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E-Article

Reserve Size and Fragmentation Alter Community Assembly, Diversity, and Dynamics

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ABSTRACT: Researchers have disputed whether a single large habitat reserve will support more species than many small reserves. However, relatively little is known from a theoretical perspective about how reserve size affects competitive communities structured by spatial abiotic gradients. We investigate how reserve size affects theoretical communities whose assembly is governed by dispersal limitation, abiotic niche differentiation, and source-sink dynamics. Simulations were conducted with varying scales of dispersal across landscapes with variable environmental spatial autocorrelation. Landscapes were inhabited by simulated trees with seedling and adult stages. For a fixed total area in reserves, we found that small reserve systems increased the distance between environments dominated by different species, diminishing the effects of source-sink dynamics. As reserve size decreased, environmental limitations to community assembly became stronger, α species richness decreased, and γ richness increased. When dispersal occurred across short distances, a large reserve strategy caused greater stochastic community variation, greater α richness, and lower γ richness than in small reserve systems. We found that reserve size variation trades off between preserving different aspects of natural communities, including α diversity versus γ diversity. Optimal reserve size will depend on the importance of source-sink dynamics and the value placed on different characteristics of natural communities. Anthropogenic changes to the size and separation of remnant habitats can have far-reaching effects on community structure and assembly.

Keywords: habitat fragmentation, mass-effects metacommunity, productivity, single large or several small (SLOSS), spatial autocorrelation, variance partitioning, wavelet.

Introduction

The theory of island biogeography is remarkable in its ability to explain island species richness with two covariates: island area and isolation, with large islands close to the mainland having the greatest species richness (MacArthur and Wilson 1963, 1967). Diamond (1975) applied these principles to the question of whether habitat reserves, analogous to islands, should be divided into many small reserves or, at the other extreme, into a single large reserve (i.e., the single large or several small, SLOSS, debate; Simberloff and Abele 1982). Diamond (1975) argued that for a fixed total reserve area, a single large reserve would preserve the most species across reserves. Invoking MacArthur and Wilson's (1967) theory, Diamond (1975) argued that larger reserve "islands" have lower extinction rates and support more species with minimum area requirements. On the contrary, Simberloff and Abele (1976) and others (e.g., Higgs 1981; Lahti and Ranta 1985; Soulé and Simberloff 1986) pointed out that island biogeography theory provides no clear guidelines for reserve size, because it does not predict β diversity across islands or γ diversity variation among sets of islands (MacArthur and Wilson 1967). As a counterexample to Diamond (1975), Simberloff and Martin (1991) made the argument that small reserves might offer greater γ diversity when competitive exclusion is important, as small reserve systems would reduce dispersal of dominant species and reduce their exclusion of inferior competitors. However, spatial turnover in community composition was ignored in MacArthur and Wilson's (1967) theory (Margules et al. 1982; Holt 1992). The reserve size question has received little attention from the perspective of spatial community theory.

Existing theory provides a starting point for hypotheses about reserve size effects on communities that exhibit spatial turnover. In MacArthur and Wilson's theory (1963, 1967), area and distance effects were assumed to emerge from stochastic extinction risk and spatial dispersal limitation. Though not accounted for by MacArthur and Wilson (1967), competition along environmental gradients can interact with dispersal patterns to drive spatial community variation (Palmer 1992; Mouquet and Loreau 2003; Tilman 2004; Schwilk and Ackerly 2005; Gravel et

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al. 2006). We focus on a class of competitive community models that incorporate the effects of dispersal limitation and environmental gradients but that have not been previously used to study reserve size. Specifically, when (1) species show niche differentiation along an environmental gradient, (2) dispersal is limited, and (3) demography is stochastic, source-sink dynamics may drive community assembly (also known as mass effects; Shmida and Ellner 1984; Shmida and Wilson 1985; Palmer 1992; Mouquet and Loreau 2003; Gravel et al. 2006). In source-sink communities, superior competitors coexist locally with sink populations of inferior competitors subsidized by propagules from source populations in other habitats (Mouquet and Loreau 2003). Enhanced dispersal can increase source-sink effects, decrease the role of environmental constraints in community assembly, and reduce local productivity by depressing populations of the best local competitor (Mouquet and Loreau 2003; Gravel et al. 2006). In particular, plant communities may be subject to source-sink effects due to their limited ability for directed dispersal (Eriksson 1996). While the general characteristics of source-sink communities have been studied, their sensitivity to spatially explicit landscape variation and disturbance are not well known (Palmer 1992; Chase et al. 2005).

Researchers have studied reserve size effects on populations using spatially explicit metapopulation theory, which is akin to island biogeography in its emphasis on patch area and isolation. For a single species, Ovaskainen (2002) found that a few large reserves were theoretically optimal for maximal patch occupancy, while more intermediate reserves maximized time to extinction. When metapopulation processes are uncertain, an intermediate number of reserves may be optimal, although the optimal strategy depends on the subjective importance of minimizing extinction risk versus maximizing robustness to uncertainty (McCarthy et al. 2011). In one of the few multispecies (noncompetitive) models parameterized with empirical data, Nicholson et al. (2006) studied 10 species and found that a set of mostly large reserves maximized time to extinction. Additionally, empirical studies have documented how habitat fragmentation affects species richness of patches (Fahrig 2003; Yu et al. 2012); however, the empirical evidence is often contradictory (reviewed by Debinski and Holt 2000), and even less is known about richness in fragments in the presence of underlying environmental gradients.

Reserve size and environmental autocorrelation can affect communities by altering dispersal success and post-dispersal recruitment. For example, the spatial configuration of habitat reserves affects dispersal between reserves (Gustafson and Gardner 1996; Keitt et al. 1997), while the overlay of reserve structure and environmental gradients affects dispersal between different types of preserved habitat (Palmer 1992). We hypothesize that reserve size effects in source-sink communities strongly depend on organisms' dispersal ability relative to the spatial scale of environmental autocorrelation. Previous studies support this assertion (Palmer 1992; Schwilk and Ackerly 2005; Gravel et al. 2006; Mouquet et al. 2006), but few explicitly relate dispersal scale with the scale of environmental gradients. A key distinction is that "small-scale" and "large-scale" dispersal and environmental autocorrelation are relative terms. For example, when the scale of environmental autocorrelation is low, dispersal between different habitats is not limiting, and communities will likely be insensitive to changes in dispersal (Mouquet and Loreau 2003). Thus, we study reserve size variation in landscapes with different scales of environmental autocorrelation and across varying organismal dispersal ability. While previous authors have questioned whether any reserve size generalizations could emerge (Simberloff and Abele 1982), we show that simple simulations based on a few key underlying processes can illuminate important reserve size effects on community assembly.

