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LETTER

Characterising extinction debt following habitat fragmentation using neutral theory

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Abstract

Habitat loss leads to species extinctions, both immediately and over the long term as 'extinction debt' is repaid. The same quantity of habitat can be lost in different spatial patterns with varying habitat fragmentation. How this translates to species loss remains an open problem requiring an understanding of the interplay between community dynamics and habitat structure across temporal and spatial scales. Here we develop formulas that characterise extinction debt in a spatial neutral model after habitat loss and fragmentation. Central to our formulas are two new metrics, which depend on properties of the taxa and landscape: 'effective area', measuring the remaining number of individuals and 'effective connectivity', measuring individuals' ability to disperse through fragmented habitat. This formalises the conventional wisdom that habitat area and habitat connectivity are the two critical requirements for long-term preservation of biodiversity. Our approach suggests that mechanistic fragmentation metrics help resolve debates about fragmentation and species loss.

Keywords

Biodiversity, connectivity, extinction debt, fragmentation, habitat loss, modelling, neutral theory, spatially explicit.

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INTRODUCTION

Habitat loss drives extinction (Millenium Ecosystem Assessment 2005; Rybicki & Hanski 2013). If all remaining individuals of a species immediately perish during habitat loss, then that species becomes extinct. Surviving species may still be driven to extinction after the habitat loss via ongoing processes. These delayed extinctions constitute an 'extinction debt' resulting from past landscape changes (Tilman *et al.* 1994). Forecasting extinction debt is challenging and requires understanding how many species exist immediately after habitat loss and how many will persist at equilibrium in the long term (Hanski & Ovaskainen 2002; Hanski 2011).

Habitat loss is often accompanied by habitat fragmentation: the process of dividing a large contiguous region of habitat into smaller, spatially disjunct remnants. In a fragmented landscape, edge effects, patch size and isolation between patches – in addition to habitat area – all influence species richness (Didham & Lawton 1999; Wilson *et al.* 2016) and thus have a bearing on extinction debt. Furthermore, different taxa can exhibit different responses to habitat loss, even within the same area (Carrara *et al.* 2015). These differences are dependent on both local and regional habitat configurations (Tischendorf & Fahrig 2000).

While it is uncontroversial that species richness decreases with loss of total habitat area, the relationship between species richness and habitat fragmentation for a specific level of habitat area (habitat fragmentation *per se*) remains the subject of fervent debate. Some authors claim the relationship is generally positive (Fahrig 2017, 2019; Fahrig *et al.* 2019; May *et al.* 2019), whereas others claim it is negative (Wilson *et al.* 2016; Thompson *et al.* 2017; Fletcher *et al.* 2018). Part of the problem is that observational studies informing the debate are relatively few, and experimental studies are even fewer (see Fahrig 2017 for a review). Even modelling studies on fragmentation and biodiversity are restricted in scale because the spatially explicit models needed are computationally expensive.

One way to avoid the computational cost of simulation modelling is to develop formulas that relate species richness to fragmentation. Standard formulas for estimating species loss from habitat loss ignore fragmentation entirely. A typical method is to take a species–area relationship (SAR) formula, such as the power law, and estimate species loss as the difference between the estimated species richness of the original area and that of the smaller area remaining after habitat loss (Brown 1984; Durrett & Levin 1996; Thomas *et al.* 2004; Foster *et al.* 2013). In addition to their failure to account for fragmentation, another limitation of standard SAR methods is that they ignore the temporal component of species loss, that is, they are insensitive to the differences between species richness in the short term compared with the long term following habitat loss. Attempts to salvage the power-law SAR by parameterising it for different temporal scales (Rosenzweig 1995; Rosenzweig & Ziv 1999) or different degrees of fragmentation (Hanski *et al.* 2013; Haddad *et al.* 2015) still do not avoid the basic limitation that the power law is a phenomenological model. Such models cannot yield ecological insights or accurate predictions outside the range of the data used for parameterisation. This is particularly problematic when applied to extinction debt as there is a paucity of long-term data. New mechanistic formulas relating the effects of fragmentation to species loss and extinction debt are sorely needed.

One fundamental issue, which we believe has confounded both the fragmentation–diversity debate and efforts to develop species–area–fragmentation formulas, is the lack of clarity about how to measure fragmentation (Ewers & Didham 2007; Lindenmayer & Fischer 2007). A host of metrics exist for characterising features of spatially intricate habitat structure (Wang *et al.* 2014; Turner & Gardner 2015). No single metric has prevailed as a way to define or quantify fragmentation and it is not clear which existing metrics are most relevant. An alternative approach is to avoid fragmentation metrics by simulating a mechanistic community model on a spatially explicit replica of the fragmented landscape (Hanski *et al.* 2013; Rybicki & Hanski 2013). However, the simulation approach is computationally expensive and only narrowly applicable to the simulated scenario. This again points to the need for formulas, but more specifically, for formulas that quantify fragmentation – through an appropriate fragmentation metric – in a way that is relevant to biodiversity.

What kinds of models may be suitable for deriving species–area–fragmentation formulas? Ideally, the models should be mechanistic and parsimonious, to facilitate generality and tractability. One such class of models is individual-based neutral models (Hubbell 2001), which assume that an individual's species identity does not influence its chances of survival or reproduction. Despite their assumptions, neutral models can reproduce numerous patterns of biodiversity (Volkov *et al.* 2003, 2007; Alonso *et al.* 2006) and non-spatial versions have been applied to predict species loss (Gilbert *et al.* 2006; Hubbell *et al.* 2008; Halley & Iwasa 2011; Halley *et al.* 2014). More germane to the inherently spatial problem of extinction debt are spatially explicit neutral models (Chave & Leigh 2002; Chave & Norden 2007; Rosindell & Cornell 2007, 2009), which are less comprehensively studied. While most studies of spatially explicit neutral models assume 100% habitat cover, a few have considered more general landscapes with habitat configurations that could represent real habitat-loss scenarios (Pereira *et al.* 2012; Campos *et al.* 2013). Analytical formulas for species richness in spatially explicit neutral models have recently been derived for the special case where habitat is contiguous and has not been destroyed or fragmented (O'Dwyer & Cornell 2018). These formulas have been extended to predict immediate species loss following special kinds of fragmented habitat loss (Chisholm *et al.* 2018), but the problem of long-term species losses and extinction debt in such models has yet to be tackled.

