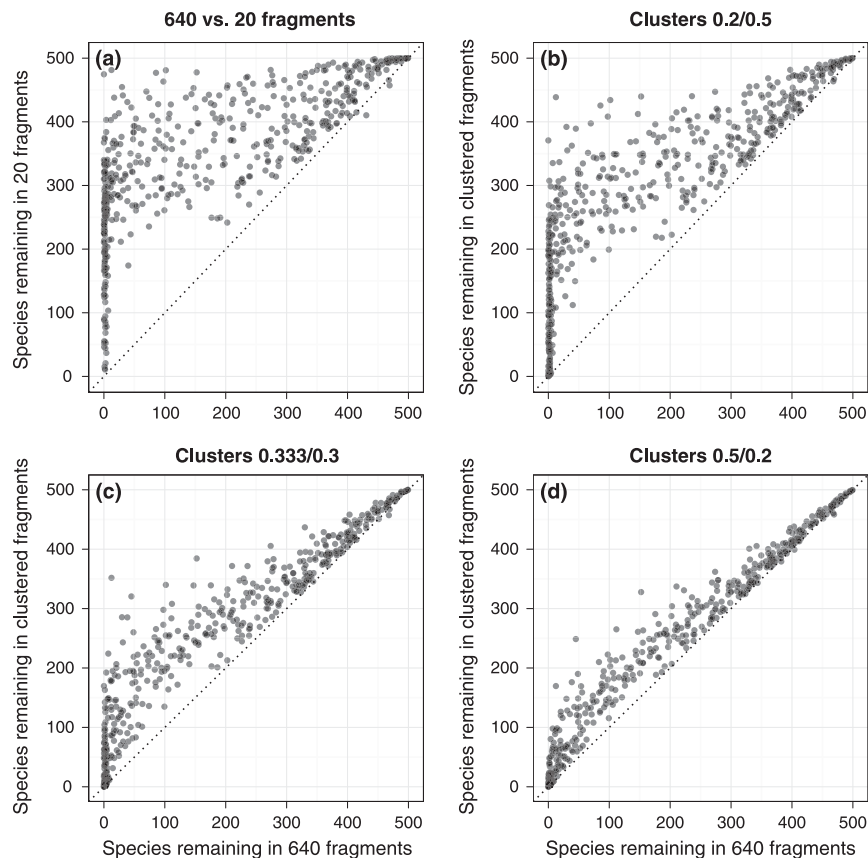


Figure 6 The number of surviving species in fragmented landscapes for different parameter combinations, contrasting the case when the fragments are clustered (on the vertical axis) vs. randomly located across the landscape (on the horizontal axis). The degree of clustering decreases from panel (a) with 20 contiguous fragments to (b) with 20 clusters in which 50% of the total area is covered by habitat fragments, to (c) with 30% covered, and to (d) with 20% of the cluster area covered by fragments. Only parameter values giving > 300 species in the quasi-stationary state prior to habitat loss are included. See the text for further explanation.

ments per cluster, respectively. The number of surviving species is higher for a smaller number of larger clusters, though the differences are not large. In all cases, clustering markedly increases the number of surviving species over the case of random distribution of habitat fragments (Figs. 4c and d).

DISCUSSION

Species–area relationships and extinctions

He & Hubbell (2011) found that the slope of SAR (average 0.174) was nearly twice as large as the slope of RAR (average 0.094) in data sets for forest trees in small study plots and in data for passerine birds in the continental USA. Assuming spatially correlated habitat type ($\omega = 2$), our modelling results are in good agreement with their empirical results as far as the relative values of SAR (average 0.07) and RAR (0.04) are concerned. The model parameters have systematic effects on the slope values (Table S3), but we do not know which values would be most realistic for the data analysed by He & Hubbell (2011). In the case of randomly distributed species, the slopes of RAR and SAR are expected to be equal (He & Legendre 2002; Green & Ostling 2003; He & Hubbell 2011), which is also what we found in our simulations with spatially uncorrelated habitat type. The average value of the slope of the OF-SAR was 0.24, which is close to 0.25, the commonly cited average value for empirical studies (Rosenzweig 1995). Thus, our dynamic, spatially

explicit model predicts SARs that are consistent with previous empirical and theoretical results.

Kinzig & Harte (2000) found that SARs generally overestimate extinctions due to habitat loss, and He & Hubbell (2011) concluded even more strongly that SAR always overestimates extinctions, while RAR yields more accurate predictions. Though the latter conclusion is correct, by definition, as far as the immediate extinction of endemic species is concerned, Kinzig & Harte's (2000) and He & Hubbell's (2011) conclusion is nonetheless misleading about extinctions following habitat loss at the regional scale, where dispersal and spatial dynamics influence the distribution of species. The reason: many non-endemic species go extinct soon following habitat loss, because these species, though initially present in some numbers in the remaining (non-destroyed) habitat, nonetheless fail to survive on the long term. In our results for 90% habitat loss, many non-endemic species went extinct so quickly after habitat loss that short-term extinctions were much better predicted by SAR than by RAR (Fig. 3). Note that the slope value that is appropriate here is the slope of the continental SAR with average less than 0.1 rather than the frequently cited 0.25, which stems from island studies and is consistent with the slopes of OF-SARs in our results.