We present the first theoretical results for how communities with source-sink dynamics along an abiotic gradient are affected by a large reserve strategy (Diamond 1975) compared to a small reserve strategy. Here, the total amount of habitat preserved is constant across different reserve size strategies; thus, our study also reveals effects of habitat fragmentation independent of habitat loss. Our approach is to simulate community dynamics across disjunct reserves with an underlying environmental gradient, bridging the discrete landscape representations of metacommunity ecology (Leibold et al. 2004) with continuous representations in landscape ecology (Holt 1992; Biswas and Wagner 2012). We focus our attention on a system that approximates tree communities. We propose that reserve size variation affects the dispersal of propagules across the landscape and thus affects community structure. We expect that reserve size effects are strongest when dispersal limitation is a major factor in community assembly, that is, when dispersal occurs at a small scale relative to the scale of environmental autocorrelation (Palmer 1992). We study reserve size effects on multiple assembly processes and community characteristics: species richness, spatiotemporal distribution of diversity, community determinism versus stochasticity, and productivity.

Methods

We developed an individual-based, spatially explicit simulation model (supplementary computer code available from the Dryad Digital Repository, http://dx.doi.org/10

.5061/dryad.1vp3j; Lasky and Keitt 2013).[1] For clarity, we follow the widely employed ODD (overview, design concepts, and details) protocol for individual-based model description (Grimm et al. 2006, 2010).

Overview

The purpose of our model is to understand how reserve size affects communities that are subject to dispersal limitation and trade-offs along environmental gradients. We studied generic simulated tree communities (e.g., Shugart et al. 1992; Hurtt and Pacala 1995; Gravel et al. 2006) undergoing deforestation. Our model emulates a simplified plant life history, with sessile individuals postgermination and seed dispersal among sites. Trees competed for exclusive access to the canopy of grid cells, leading to strong competition for space (Hurtt and Pacala 1995; Pacala et al. 1996). Adult trees had equivalent probability of mortality. However, seedling mortality was based on species environmental niches, and species identity of seedlings recruiting to canopy in gaps was a weighted lottery processes (Hurtt and Pacala 1995). Individual-based simulation models are useful for studying the effects of individual-scale mechanisms on the global properties of a system, even when analytical theory of the system is intractable (Grimm et al. 2005). Computer simulations of forest disturbance are convenient because they provide faster results than physical experiments (Coates et al. 2003; Pearson and Dawson 2005; Uriarte et al. 2009).

Design Concepts

We based our model on that of Gravel et al. (2006) and applied it in a novel way to study communities under different reserve size strategies. The model incorporates major elements required for our investigation of reserve size: a spatially explicit environmental gradient, dispersal limitation, environment-mediated competition for canopy space, and stochastic demography. Stochastic mortality, recruitment, and dispersal allow species to exist in locations where they are inferior competitors (i.e., sink populations). The combination of these elements allows us to observe community dynamics that emerge from the interplay of reserve size and source-sink dynamics (Mouquet and Loreau 2003).

Dispersal success depends in part on the scale of dispersal relative to spatial separation of suitable habitats (Keitt et al. 1997). We therefore established a common basis for specifying the scales of habitat reserves (though total area in reserves was equal in all scenarios), environmental autocorrelation, and dispersal ability. All three scales were related to a Gaussian density function via the standard deviation parameter. In the case of reserve size and environmental gradients, we simulated patterns with Gaussian spatial dependence. Dispersal distances were also simulated from a Gaussian function. As a result, we are able to directly relate the scale of dispersal to the scale of landscape structure. The choice of a Gaussian dispersal function, while not particularly realistic, simplified our analysis. Future work will consider more peaked “leptokurtic” dispersal kernels.

Entities, State Variables, and Scales

Entities in the model are individual trees and a two-dimensional grid of cells. Trees have four ontogenetic states: (1) seed, (2) live seedling, (3) live adult, and (4) dead. Trees have two-dimensional spatial coordinates that determine which grid cell they occupy. Trees also have a species state, which defines the optimal cell environmental state for the tree. Each cell has an environmental state. First, cells are either habitat or nonhabitat. Second, habitat cells have a fixed environmental state, with potential values between 0 and 100. Landscape grids consisted of 128 × 128 cells (16,384 total cells) with periodic (i.e., wrapping) boundaries, with each cell representing the canopy space occupied by an adult tree. Simulations were run for 400 time steps, with each time step representing the interval between reproduction and mortality events.

Process Overview and Scheduling

Individual tree processes include birth, dispersal, germination, recruitment to canopy, reproduction, and death (fig. A1). At each time step, adult trees reproduce, creating seeds. Adults face random mortality after reproduction at each time step. After seeds are born, they are instantly dispersed a distance and direction drawn from a dispersal kernel. Seeds arriving in nonhabitat cells instantly die, while seeds arriving in habitat cells instantly become seedlings. At each time step, seedlings face environment-dependent mortality and environment-independent mortality. Probability of environment-dependent mortality is determined by the similarity between the environmental state of the seedling’s grid cell and the optimal environmental state for the seedling’s species (Gravel et al. 2006). If an adult dies, a surviving seedling occupying the same cell is chosen at random to recruit to adulthood. At the end of a time step, the location and identity of surviving adults and seedlings are passed to the next time step.

The only grid cell process is habitat loss. All cells begin as habitat. Habitat loss occurs only once in each simulation. Cells are converted from a habitat to nonhabitat state

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[1] Code that appears in the *American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

according to neutral, spatially dependent functions that determine the characteristic size of remaining habitat reserves (see below). Simulations were initiated with a landscape occupied by source populations; the first 50 time steps were subsequently run with intact continuous habitat to allow establishment of sink populations (cf. Gravel et al. 2006). After 50 time steps, the habitat loss surface was imposed on the grid and simulations were run for 350 more time steps. Community metrics changed very little after 350 time steps (data not shown). For comparison, we conducted simulations for 400 time steps on unfragmented, intact landscapes never experiencing habitat loss.

Initialization and Inputs

Simulations began on an intact landscape of cells, that is, all cells were initially habitat. Twenty species occupied landscapes at the beginning of simulations. There was no immigration from a regional species pool to rescue species from extinction (cf. Schwilk and Ackerly 2005; Gravel et al. 2006). Species s differed only in their optimal environmental state μ_s (niche optimum), thus $s \equiv \mu_s$. Species niche optima were evenly distributed from 0 to 100, which was the range of environmental states E_i of cells i, resulting in μ_s being separated by five environmental units. At the beginning of a simulation, each grid cell i was occupied by a single adult of the species that minimized $|E_i - \mu_s|$, defined as the best local competitor. Species were initially located in their optimal habitat in order to begin with seminatural distributions and to avoid dispersal limitation at the beginning of simulations (Gravel et al. 2006).

Submodels

Simulated Landscapes. Each cell was given an environmental state drawn from a standard Gaussian distribution. To control the level of spatial autocorrelation in the environment (i.e., spatial dependency), we used wavelet transformations (Keitt 2000). Wavelet coefficients w describe scale-specific variance in environmental structure and can be transformed to alter the scale of environmental spatial autocorrelation. We conducted a two-dimensional discrete wavelet transform of the landscape using the "la8" wavelet from the waveslim package in R statistical software. Scale-specific environmental variation was determined by σ_E, according to

$$\mathrm{Var}\,(w;\sigma) \propto \exp\,(-2\sigma_E^2 f^2), \qquad (1)$$

where w represents wavelet coefficients, and f is the frequency or inverse scale of analysis (Keitt 2009). By tuning σ_E, we were able to generate smooth surfaces with longer-range spatial dependence (larger values of σ_E) versus rougher surfaces exhibiting fine-scale heterogeneity (smaller values of σ_E). Environmental values E_i in cells i were scaled so that each landscape had E_i ranging from 0 to 100. Examples are shown (fig. 1). For each value of σ_E tested, we created five intact landscapes for parallel simulations that were each subject to varying reserve size strategies, including no habitat loss.