Here we help bring clarity to the fragmentation–diversity debate by developing what are, to our knowledge, the first analytical solutions for quantifying long-term species loss and extinction debt under fragmentation scenarios in a mechanistic model. We use the spatially explicit neutral model, but highlight how our approach can be generalised to environments with multiple niches. Our formulas predict extinction debt based on the change in a habitat's 'effective area', which captures the number of individuals supported in the remaining habitat, and 'effective connectivity', which captures ease of movement through the landscape from the perspective of the taxa being studied and their dispersal ability. These two novel metrics give a rigorous analytical grounding to the long-held view of conservation biologists that habitat area and habitat connectivity are what drive long-term biodiversity preservation.

METHODS

Our methods comprised three steps. First, we derived new analytical formulas for estimating long-term species loss in fragmented landscapes under a mechanistic neutral model. Second, we verified our formulas by comparing their predictions to individual-based neutral simulations on fragmented landscapes including real landscapes from satellite data and synthetic landscapes generated algorithmically. Third, we used the formulas to get new conceptual insights about the general relationship of extinction debt to landscape and taxa.

Spatially explicit neutral models

Our model generates spatially explicit neutral communities in a manner broadly similar to the simulations used in Rosindell & Cornell (2007). Every time step, an individual is killed and the replacement is chosen from the propagules landing at the newly vacated cell. Each individual rains propagules onto the surrounding landscape in a radially symmetric pattern according to a dispersal kernel. With some small probability ν, the individual mutates into a new species (speciation). Eventually, a dynamic equilibrium between speciation, immigration and extinction is reached at the landscape scale. Predictions from these models are robust to changes in the dispersal kernel (Rosindell & Cornell 2007, 2009) and coincide with those of the non-spatial model at large scales (Rosindell & Cornell 2013). Coalescence methods enable efficient simulations on a subset of individuals within effectively infinite landscapes (Rosindell *et al.* 2008). They work by progressing backwards in time, tracking only the ancestors to present-day individuals of interest. We tracked the species richness within a single tile (a 'focal region') of an infinite landscape constructed by tiling a given landscape structure. Simulations were implemented in C++ and Python using the pycoalescence package (available on bitbucket: https://bitbucket.org/thompsonsed/pycoalescence).

Analytical approach

We sought to derive analytical formulas for long-term species loss following habitat loss in a spatially explicit neutral model. In contrast to Chisholm *et al.* (2018), who studied a similar system and focused on species loss immediately following habitat clearing, we focused on the long-term outcome. We used a method common in physics whereby a complex system can be re-written in terms of a reduced number of parameters. The approach involves determining combinations of parameters that are codependent, meaning the full solution for the system can ultimately be reduced to simpler, analytically tractable cases (as in Rosindell & Cornell 2007; Chisholm *et al.* 2018). Such approaches are typically developed by examination of simulation results, heuristic arguments and inspired guesswork; they are later verified by extensive simulation.

In the standard spatially explicit neutral model using Gaussian dispersal and point mutation, species richness in a defined region of a contiguous, infinite landscape reaches a dynamic equilibrium between speciation, immigration and extinction and can be described by a two-parameter function known as the 'Preston function' Ψ (Chisholm *et al.* 2018; O'Dwyer &

Cornell 2018; Appendix 1). Following a tradition of naming special functions in mathematics, the Preston function was named (Chisholm *et al*. 2018) to highlight its importance and to abstract away the complicated analytical solution (O'Dwyer & Cornell 2018). Specifically, the species richness of a disc-shaped focal area, set within an infinite contiguous neutral landscape, can be approximated as

$$S_{\text{contig}}(A_e, \nu, \sigma^2) \sim \sigma^2 \Psi\left(\frac{A_e}{\sigma^2}, \nu\right), \tag{1}$$

where ν is the point speciation rate, σ^2 is a measure of dispersal ability (the variance of a bivariate normal dispersal kernel) and A_e is the number of individual organisms in the focal area (O'Dwyer & Cornell 2018). Chisholm *et al*. (2018) extended this result to produce equations giving upper and lower bounds on species loss immediately after habitat loss. We calculated extinction debt in the same model by deriving the long-term species richness following habitat loss and taking the difference between this and the species richness immediately after habitat loss. To distinguish our results from previously derived formulas for S the species richness immediately following habitat loss, we developed a hat notation $\hat{S}$ to indicate long-term species richness at equilibrium following habitat loss. Whilst both S and $\hat{S}$ are expressed in terms of Preston functions, their mathematical forms and biological meanings are very different. Estimating S is a relatively simple spatial sampling problem; estimating long-term species richness $\hat{S}$ involves community dynamics on the fragmented landscape.

Landscape generation

To verify our analytical results, we performed simulations on a wide variety of 'synthetic' and 'real' landscapes. Two parameters defined the landscapes: h, the percentage of habitat cover after loss; and $A_{\max}$, the maximum possible 'effective area' in the landscape with 100% habitat cover, where we define effective area as the number of individual organisms present in a focal landscape. The effective area after habitat loss is given by $A_e = h \cdot A_{\max}$. We used $A_{\max}$ values of 50^2, 500^2 and 5000^2, and h values of 10, 20 or 40% yielding nine values of A_e. All habitat pixels within our landscapes had equal value to organisms, and all non-habitat pixels had zero value.