We conclude that considering even short periods of time following habitat loss, RAR always underestimates extinctions, while SAR gives a satisfactory short-term prediction. Over longer time periods, the number of surviving species in the remaining habitat approaches

a new quasi-stationary state that is given by the OF-SAR if the remaining habitat occurs as a single continuous block. In reality, habitat loss is typically accompanied by fragmentation, which may greatly reduce the number of surviving species (below). It should also be noted that following the dynamic response of species to substantial habitat loss, the parameters of the SAR will gradually change. Typically, the slopes of OF-SAR and other 'island' SARs (Table 2) are steeper than the slope of continental SAR (Pimm & Askins 1995; Tjorve & Turner 2009; though see Drakare *et al.* 2006). The contrast between continental and OF-SARs has been used as an indication of extinction debt (Kuussaari *et al.* 2009), which is also supported by our results.

Storch *et al.* (2012) have recently reported EAR slopes between 1 and 2 for continental faunas of birds, mammals and amphibians. In contrast, He & Hubbell (2011) reported EAR values < 0.1 for North-American birds. The reason for the apparent conflict is that He & Hubbell (2011) estimated the value of α in eqn 2, which we have dubbed RAR, while Storch *et al.* (2012) fitted data to the power-law EAR, $S_{loss} = a\alpha^z$. The value of α in eqn 2 is helpful because it can be directly compared with the value of α in the power-law SAR (eqn 1), as we have done in this article (Fig. 1).

Habitat fragmentation and extinctions

All SARs implicitly assume that habitat occurs as a continuous area in the landscape. It has been frequently observed that the shape of the habitat area may influence SAR and EAR (Drakare *et al.* 2006; Pereira *et al.* 2012) and hence also their predictions concerning extinctions. Kinzig & Harte (2000) present an example in which half of a square area is destroyed leaving 2 one-quarter quadrants in the diagonal corners of the original square. SAR with $\alpha = 0.2$ predicts that 13% of the species will be lost, but using their formula that takes into account the geometry of the remaining habitat, they calculated that only 5% of the species are lost. However, informative as this calculation is, it is based on the assumption that SAR applies with the same slope at all spatial scales (self-similar spatial distributions), which is unlikely to hold at scales where the distributions of species are much affected by spatial dynamics.

There has been much discussion in the literature about the relative roles of habitat loss vs. fragmentation in affecting population dynamics and extinction risk of single species (Fahrig 1997, 1998, 2002, 2003). It is now recognised that fragmentation decreases habitat occupancy and increases extinction risk when the total amount of remaining habitat is small (Hanski 2005). When there is much habitat, fragmentation does not make much difference, because all habitat is well within the dispersal range of the species, but with decreasing amount of habitat an increasing fraction of habitat occurs in isolated fragments and remains unoccupied for a part of the time. Ultimately, the species goes extinct from the entire landscape when the species' extinction threshold has been crossed (Hanski & Ovaskainen 2000; Hanski 2011). Equation 4 adds to the power-law SAR an additional term that accounts for the fragmentation effect on the number of surviving species. In the example in Fig. 5, the extended model fits well the simulated data, and we conclude that this model has potential for describing the combined effects of habitat loss and fragmentation on species richness.

The important message for conservation is that when the total amount of remaining habitat is small, a high degree of fragmenta-

tion is highly detrimental to long-term persistence of species. An example of ill-informed expectations about the effectiveness of small habitat fragments in supporting biodiversity is the scheme of woodland key habitats (WKH) in production forests in Finland (Hanski 2008). Around 96 000 WKHs with the average area of 0.6 ha have been delimited in privately owned forests within the total area of 15 million ha (Yrjönen 2004). Empirical studies indicate that such small and isolated habitat fragments are not effective in retaining local populations of threatened species (Gustafsson 2000; Sverdrup-Thygeson 2002; Pykälä 2004; Ericsson *et al.* 2005; Hottola & Siitonen 2006; Junninen & Kouki 2006; Pykälä *et al.* 2006). Our simulations suggest that a much more cost-effective way of protecting forest biodiversity would be to distribute the total area of 600 km² in the WKHs (96 000 times 0.6 ha) among a much smaller number of fragments than 96 000 fragments, or to aggregate the small fragments (below). On the other hand, regardless of how the 600 km² is distributed in space, it amounts to only 0.5% of 15 million ha, for which reason alone the WKHs cannot be expected to make a significant contribution to conservation of forest biodiversity. For other conservation and management implications of the present results see the box on p. 11.