The wavelet transformation was also used to simulate habitat loss and hence determined reserve size. Random surfaces were generated with a specified spatial dependence σ_H (as in eq. [1]) and then thresholded to produce a binary reserve/nonreserve template. In some cases, small reserves could merge because of grid effects. We therefore chose a threshold for the habitat loss surface that yielded 75% habitat loss and 25% of the landscape in reserves, values that were equal across different reserve size strategies. This threshold ensured that even small-scale habitat loss resulted in distinct, spatially separated reserves. Nonreserve areas were considered to be converted and unsuitable for occupancy. Small values of σ_H generated small habitat reserves, whereas the largest value gave Diamond's (1975) single reserve strategy (fig. 1).

Reproduction and Dispersal. Adults released seeds that dispersed based on a kernel with random variables for distance and direction. At each time step, adults released 5 seeds, which dispersed in a direction drawn from a uniform distribution to distances drawn from a Gaussian distribution centered at zero. Here $\Pr(d)$ is the probability a seed disperses distance d,

$$\Pr\,(d) = \frac{\exp\left(-\frac{d^2}{2\sigma_D^2}\right)}{\sigma_D\sqrt{2\pi}}, \qquad (2)$$

where σ_D determines the scale of dispersal. Larger values of σ_D allowed dispersal over large scales, while smaller σ_D limited dispersal to small, local scales. Seeds that landed in deforested matrix perished, while those landing in habitat reserves became seedlings.

Recruitment. When an adult died, one seedling in each grid cell was chosen based on a random draw from a categorical probability distribution where species recruitment probabilities were the vector $\boldsymbol{R} = \{R_1, R_2, \ldots, R_S\}$. Thus, the probability R_s of species s recruiting into the adult state in a canopy gap was

$$R_s = \frac{a_s}{\sum_{s=1}^{S} a_s}, \qquad (3)$$

where a_s is the abundance of seedlings of species s in the cell, with S total species. Stochastic community dynamics

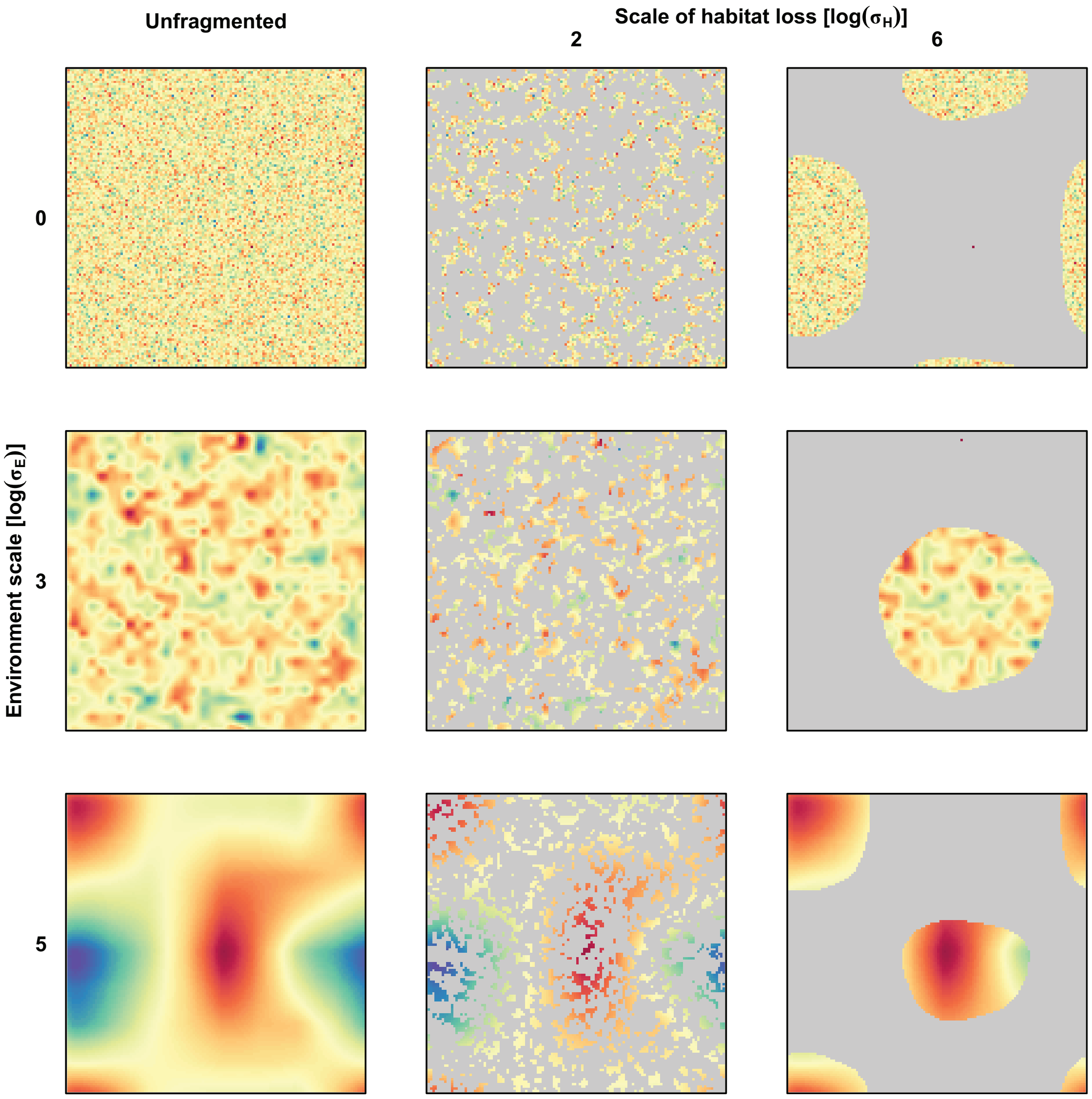

Figure 1: Examples of the range of random, wavelet-generated landscapes studied. Color indicates the environmental gradient within habitat, while gray indicates unsuitable areas of habitat loss. Landscapes ranged from those with small-scale environmental spatial autocorrelation (*top row*) to large-scale spatial autocorrelation (i.e., spatial dependency, *bottom row*). In all simulations of reserve size, the proportion of habitat preserved was fixed at 0.25. As the scale of habitat loss increases from small (*middle column*) to large (*right column*), reserve size increases and fragmentation decreases (small reserves in *middle column*, large reserves in *right column*). Note that the same unfragmented, intact landscape in each row underlies the different reserve size scenarios in columns.

were partly a result of this random recruitment process. Seedlings that did not recruit remained seedlings.