Our synthetic landscapes comprised two types: 'random' (Fig. 1a) and 'clustered' (Fig. 1b). Random landscapes were produced from a landscape with 100% habitat by randomly removing pixels until the desired habitat cover was achieved. Ten random landscapes were generated for each value of landscape size $A_{\max}$ and per cent cover h, giving a total of 90 maps. Clustered landscapes consisted of evenly spaced disc-shaped clusters of habitat and had one additional parameter: the number of fragments n. Clustered landscapes were produced for $n = 2^i$ where i ranges from 0 (a single large fragment) to $\log_2 A_e$ (every individual an isolated patch).

Our real landscapes (Fig. 1c) came from satellite maps of South American forest cover (Hansen *et al*. 2013). Our models on these maps are not intended to represent Amazon tree community dynamics specifically; the maps provide a selection of realistic landscape patterns for testing our formulas. For each value of h, regions with habitat cover within 1% of h

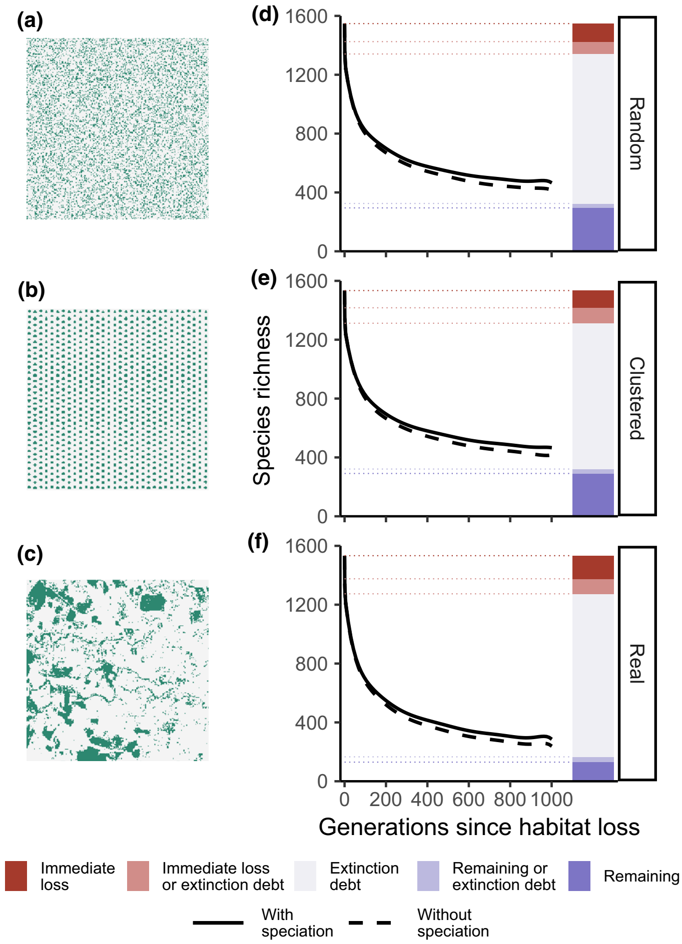

Figure 1 Three habitat-loss scenarios (a–c) and species richness over time averaged across 10 simulations (d–f). The solid and dashed curves represent the result with and without speciation, respectively; over a 1000 generation timeframe the ability for speciation to offset extinction debt is negligible (as indeed one would expect in most real situations). The coloured areas on the right represent the ranges of outcomes of species richness within the respective scenario, with uncertainty obtained from repeated simulations indicated by paler red or blue. For comparison, an SAR approach for species richness estimation that ignores extinction debt and fragmentation would predict a species richness of 1020–1400 (z between 0.1 and 0.3) in all three scenarios (Appendix 1). For all simulations, we used parameters $A_{\max} = 500^2$, $h = 20\%$, $\nu = 0.0001$, $\sigma = 16$.

were identified and pixels added to or removed from habitat boundaries to produce maps that had exactly the desired habitat cover (but still closely resembled real landscapes). For $A_{\max} = 5000^2$, there were insufficient regions with habitat areas within 1% of the target parameter values so instead 100 randomly chosen real maps each of size $A_{\max} = 500^2$ were tiled to create these landscapes.

Empirical example

To provide examples of how our methods can be applied, we also estimated actual extinction debt for tropical trees in five specific regions of the Amazon. The forest cover satellite maps from Hansen *et al*. (2013) provided the spatial arrangement of trees within each region. The five sites experienced significant deforestation in the last 20 years and were chosen with relatively similar patterns of fragmentation across a large area surrounding the focal landscape. The model parameters were taken from the tropical forest literature (Condit *et al.* 2012): a density of 0.0512 individual adult trees per m^2, a dispersal parameter of $\sigma = 8.5$ (approximately 40.2 m) and a speciation rate of $\nu = 6 \times 10^{-6}$.

RESULTS

Analytical solutions for long-term species richness in simple landscapes

Finding a general analytical solution from our neutral models for long-term (equilibrium) species richness, $\hat{S}$, of the focal region within an infinite landscape $\boldsymbol{L}$ requires understanding which features of $\boldsymbol{L}$ are most important for ecological processes. In the special case of a contiguous landscape $\boldsymbol{L}_{\text{contig}}$ with 100% habitat cover, no habitat has been lost and $A_{\text{e}} = A_{\max}$. The long-term equilibrium species richness is therefore equal to the original species richness:

$$\begin{aligned}\widehat{S}\left(\boldsymbol{L}_{\text{contig}}, \nu, \sigma^2\right) &= \widehat{S}_{\text{contig}}\left(A_{\max}, \nu, \sigma^2\right) \\ &= S_{\text{contig}}\left(A_{\max}, \nu, \sigma^2\right) \sim \sigma^2 \Psi\left(\frac{A_{\max}}{\sigma^2}, \nu\right). \end{aligned} \quad (2)$$