Practical conservation: the third-of-third rule

Virtually everywhere on Earth where the terrestrial habitats are productive, the human population density is so high and land use is so intensive that only a small fraction of natural habitats remains and biodiversity is consequently on steep decline. This is consistent with model predictions: the SAR indicates that only a fraction of species will survive when the vast majority of their habitat is gone, and our results demonstrate that scattered small or relatively small habitat fragments are especially ineffective in protecting biodiversity. Unfortunately, even if there would be the political will to protect more natural habitats, there are either no or only limited opportunities to establish large continuous protected areas outside the species-poor biomes at high latitudes and altitudes. In this situation, how can the nations achieve the target of halting biodiversity decline by protecting at least 17% of land area by 2020, as agreed in the UN biodiversity summit in Nagoya in 2010? The Nagoya agreement further recognises that the protected areas should not be located primarily in marginal areas but protection should cover 'especially areas of particular importance for biodiversity and ecosystem services, ... ecologically representative and well-connected systems of protected areas ... integrated into the wider landscapes' (<http://www.cbd.int/doc/strategic-plan/2011-2020/Aichi-Targets-EN.pdf>, strategic goal C, target 11).

In practice, the only short-term option is to protect what remains, which in many parts of the world is mostly small and relatively small areas of habitat – and the challenge is to try to minimise the adverse effects of fragmentation. To achieve that, our results lead to the recommendation that habitat fragments should be protected in clusters rather than as randomly scattered fragments, which will generally increase the conservation benefits for a given total area protected. In the examples in Fig. 4, and assuming that 10% of the total area is protected, clustering 520 habitat fragments into 5, 20 or 52 clusters increased the number of surviving species by 75% (panel 4d) to 300% (panel 4c) in comparison with randomly located fragments. Hanski (2011) suggested the rule-of-thumb of protecting a third-of-third, such that the clusters of habitat fragments, dubbed as conservation landscapes, would cover one-third of the total land-

scape area, while one-third of the area within the clusters would be covered by the actual habitat fragments. In this case, roughly 10% of the total area would be protected (0.3×0.3). In the present results, an even greater degree of clustering was slightly more beneficial, for example, protecting half of the area covered by the clusters, which themselves would cover 20% of the total landscape area, giving the same 10% of land protected. Exactly what these proportions would be in practice is naturally constrained by what is possible in particular regions, and the coverage would vary from one cluster to another, but the principle of clustering remains an important message for conservation, and also a practical one, as there often are alternative sets of habitat fragments to protect, or to restore, when land-use patterns change.

Another advantage of clusters of habitat fragments for biodiversity conservation stems from the fact that the clusters themselves may be relatively evenly distributed across large areas. Though movements of individuals are especially frequent among fragments within clusters, because of relatively short distances, some less frequent movements would occur among the clusters, which would

facilitate, for example, range shifts of species in changing climates. Thomas *et al.* (2012) have recently shown that a network of protected areas facilitates the expansion of species' ranges. Aggregating protected habitat fragments into clusters strikes a compromise between facilitating survival of species within clusters and facilitating the movements of species at larger spatial scales. We emphasise that we are not arguing for degazetting existing national parks and other large protected areas, which are invaluable for many reasons and are needed for the achievement of the Nagoya targets. We are suggesting possible new ways of planning protected areas in a cost-effective manner while recognising the realities of the densely populated world.

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Conservation and management implications of the results

- (1) To calculate the number of species that survive the loss of habitat in a certain area, one may use the remaining species–area relationship (RAR) (Table 1). In this assessment, the surviving species are the ones that have populations outside (as well as possibly inside) the area where the habitat is converted. However, as demonstrated by the example in Fig. 3, not all these species are expected to survive for a long time, because the viability of their populations may be lost due to loss of the populations that resided in the converted area. These species represent the extinction debt in the community. Compared with RAR, the species–area relationship (SAR) gives a more realistic prediction about the number of species going extinct due to habitat loss. However, it is important to realise that the slope of SAR, which determines how many species will go extinct, can be calculated in many different ways (Table 2) that lead to different predictions (Fig. 1). In our example (Fig. 3), the short-term extinctions are predicted well by the continental SAR (Table 2), with slopes typically being ~ 0.1 or somewhat less. The OF-SAR, calculated for isolated fragments of habitat and with slopes ~ 0.25 , predicts the numbers of surviving species on the long-term, but only if the remaining habitat occurs as one or a few fragments.
- (2) If the total amount of remaining area-covering habitat such as forest is small, roughly $< 20\%$ of the landscape area, and the habitat is fragmented, SARs underestimate the number of species going extinct (Fig. 4a–b). The reason is that with decreasing amount and increasing degree of fragmentation of the habitat, more and more species pass their extinction threshold in the fragmented landscape and go regionally extinct.
- (3) The adverse effects of fragmentation can be countered to some extent by aggregating the remaining habitat fragments into clusters rather than distributing them evenly or in random across the landscape (see Fig. S3 in the supporting information). Aggregation effectively reduces fragmentation for most species and allows more species to persist (Fig. 4c–d).

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