Neutral Mortality. At each time step, adults faced mortality M with probability $\Pr(M) = .25$, and a dying adult created a canopy gap in its cell (following the adult mortality rate of Gravel et al. 2006). While only one adult could occupy a cell at a time, local density of seedlings was not limited (Gravel et al. 2006). However, at each time step, we imposed a global carrying capacity on seedlings enforced by neutral mortality. Seedling carrying capacity was 200,000 across the landscape before habitat loss and 50,000 (for computational speed) after habitat loss, allowing an average of ~12 seedlings per habitat cell.

Environment-Dependent Mortality. Niche-mediated environmental constraints on community assembly were simulated at the stage of seedling survival (following Gravel

Table 1: Measures of landscape and community characteristics

Community characteristic	How calculated
Spatial distance from potential source to sink habitats	Average distance from a habitat cell to the nearest cell where the environmental difference between cells is ≥2.5
α species richness	Average species richness of two neighboring trees
γ species richness	Total species found on the landscape
γ functional diversity	Range of species niches μ_s among surviving adults
Productivity	Gaussian function of how well matched the average adult is to its cell environment (productivity $= 1 - \Pr(M)$ from eq. [4])
Proportion of community variation explained by environment	Proportion of spatial variation in adult composition explained by cell environmental values, using variance partitioning (Peres-Neto et al. 2006)
Temporal community turnover	Mean niche difference between adults in cell i at time t versus $t-l$, across the last eight time steps, where l is the lag for comparison: $\sum_{t=393}^{t=400} \lvert \mu_{it} - \mu_{i(t-l)} \rvert /8$

et al. 2006). At each time step, seedlings perished with a probability determined by the difference between their niche optimum and the environmental state of their cell. The probability of mortality due to environment, $\Pr(M_E)$, increased with increasing difference between the niche optimum μ of species s and the local environmental state E_i of cell i, according to a Gaussian function with a standard deviation of 35 (i.e., 35% of the environmental range),

$$\Pr(M \vert E_i, \mu_s) = 1 - \exp\left(-\frac{[E_i - \mu_s]^2}{2 \times 35^2}\right). \tag{4}$$

Seedlings in a cell with environment equal to their niche optimum had $\Pr(M_E) = 0$, that is, when $E_i = \mu_s$. The standard deviation of equation (4) is a measure of species fundamental niche breadth, and its value was chosen to allow a modest amount of niche overlap among species, which allows sink populations to exist (Gravel et al. 2006).

Exploration of Parameter Space

We explored variation in three parameters, σ_H, σ_E, and σ_D, which determine reserve size, the scale of environmental spatial autocorrelation, and the scale of dispersal, respectively. We tested an exponential series of parameter values for all three scale parameters: $\sigma = \exp(x)$, $x = \{-\infty, 0, 1, 2, 3, 4, 5, 6\}$. For each value of σ_E, an original intact landscape was created, giving eight intact landscapes with different spatial autocorrelation of environment. Five replicate simulations were conducted on these intact landscapes without habitat loss for each level of σ_D, giving 320 simulations on intact landscapes. In parallel simulations of reserve size variation, each intact landscape was subject to habitat loss under each value of σ_H (determining reserve size). Five replicate reserve systems were created for each value of reserve size (σ_H) for each σ_E. Tree communities were simulated at each value of σ_D for each combination of σ_E and σ_H, giving 2,560 simulations in reserves (5 replicates × 8^3 for eight values of the three σ parameters). We studied a reduced parameter space for effects of parameter variation on temporal community turnover, $\sigma = \exp(x)$, $x = \{-\infty, 1, 3, 5\}$.

Characterizing Landscapes and Resulting Communities

We analyzed resulting landscapes and adult tree communities with seven metrics of community assembly, diversity, and dynamics (summarized in table 1). Local coexistence in source-sink metacommunities depends on dispersal from a species' optimal environment into one where it is an inferior competitor (Shmida and Wilson 1985; Mouquet and Loreau 2003). However, splitting a single reserve into multiple reserves necessarily increases the average distance between sites with habitat (assuming reserves are not extremely irregular in shape). Thus, we measured the structure of each landscape to estimate potential dispersal limitation between potential source and sink environments. We assumed potential sources for species s were found in the cells where it was the best competitor, defined as all cells i for which μ_s gives the minimum $\lvert E_i - \mu_s \rvert$ among all species S. Potential sinks were defined as cells with environments sufficiently different so as to be sources for a different species. Thus, the environments of a potential source and sink differed by at least half the environmental distance between species niche optima ($5/2 = 2.5$ environmental units). For each landscape, we selected 100 random habitat cells i and calculated the average distance in landscape space from each cell i to the nearest cell j such that $\lvert E_i - E_j \rvert \geq 2.5$ was satisfied. The use of distance as a proxy for dispersal limitation is justified because dispersal kernels were solely a function of distance (eq. [2]).

The second and third metrics were α species richness and γ species richness, respectively. We measured α species richness of adults at the smallest scale possible, between two neighboring individual trees. The neighborhood of each cell was defined as the four adjacent cells. We randomly sampled 100 exclusive neighbor pairs from each community and calculated the average species richness of pairs ($\alpha \in [1, 2]$). We calculated γ richness as the total number of species of adults across the landscape. Note that because the range of possible α richness ($\alpha \in [1, 2]$) was much less than that of γ ($\gamma \in [1, 20]$), the great majority of variation in β diversity is contained in γ. Thus, we do not present results on β diversity, though they can be obtained by subtracting average α richness from γ richness (Lande 1996; Mouquet and Loreau 2003). The fourth metric was γ functional diversity. We calculated γ functional diversity as the range of niche optima μ_s represented by species of surviving adults at the end of simulations. This allowed us to determine when differences in γ richness were due to loss of species with niches at environmental extremes.

The fifth community characteristic we measured was average cell productivity, ϕ. We considered productivity ϕ_i of cell i as a function of the performance of the resident adult species given the environment, following previous authors (Tilman et al. 1997; Mouquet and Loreau 2003). Adults occupying environments far from their niche optimum were assumed to have low productivity (MacArthur and Levins 1967). Productivity was calculated as a Gaussian density of $E_i - \mu_s$, with the greatest density at zero, as with seedling survival (Palmer 1992). Thus, we assumed that the adult in cell i of species s was most productive if it was at its niche optimum, that is, when $E_i = \mu_s$, $\phi_i = 1$. Productivity of an adult in a cell was the same as the environment-dependent probability of seedling survival ($\phi_i = 1 - \Pr(M_E)$ in eq. [4]).

The sixth community characteristic quantified the effect of deterministic environmental constraints on community composition. For each community, we randomly sampled 100 individuals from across the landscape. We used variance partitioning (Peres-Neto et al. 2006) to calculate how much spatial community turnover was explained by the environmental states of cells. We used functional community composition, that is, μ_s niche optima of adults, as the response variable. Because μ_s are ordinal, μ_s are more informative than categorical species identity. We also explored using variance partitioning to estimate the contribution of dispersal limitation to spatial community turnover. One of the most commonly employed methods is to use eigenvectors of the pairwise distance matrix among sampling locations as proxies for dispersal ("spatial structure"; Borcard and Legendre 2002). However, we were not able to separate the contribution of environment from spatial eigenvectors, because spatial structure was nearly collinear with environmental pattern.