Randomly fragmented landscapes represent another special case: here habitat cells are uniformly distributed in space, just like the contiguous case, only now they are randomly mixed with non-habitat cells that cannot be occupied. The average distance between adjacent habitat cells is $\sqrt{\frac{A_{\max}}{A_e}}$ cell widths instead of one cell width in the contiguous case. A heuristic solution to long-term species richness can be obtained as follows: if we imagine compressing the spaces between habitat cells by $\sqrt{\frac{A_e}{A_{\max}}}$ and reducing the dispersal distance σ by the same factor, the community dynamics of the system would be unchanged, but now the habitat cells would be contiguous in space. For the randomly fragmented landscape $\boldsymbol{L}_{\text{random}}$, the equilibrium long-term diversity $\hat{S}_{\text{random}}$ can thus be calculated in terms of Preston functions by substituting $\sqrt{\frac{A_e}{A_{\max}}}\sigma$ for σ in eqn 2:

$$\begin{aligned}\hat{S}\left(\boldsymbol{L}_{\text{random}}, \nu, \sigma^2\right) &= \hat{S}_{\text{random}}\left(A_{\max}, A_e, \nu, \sigma^2\right) \\ &= \hat{S}_{\text{contig}}\left(A_e, \nu, \frac{A_e}{A_{\max}}\sigma^2\right) \sim \frac{A_e}{A_{\max}}\sigma^2 \Psi\left(\frac{A_{\max}}{\sigma^2}, \nu\right). \end{aligned} \quad (3)$$

We verified this result numerically (Appendix 3); the mean percentage error (MPE) was < 4% and can be attributed to the error inherent to the current methods for evaluating the Preston function itself (O'Dwyer & Cornell 2018).

Analytical solutions for complex landscapes: incorporating effective connectivity

We have thus far considered the idealised contiguous and random habitat patterns, but most landscapes exhibit some intermediate fragmented spatial structure (Fig. 1) that is described by neither of the extreme cases corresponding to eqn 2 and 3 (Appendix 3). There is no single metric that entirely captures fragmentation, or even an agreement among ecologists on the strict definition of fragmentation. Our strategy here is to sidestep this definitional issue and instead introduce metrics of the landscape that are mechanistically important for species diversity.

We conjectured that a fruitful approach for developing fragmentation metrics relevant to biodiversity would be to consider fragmentation from the perspective of a dispersing organism. Due to the shape of a fragmented habitat, the effective dispersal – the actual movement across a fragmented landscape – may differ considerably from the intrinsic dispersal – the expected movement of the same taxa on a contiguous landscape. We developed an 'effective dispersal' metric σ_e, which is calculated algorithmically by sequentially applying n dispersal events and recording the total distance between the overall start and end points. By repeating the process starting from different habitat cells, we generated the mean distance μ_n travelled over n generations for the landscape. Relating this distance back to a per-generation equivalent gives our effective dispersal parameter $\sigma_e^2 \approx \mu_n^2 \cdot \frac{2}{n\pi}$ (Appendix 2). For $n > 1$, this metric adds weight to the connectivity in critical regions through which many lineages pass over longer timescales. In our calculations, we used $n = 1/\nu$, the expected species' lifetime. This means that the landscape structure surrounding the focal area has influence growing weaker with distance, but decaying to zero only on passing the range boundary of an average species present in the focal region. In most cases, the estimate of σ_e converged for much lower values of $n \approx 1000$.

We then defined another novel metric that we call 'effective connectivity' c_e, which combines the proportional habitat coverage with effective dispersal. This makes our metric a function of both habitat configuration and properties of the taxa of interest, distinguishing itself from other landscape metrics that statically capture habitat configuration only. We define effective connectivity for a single cell in terms of its squared value, which is the squared mean distance travelled per generation for lineages starting from that cell, if the cell is habitat, or zero, if the cell is not habitat (i.e. it contains no individuals). Averaging over all cells gives the effective connectivity of the whole landscape:

$$c_e^2 = h \cdot \sigma_e^2, \quad (4)$$

where h is the proportion of habitat cover $\left(h = \frac{A_e}{A_{\max}}\right)$ and σ_e is the effective dispersal, as defined above.

We found that the calculation for effective connectivity can be performed with reasonable accuracy in equivalent computational time to other landscape metrics such as average patch size and edge-to-area ratio (see Hesselbarth *et al.* 2019). We used heuristic arguments involving the effective connectivity metric to develop the following ansatz for equilibrium species richness in a neutral model on a fragmented landscape:

$$\hat{S}\left(\boldsymbol{L}, \nu, \sigma^2\right) = \hat{S}_{\text{contig}}\left(A_e, \nu, c_e^2\right) \sim c_e^2 \Psi\left(\frac{A_e}{c_e^2}, \nu\right). \quad (5)$$

The motivation for this formula comes from the intuition that a generic landscape gives the same long-term result as a contiguous landscape with augmented dispersal to account for the change in connectivity. As expected, eqn 5 reduces to eqn 2 in the special case that the landscape is contiguous and to eqn 3 in the special case that the landscape is randomly fragmented.

Verifying analytical results

We confirmed by simulation that our new general solution for long-term species richness (eqn 5) accurately matches simulated species richness values (Appendix 3 Fig. S3). The analytical values have under 10% MPE across landscape types (8.1%, 9.1% and 4.2% for real, clustered and random landscapes, respectively) when compared against simulated values. The power of our approach can be seen by rearranging eqn 5 to give

$$\frac{1}{c_e^2}\hat{S}(\boldsymbol{L}, \nu, \sigma^2) \sim \Psi\left(\frac{A_e}{c_e^2}, \nu\right). \tag{6}$$

Equation 6 predicts that plotting species richness and effective area both rescaled by effective connectivity (i.e. $\frac{\hat{S}}{c_e^2}$ vs. $\frac{A_e}{c_e^2}$) should cause the SARs for all fragmented landscapes to collapse on to one curve. We verified this was true for all our simulated data (Fig. 2b) despite the huge variability displayed by the unscaled SARs (Fig. 2a). This scaling collapse verifies that we can estimate species loss by calculating just two parameters from our fragmented landscape (effective area A_e and effective connectivity c_e) and plugging the numbers into our eqn 5. Doing so produced noteworthy errors only for a small number of special cases corresponding to clustered landscapes with extremely low effective connectivity due to the presence of highly isolated habitat 'islands'. On such landscapes, the simulated long-term richness was relatively high because of endemism on the 'islands', but the scaling used to produce eqn 5 cannot account for such endemics and thus underestimates species richness (see Appendix 3).