The last characteristic we studied was temporal community turnover. When community assembly is ecologically neutral, there may be high turnover in species composition even when the environment is constant (Gravel et al. 2006). We measured temporal functional turnover, that is, how μ_s of species occupying a given cell changed across time steps. For the last eight time steps t, we calculated the mean change in μ_s of the adult occupying the cell at time t versus μ_s of the adult at time $t - l$. In each community, we sampled 100 cells and averaged their mean temporal turnovers. We tested turnover for values of l from 1 to 5 (table 1).

We tested the statistical significance of monotonic reserve size effects by comparing metrics at a given level of relative dispersal (σ_D/σ_E) across different reserve size scenarios. For each value of relative dispersal, there were replicate simulations with different reserve sizes (i.e., scales σ_H of habitat loss). The effects of reserve size (measured with σ_H) were tested separately for each level of relative dispersal using linear mixed-effects models. The prehabitat loss, intact landscape identity was a random effect because simulations were conducted with replicates of habitat loss on the same eight underlying landscapes. Reserve size and community metrics were rank transformed to allow flexible modeling of nonlinear (though monotonic) relationships. We tested the effect of reserve size on distance between potential sources and sinks separately for each value of σ_E using Spearman's rank correlation.

Results

Landscape Structure

For the largest value of σ_H, a single large reserve was created (Diamond 1975), habitat loss occurred at large scales, and the remnant habitat was unfragmented. Large reserves had less spatial distance between potential source and sink cells (i.e., cells with environmental difference ≥ 2.5) relative to small and highly fragmented reserves, even though total area in reserves was equal for different reserve size strategies (significant for all but one scale of environmental spatial autocorrelation, Spearman's rank correlation, hereafter $\alpha = 0.05$; fig. 2). Thus, when habitat was maintained in large reserves, seeds had to travel less distance to reach environments where a different species would be the best competitor, compared to distances in small reserve systems.

Species Richness

Reserve size also affected α and γ species richness. Reserve size effects were strongest when dispersal occurred at a small scale relative to the scale of environmental spatial autocorrelation. At the five smallest nonzero relative scales of dispersal (scale of dispersal divided by environmental

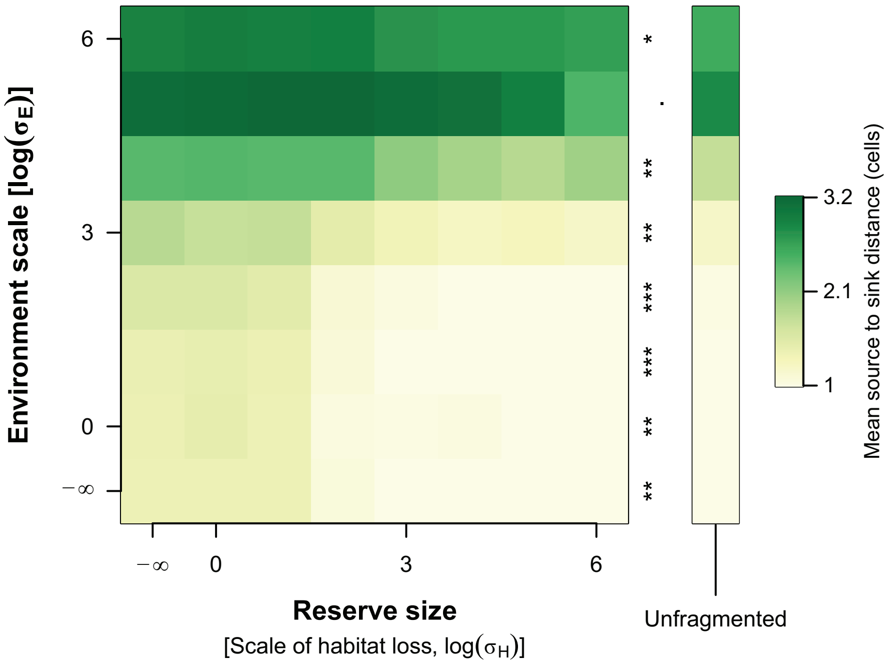

Figure 2: Spatial separation between potential source and sink habitat cells increased in smaller reserves, that is, at smaller scales of habitat loss. A potential sink environment is defined as one that has an environmental value distinct enough from a potential source so that a different species is the best competitor (environmental difference between cells ≥2.5). Note that in all simulations of reserve size, the proportion of habitat preserved was fixed at 0.25. Asterisks indicate the significance of the reserve size effect, that is, the correlation between distance to different environment and the scale of habitat loss (Spearman's rank correlation; period, $P < .1$; one asterisk, $P < .05$; two asterisks, $P < .01$; three asterisks, $P < .001$).

scale, σ_D/σ_E), α richness was significantly greater in large reserves than in small reserves (linear mixed-effects model; fig. 3*A*; for display of absolute scales σ, see fig. A2). Reserve size impacts on diversity are demonstrated in example simulation outcomes (fig. 4). For three larger scales of relative dispersal, the relationship between reserve size and α richness reversed, with significantly less α richness occurring in large reserves, though the effect was of less magnitude than at small-scale dispersal (linear mixed-effects model).

Reserve size altered the scale of relative dispersal at which α richness was maximized (fig. 5). In intact landscapes and large reserves, α had a unimodal relationship with relative dispersal, with a peak at $\log(\sigma_D/\sigma_E) = -2$. However, in landscapes with small reserves, α had a saturating relationship with dispersal, whereby α increased with greater dispersal until $\log(\sigma_D/\sigma_E) = 1$, beyond which α was nearly constant. In general, the effects of dispersal on α and γ richness were weaker in large reserve systems compared to small reserve systems (fig. 5).

There was a strong and monotonic relationship between γ richness and reserve size. Large reserve systems had significantly less γ richness than small reserve systems at small scales of dispersal and up to $\log(\sigma_D/\sigma_E) = 3$ (linear mixed-effects model; fig. 3*B*). Large reserve systems harbored significantly less γ richness even when there was no intercell dispersal, that is, when $\log(\sigma_D) = -\infty$. We found that γ richness variation was closely correlated to γ functional diversity, as quantified by the niche range of surviving adult species at the end of simulations (Spearman's rank correlation, $\rho = 0.99$, $P < 10^{-16}$). As with γ richness, γ functional diversity was significantly reduced in large reserve systems at small scales of dispersal and up to $\log(\sigma_D/\sigma_E) = 3$ (fig. 3*C*).

Community Function and Assembly

Reserve size effects on other community metrics were roughly similar to species richness, in that reserve size had its strongest effects when dispersal occurred at relatively small scales. The average productivity of a cell decreased significantly as reserves became larger for all but two scales of relative dispersal (linear mixed-effects model; fig. 6*A*).