Extinction debt

We applied our new analytical methods to the problem of estimating extinction debt in fragmented landscapes. The upper and lower bounds on species richness immediately after habitat loss, for given values of the fragmentation-independent parameters (A_e, $A_{\max}$ and σ), are given by formulas in Chisholm *et al.* (2018). Our new results provide the corresponding estimates of long-term loss. We calculated upper and lower bounds on σ_e for each $A_{\max}$ from the minimum and maximum values across all the real and synthetic landscapes; this, in turn, gives bounds on effective connectivity c_e and ultimately on $\hat{S}$ (via eqn 4), representing the best- and worst-case scenarios for long-term species richness on fragmented landscapes (Appendix 4). Corresponding estimates of extinction debt are given in absolute terms as $S - \hat{S}$ or in relative terms as $\left(S - \hat{S}\right)/S_0$, where S_0 is the species richness of the original landscape.

Across a range of spatial scales ($A_{\max}$), levels of habitat cover $\left(\frac{A_e}{A_{\max}}\right)$ and intrinsic dispersal parameters (σ), immediate species loss was consistently substantial, but usually represented < 50% of species richness (Fig. 3). By contrast, when

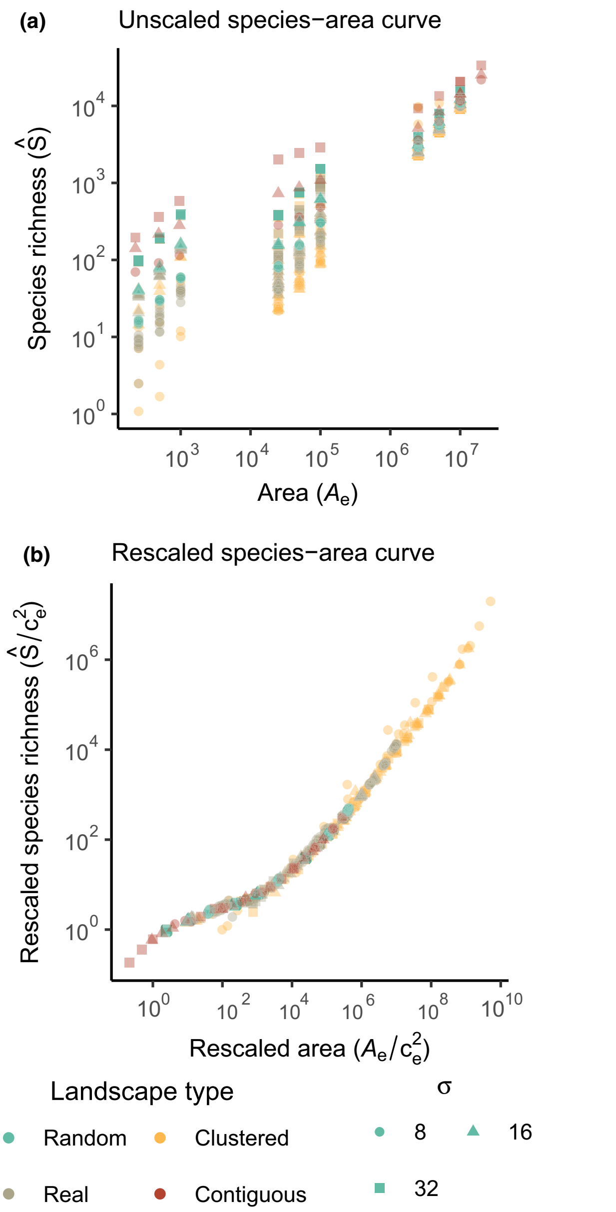

Figure 2 The unscaled (a) and rescaled (b) SARs from our simulations (obtained by dividing the effective area axis and the species richness axis, by the squared effective connectivity, c_e^2). The re-scaling collapses the parameter space to its equivalent in a contiguous landscape, and the resulting points fall approximately on a single curve. MPEs are 4.91% (contiguous), 9.09% (clustered), 4.17% (random) and 8.08% (real). Parameters used were all combinations of σ in {8, 16, 32}, $A_{\max}$ in {50^2, 500^2, 5000^2} and h in {10, 20, 40} for each landscape type, with $\nu = 0.0001$.

extinction debt was accounted for, total long-term losses were usually over 50% and in many cases close to 100%. The qualitative relationship of immediate and long-term loss to spatial scale was consistent across parameter sets (Appendix 4): extinction debt (in relative terms) was generally maximal at intermediate scales but remained sensitive to the spatial structure of each habitat.

Among the suite of landscapes in our testbed, the real landscapes from satellite data are most relevant for empirical

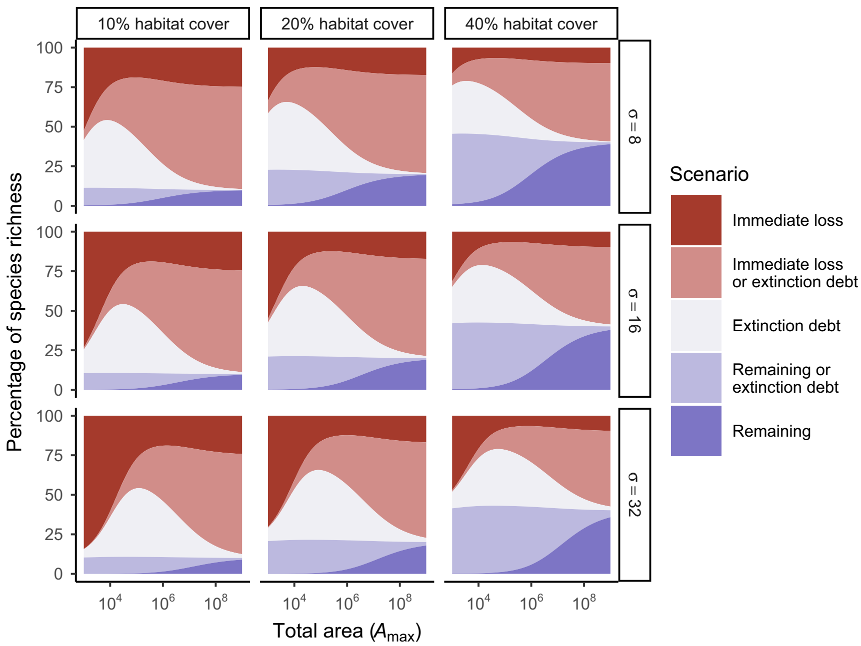

Figure 3 The equilibrium percentage of species richness remaining after habitat loss, including the uncertainty range obtained from differences in fragmentation, as a function of total area, A_{max}. Dark red indicates best-case immediate loss after habitat loss. Paler red indicates worst-case immediate loss and thus shows the uncertainty around immediate loss based on habitat configuration. Dark blue areas show the remaining species at equilibrium in the longer term, after extinction debt has been paid. Paler blue shows species that remain in the longer term in the best-case scenario depending on the habitat configuration. Pale grey represents the definite extinction debt as the gap between the worst-case immediate loss and best-case long-term loss results. The actual values of richness after immediate loss and in the long term will occur in the pale red and pale blue pale coloured areas, respectively, and depend upon the structure of the fragmented landscape (see Fig. 4 for an example of equilibrium richness corresponding to the centre panel). Here $\nu = 0.0001$.

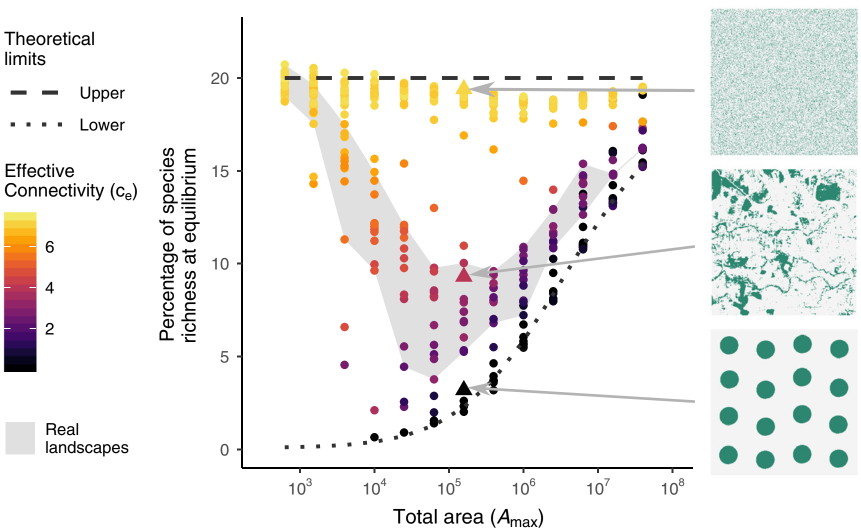

Figure 4 Percentage of species richness remaining in the long term as a function of total habitat area. Each point represents the mean value of species richness (vertical axis) from simulations on one landscape of area A_{max} (horizontal axis) and effective connectivity c_e (colours). For all points, habitat cover is $h = 20\%$ and the dispersal parameter is $\sigma = 16$, corresponding to the central panel from Fig. 3. Theoretical bounds our formulas are given by the dashed and dotted lines for the upper and lower bounds, respectively. The region (Appendix 3) between these bounds corresponds directly to the pale blue region in the central panel of Fig. 3. Real landscapes occupy a subset of parameter space, indicated by the grey shaded region. The three triangles represent the results from simulations performed on three landscapes of equal effective area ($A_e = hA_{max}$) indicated on the right.

problems. Our simulation-based estimates of long-term species loss on these real landscapes fell within the theoretical bounds from our formulas, as expected, but exhibited a much narrower range of values than those from our synthetic landscapes. For small real landscapes, the percentage long-term species loss was approximately equal to the percentage of habitat loss (Fig. 4). At intermediate spatial scales, the percentage of long-term species loss was greatest: for example, for the parameter values in Fig. 4, long-term species loss on real landscapes was 90–95% at intermediate spatial scales when 80% of habitat was lost. At very large scales, we found that the structure of real landscapes tended to impede dispersal, leading to low c_e values and long-term species richness values close to the theoretical lower bound (Fig. 4).

In an example application of our methods, estimating tree species losses in the Amazon (Fig. 6), the predicted species richness was consistently closer to the theoretical lower bound. Overall, the percentage of species remaining as a function of spatial scale follows a U-shaped curve on real landscapes (Fig. 4), and accordingly the total percentage of species lost (extinction debt and immediate loss together) follows a hump-shaped curve. In Fig. 5, we summarise graphically the expected percentage of species remaining for a range of levels of habitat loss and connectivity and across a range of spatial scales.