Increasing reserve size decreased the strength of environmental constraints to community composition, as measured by the proportion of spatial community variation explained by the environment (fig. 6*B*). More community variation was explained by environment when habitat was

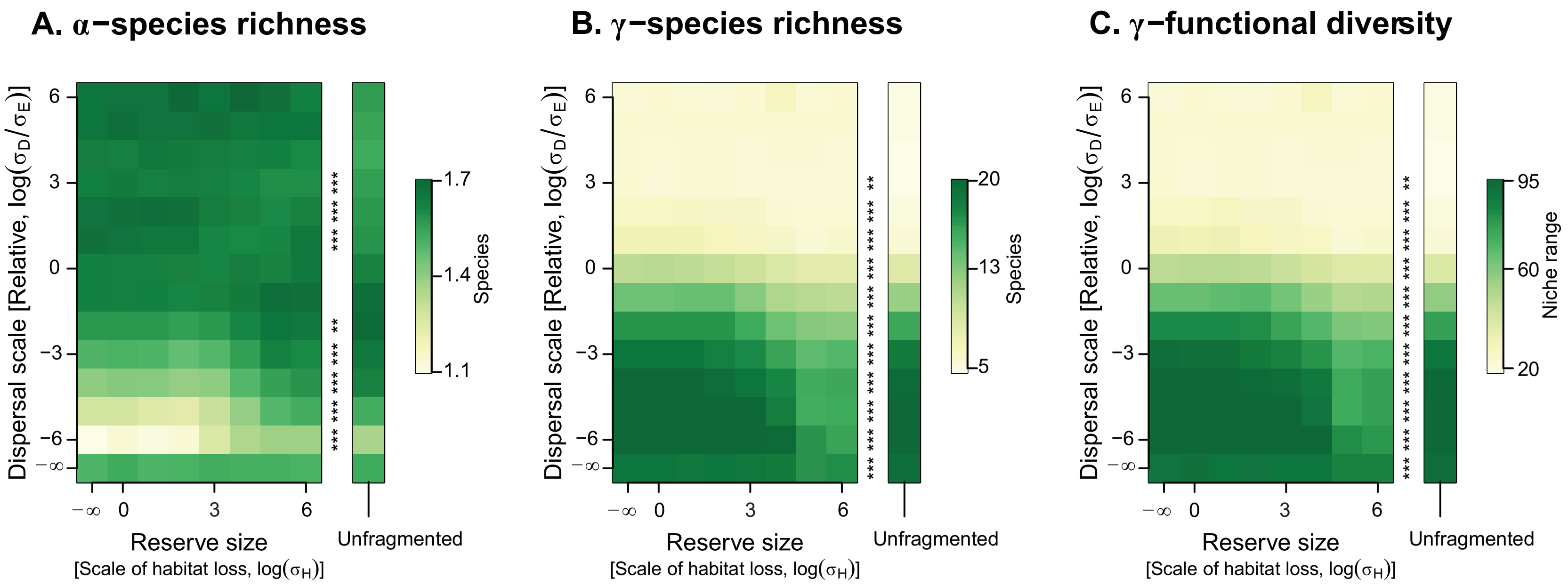

Figure 3: Change in diversity patterns across landscapes of varying reserve size (scales of habitat loss, *X*-axes) and scales of dispersal (relative to environment, *Y*-axes). *A*, α species richness. *B*, γ species richness. *C*, γ functional diversity, that is, the range of environmental niches represented by species on the landscape. Note that in all simulations of reserve size, the proportion of habitat preserved was fixed at 0.25. Asterisks indicate the significance of the reserve size effect for a given level of relative dispersal, that is, the correlation between the diversity response variable and the scale of habitat loss (linear mixed-effects model; period, $P < .1$; one asterisk, $P < .05$; two asterisks, $P < .01$; three asterisks, $P < .001$).

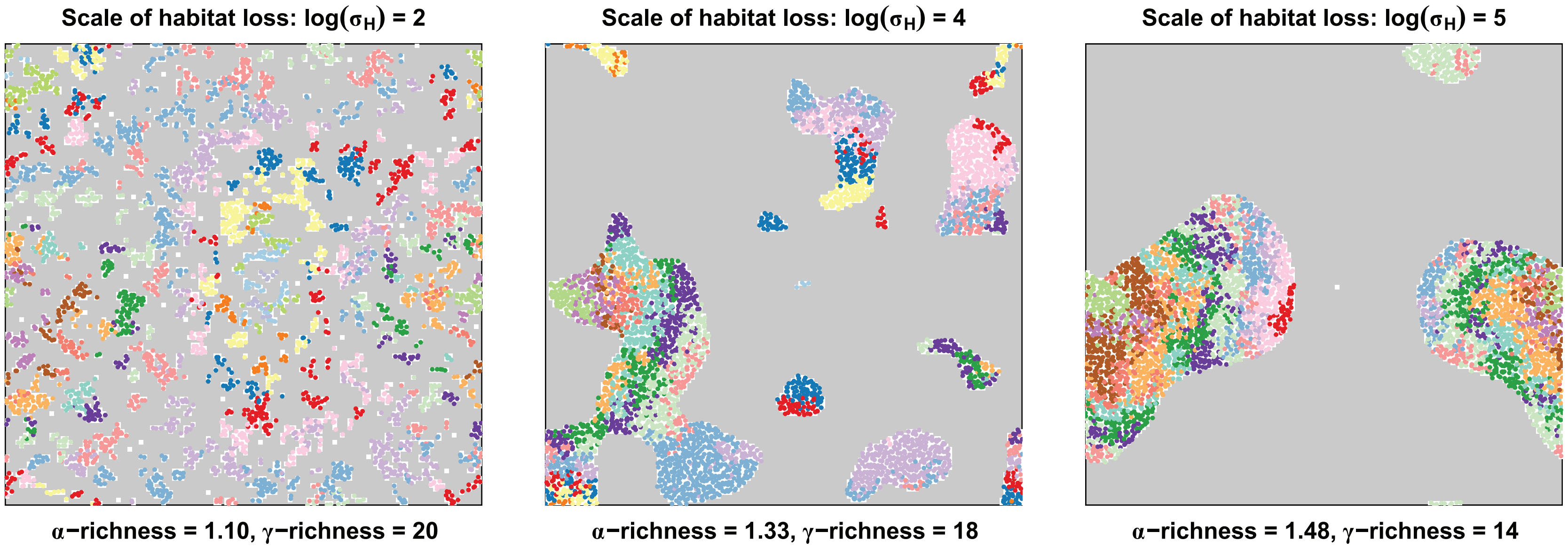

Figure 4: Comparison of three different habitat loss scenarios for the same landscape, showing how reserve size affects diversity patterns. In these simulations, the scale of dispersal (σ_D) = 1 cell. Deforested areas are shown in gray and occupy 75% of each landscape. Individual trees are represented as circles of different colors, with color indicating different species with different environmental niches. Note that similar colors here do not indicate similar niches of different species and that the environmental gradient within reserves is not shown. This was done in order to improve visualization. Note that smaller reserves (*left*) tended to be dominated by the best local competitor.