We found that the most connected scenario in our model, and the best-case scenario for long-term species richness (lowest species loss), is when habitat loss is random. We can quantify this best-case scenario by taking the long-term species richness from a randomly fragmented landscape divided by the original species richness in a contiguous landscape:

$$\frac{\hat{S}_{\text{random}}\left(A_{\max}, A_e, \nu, \sigma^2\right)}{S_{\text{contig}}\left(A_{\max}, \nu, \sigma^2\right)} = \frac{\frac{A_e}{A_{\max}}\sigma^2\Psi\left(\frac{A_{\max}}{\sigma^2}, \nu\right)}{\sigma^2\Psi\left(\frac{A_{\max}}{\sigma^2}, \nu\right)} = \frac{A_e}{A_{\max}}. \tag{6}$$

Therefore, the best-case proportion of species remaining in the long term after habitat loss is equal to the proportion of habitat remaining $h = \frac{A_e}{A_{\max}}$ (Fig. 6). This result also generalises to the case where the landscape consists of multiple habitat types each providing an independent niche for species to occupy, assuming that within each niche species dynamics are neutral (Appendix 6). Even this best-case long-term scenario is substantially worse than immediate loss scenarios, where the number of species initially remaining is always higher than $\frac{A_e}{A_{\max}}$ (Fig. 6b). The importance of accurately accounting for extinction debt is underscored by a comparison with the traditional power-law SAR approach, which in a scenario of 20% habitat remaining predicts the 62–85% of species remaining (Appendix 1), a substantial overestimate compared to our results (Fig. 6a).

DISCUSSION

Habitat loss is a ubiquitous feature of modern landscapes, yet we still lack a fundamental understanding of how it affects biodiversity both in the short term and in the long term after repayment of extinction debt. The effects of fragmentation on biodiversity in particular are hotly debated (Fahrig 2017;

Figure 5 Summary of expected species richness outcomes at different spatiotemporal scales and under different levels of habitat loss and fragmentation. This figure conveys the qualitative patterns that hold across parameter space. Here $\sigma = 16$, $\nu = 0.0001$, $A_{\max} \in \{10^4, 10^6, 10^8\}$ (for local, intermediate and regional spatial scales, respectively) and $h \in \{0.8, 0.4, 0.2\}$ (for low, medium and high habitat loss, respectively). The extremes of habitat connectivity c_e at each spatial scale were determined using our full range of real landscapes to determine the lower bound and using random landscapes to determine the upper bound. Warmer colours indicate fewer species remaining (more severe species loss).

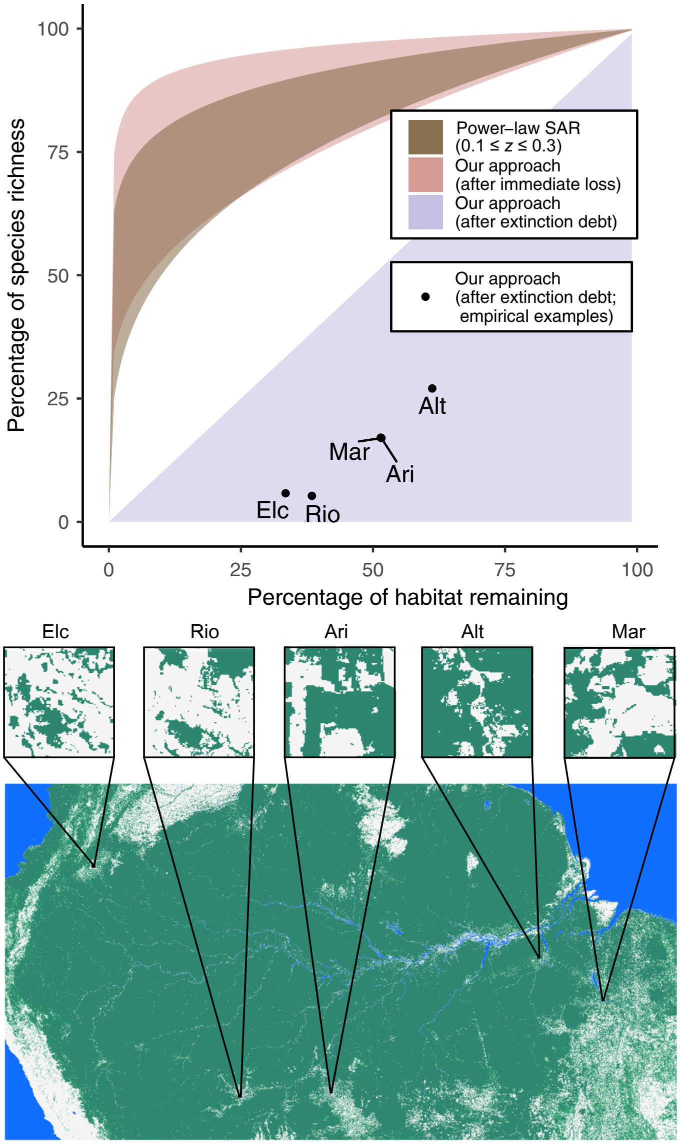

Figure 6 Different methods of estimating species richness in a fragmented landscape. The approach of Chisholm et al. (2018) gives bounds for the species richness immediately following habitat loss (red area). Our approach gives bounds for the long-term species richness (blue area). The traditional power-law approach provides a phenomenological estimate of species richness without reference to temporal scale (brown area). Predictions for tree species losses in five 100 km^2 areas of the Amazon are shown using the effective connectivity metric with $\sigma = 8.5$ (approximately 40.2 m) and $\nu = 6 \times 10^{-6}$ (Condit et al. 2002). The approach for predicting the tree species losses is outlined in Appendix 7. Abbreviations for locations: Elc, El Cayman, Colombia; Rio, Rio Branco, Brazil; Ari, Ariquemes, Brazil; Atl, Altamira, Brazil; Mar, Maraba, Brazil.