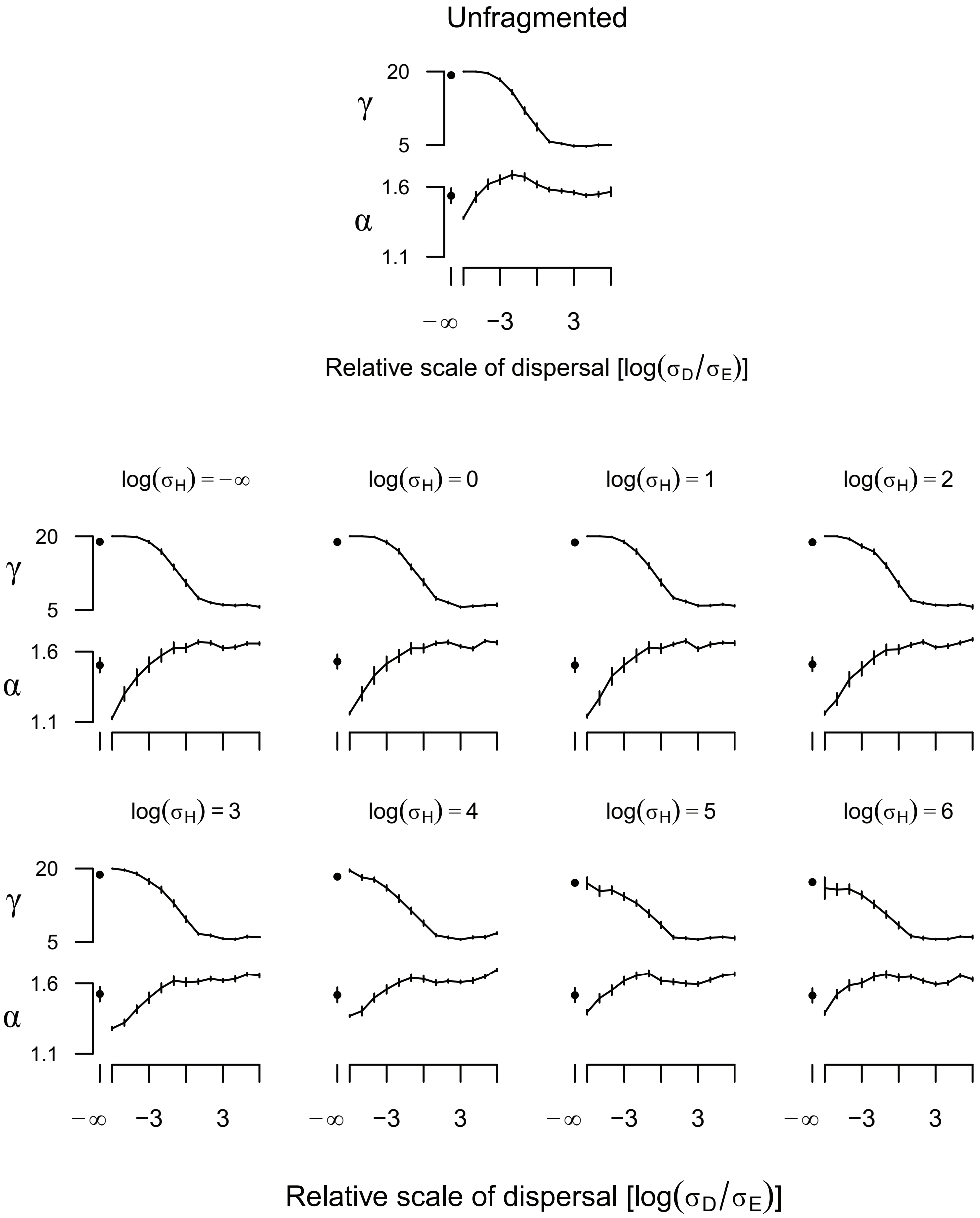

Figure 5: Change in effects of dispersal on communities under different reserve sizes. In unfragmented landscapes, there was a unimodal relationship between α richness and relative dispersal. In small reserve systems (e.g., $\log(\sigma_H) = -\infty$), there was a strong monotonic increase in α with greater dispersal. Both α and γ richness showed weaker responses to increased dispersal when in large reserves (e.g., $\log(\sigma_H) = 6$). Note that in all simulations of reserve size, the proportion of habitat preserved was fixed at 0.25. Vertical bars show standard errors.

divided into many small reserves. This increase in determinism in small reserve systems was significant when dispersal occurred at small scales and up to $\log(\sigma_D/\sigma_E) = 3$ (linear mixed-effects model). At the smallest scale of nonzero dispersal, temporal community turnover in a given cell (as measured by average difference in adult niches from one time step to the next, $l = 1$) significantly increased as reserves became larger (linear mixed-effects model, $P = .0463$), while the reverse was true when $\log(\sigma_D/\sigma_E) = 1$ ($P = .0498$; fig. A3). Reserve size effects were not significant at other scales of dispersal, though temporal turnover exhibited a strong peak at intermediate dispersal. Results were similar when comparing temporal niche difference at time lags from 1 to 5 time steps.