Fletcher *et al.* 2018) fuelled partly, in our view, by lack of clarity around how to quantify fragmentation. The true response of biodiversity to fragmentation likely varies across spatial and temporal scales and is affected by properties of both species and landscapes (Lindenmayer *et al.* 2000, 2015; Evans *et al.* 2017). Here we have focused on the knowledge gap surrounding habitat loss, habitat fragmentation and extinction debt by developing new analytical treatments of a spatially explicit neutral model (eqn 5). Below, we focus first on our technical results and then on the implications for the fragmentation debate more broadly.

Our neutral models account for fragmentation through new parameters, which measure landscapes through the lens of the taxa being studied. In particular, effective area A_e and effective connectivity c_e quantify concepts that have long been central to thinking in conservation. Our effective area parameter is the number of individual organisms remaining in the fragmented landscape and thus incorporates habitat quality and individual density for the taxa of interest. Our effective connectivity parameter integrates further aspects of habitat structure and dispersal mechanisms into a single value capturing broad restrictions to movement in the landscape for the taxa of interest. The broader lesson here is that any biologically meaningful metric of fragmentation must take a species-eye view of the world, rather than being based on human perceptions of what 'fragmented' looks like.

What degree of species loss can be expected in the long term in a neutral model? Even in our best-case scenario, long-term species loss is substantial (Fig. 3), with the same proportion of species lost as the proportion of habitat lost. Worryingly, all our examples based on real fragmentation maps (Figs 4 and 6) are even more severe and closer to the worst-case scenario. This suggests that realistic landscape patterns exhibit considerable structural impediments to connectivity. In the real world, where competitive exclusion and environmental stochasticity accelerate change beyond the pace of a neutral model (Kalyuzhny *et al.* 2015; Danino *et al.* 2016), and where dispersal across the matrix may increase mortality, the loss of diversity could be greater still.

One prediction of our model is that the best-case scenario for long-term species richness, under a fixed total area of habitat loss, is a randomly cleared landscape corresponding to the highest connectivity between habitat cells. This prediction should be interpreted cautiously because our model ignores edge effects (see Appendix 5), which constitute a complex variety of ecological responses, with some positive but mostly negative effects on diversity. Along edges, sensitive species can be driven to extinction by processes including altered microclimate or increased accessibility to poachers (Ewers & Didham 2006; Evans *et al.* 2017). These extinctions can also be masked along edges by increased local habitat diversity. Our model could be extended to include edge effects by appropriately adjusting effective area to penalise edges.

Our analysis has exposed one general obstacle to a rigorous conceptual foundation of 'extinction debt'. A practical definition of extinction debt in conservation biology would be based on a timescale that is long enough for a new equilibrium to be reached after fragmentation, but short enough that no significant speciation occurs. But when the ecological and evolutionary timescales overlap (e.g. in Fig. 1, which indicates roughly 50 000 years), it becomes impossible to satisfy both of these requirements simultaneously because there is no true equilibrium on the ecological timescale. This suggests that defining extinction debt means specifying a timescale of interest, and that this choice will inevitably be somewhat arbitrary: the timescale must be long enough for most extinctions to occur, but short enough that speciation is still largely irrelevant.

Moving beyond the purview of conservation biology, we see that on very long (geological) timescales, fragmentation can actually increase diversity by promoting speciation (Fig. 1). It may seem paradoxical that anthropogenic habitat fragmentation is generally thought to be bad for biodiversity whilst geological habitat fragmentation is perceived to increase diversity due to speciation and the origin of endemics in isolated habitat patches such as the islands on archipelagos. The phenomenon is of great interest in biogeography: repeated bouts of fragmentation and speciation over geological time is one hypothesis proposed to explain the high diversity and endemism of ecosystems ranging from the Amazon to the South African fynbos (Allsopp *et al.* 2014). It is pleasing that a single unified model provides explanations for why fragmentation can destroy biodiversity on short-term timescales, yet sometimes foster biodiversity on geological timescales (see Appendix 4). Also, these results highlight the conundrum that reconnecting historically fragmented landscapes can have a negative impact on biodiversity, a topic that we leave for future work.

Returning to the ongoing fragmentation debate (Fahrig 2017, 2019; Fletcher *et al.* 2018; Fahrig *et al.* 2019; Miller-Rushing *et al.* 2019), we ascribe the current impasse partly to differences in the unstated assumptions made by the opposing sides, which, in turn, is due to a reliance on mainly on verbal arguments inspired by intuition and limited empirical evidence. If even in a neutral model, the answer to the fragmentation question is non-trivial and context dependent, surely it must be so in reality as well. Therefore, we encourage participants in the fragmentation debate to take pains to make explicit their assumptions about spatial scales, temporal scales, taxonomic scope and the definition of fragmentation itself. More quantitative mechanistic modelling could help in this regard.

Beyond these general recommendations, we highlight three key messages for the fragmentation debate. First, the response of species to fragmentation depends not just on the arrangement and amount of habitat loss, but on ecological properties of the species themselves, including dispersal ability. Second, the long-term species loss following habitat loss can be drastically different to the immediate species loss. Finally, quantifying fragmentation in a mechanistic way – here using our effective connectivity and effective area metrics – is critical to properly understanding its impact.

We have presented a new analysis of a mechanistic model that allows us to hone our intuitions for how the process of fragmentation and habitat loss affects diversity over different spatial and temporal scales. In characterising the response of biodiversity to fragmentation, we show that doing so accurately requires an appropriate metric of fragmentation that specifically considers species' responses to fragmentation (effective connectivity). We hope that this will be used as the foundation for more sophisticated models forecasting diversity loss.

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AUTHORSHIP

All authors designed the study. SEDT performed simulations and analyses. All authors contributed to mathematical derivations. All authors wrote the paper.

DATA AVAILABILITY STATEMENT

Code and data are available on FigShare: https://doi.org/10.6084/m9.figshare.c.4660199. Code for simulations and analysis is available on bitbucket: https://bitbucket.org/thompsonsed/extinction_debt_eco_let.

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Additional supporting information may be found online in the Supporting Information section at the end of the article.

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