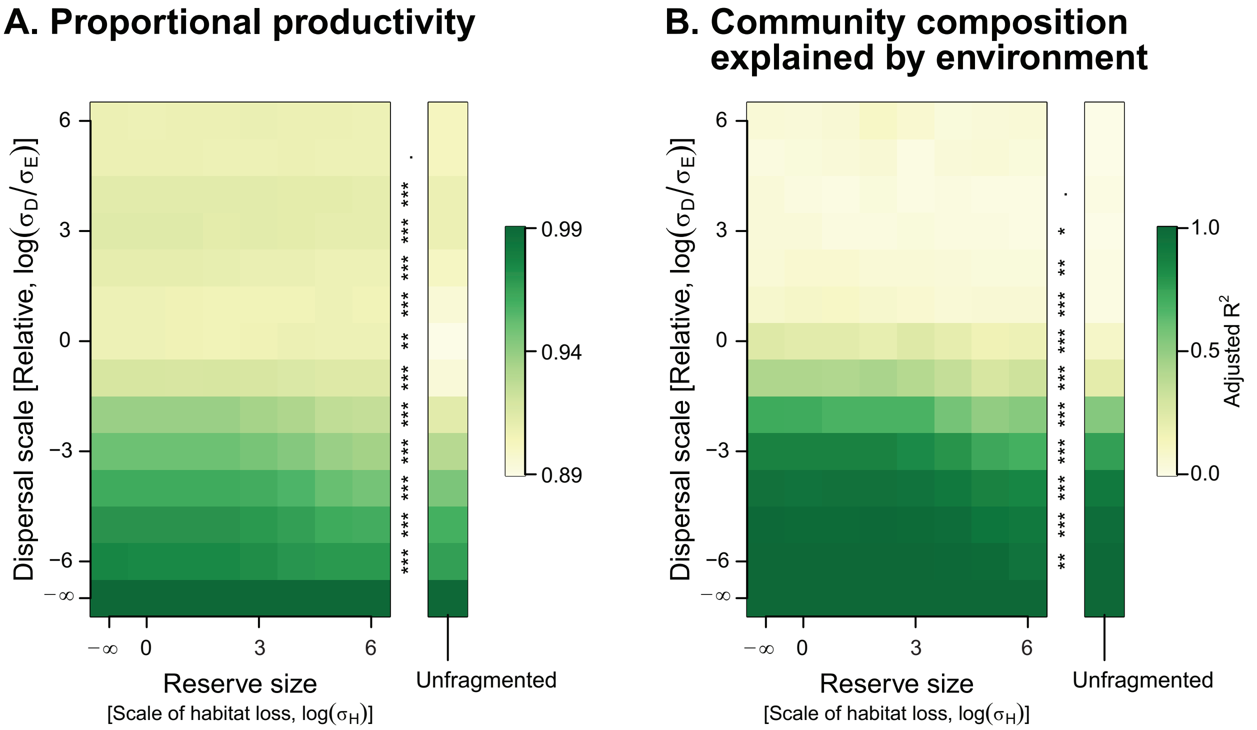

Figure 6: Change in productivity and environmental determinism across landscapes of varying reserve size (scales of habitat loss, *X*-axes) and relative scales of dispersal (*Y*-axes). Note that in all simulations of reserve size, the proportion of habitat preserved was fixed at 0.25. *A*, Proportional productivity is measured as a fraction of the maximum possible, which is attained by a species found at its niche optimum. *B*, Proportion of spatial turnover in community composition explained by environmental gradients, using variance partitioning. Asterisks indicate the significance of the reserve size effect for a given level of relative dispersal, that is, the correlation between the community response variable and the scale of habitat loss (linear mixed-effects model; period, $P < .1$; one asterisk, $P < .05$; two asterisks, $P < .01$; three asterisks, $P < .001$).

Discussion

Previous research on the effects of reserve size variation had largely overlooked competitive communities with spatial turnover driven by abiotic gradients. We found that community composition under a large reserve strategy (Diamond 1975) was heavily influenced by dispersal effects, whereas the effect of the abiotic gradient was greater in small reserves. Fragmentation into small reserves increased the distance and decreased dispersal between potential sources and sinks, which in turn homogenized local communities and enhanced environmental effects on composition. In several respects, such as α richness and productivity, communities in large reserve systems were most similar to intact landscapes. In other respects, such as γ richness and γ functional diversity, communities in small reserve systems were most similar to those in intact landscapes. Reserve size variation had the strongest impact on communities when the scale of dispersal was smaller than the scale of environmental spatial autocorrelation, as these are the conditions under which dispersal limitation maximally influences community composition.

In this study, variation in reserve size was equivalent to the degree of habitat fragmentation, independent of the amount of habitat loss, as we varied reserve size while holding total area constant. Our results may thus shed light on semantic debates over the meaning of fragmentation per se (Ewers and Didham 2007; see reviews by Fahrig 2003; Lindenmayer and Fischer 2007; Tscharntke et al. 2012). Our results highlight that fragmentation, habitat loss, and diversity effects interact in complex nonlinear ways (cf. Fahrig 2003). It is crucial to consider competing scales of landscape pattern, dispersal capacity, and underlying environmental variation in order to arrive at a predictive theory.

Reserve size effects in our model were largely determined by their influence on the spatial separation of potential source environments from sinks. All else being equal, increased distance between sites differing in environment decreases subsidies of propagules to potential sinks. These subsidies of migrants across environmental gradients are essential to generating sink populations and can play a fundamental role in determining community patterns (Palmer 1992; Mouquet and Loreau 2003; Mouquet et al. 2006). For example, mesocosm experiments have shown that dispersal variation had stronger effects on diversity when habitat gradients were present compared to when dispersal occurred across a single habitat type (Chisholm et al. 2011). Here, nearly all effects of reserve size variation weakened as dispersal became global, suggesting that limited dispersal was the mechanism of reserve size effects. With the exception of γ diversity, all community metrics were unaffected by reserve size when there was no intercell dispersal, that is, when all assembly processes were local (i.e., when $\log(\sigma_D) = -\infty$; figs. 3, 6, A2, A3).

Dispersal rates across the environmental gradient, as a function of both organismal dispersal ability and reserve size, played a central role in α richness variation. Previous studies have found that when communities are strongly dispersal limited, highly connected patches positioned centrally in the landscape have the greatest α diversity due to high immigration (Economo and Keitt 2008, 2010). However, communities affected by a combination of dispersal and environmental limitations exhibit more complex dynamics. Our results from intact landscapes were consistent with theoretical (Mouquet and Loreau 2003; Mouquet et al. 2006) and experimental findings (Cadotte 2006; Howeth and Leibold 2010) that dispersal and α richness have a unimodal relationship, with α peaking at intermediate dispersal. High dispersal decreases α because species specialized in extreme environments are driven extinct by the best average competitors across environments (Mouquet and Loreau 2003). This pattern was evident in γ functional diversity, which was consistently lower in large reserves, indicating the loss of species with extreme niches. The correlation between dispersal and α was largely positive in reserve systems (fig. 5). The weak or nonexistent α peak at intermediate dispersal in reserves suggests that interreserve dispersal was not high enough to cause sufficient extinctions to decrease α, possibly because of propagule loss to the matrix. However, at some large scales of dispersal, large reserves had significantly less α richness than small reserves, as expected from a unimodal relationship between dispersal and α (Mouquet and Loreau 2003), though the effect was weak.

Contrary to α, γ species richness in highly fragmented small reserves was more similar to γ in intact landscapes, likely for two reasons. By studying scenarios with zero and nonzero dispersal, we were able to separate the roles of environmental sampling and dispersal in causing greater γ species richness in small reserves, a novel achievement for reserve size and fragmentation studies (Tscharntke et al. 2012). First, when environmental variation was shallow and autocorrelated across large scales, a widely dispersed set of reserves was required to sample the range of environments present in the landscape. The effect of more extensive environmental sampling on γ richness was demonstrated by the greater γ in small reserves versus large reserves even when dispersal was zero (when $\log(\sigma_D) = -\infty$ in fig. 3*B*). Spatial autocorrelation of environmental conditions is pervasive in natural landscapes. However, the spatial sampling effect of small reserves depends on the segregation of species niches along those environmental gradients and thus depends on spatial autocorrelation in environmental niche axes. Authors have previously argued that many small reserves should have greater spatial sampling of species (Simberloff and Abele 1976) and that habitat preservation with low spatial autocorrelation better samples γ richness than a few large reserves (Seabloom et al. 2002). Likewise, the use of complementarity indices to maximize γ richness in reserves often prioritizes a large number of fragmented reserves (Margules and Pressey 2000; Economo 2011).

Dispersal limitation also contributed to greater γ in small reserve systems. Increasing σ_D from zero to small scales magnified the increase in γ richness in small reserves versus large reserves (fig. 3*B*). Thus, the high γ richness in small reserve systems is due to both dispersal limitation and environmental sampling. Species that specialized in extreme, uncommon environments were the source of extinctions in large reserves, indicating that decreased distances between potential sources and sinks as well as increased dispersal likely caused the best average competitors to exclude marginal species. The effect of dispersal on γ as the best average competitors dominate has been demonstrated previously (Palmer 1992; Mouquet and Loreau 2003; Cadotte 2006). We place previous findings in the context of reserve size strategy in landscapes with environmental gradients and provide quantitative results to support previous verbal arguments against a universal large reserve strategy (Simberloff and Abele 1976; Soulé and Simberloff 1986).

In landscapes with greater disturbance and smaller populations than ours, extinction-colonization dynamics of patches may become more important. Community-wide, populations were controlled largely by adult mortality and the carrying capacity of seedlings. In our simulations, nearly all habitat cells were occupied, and the best local competitors dominated small reserves even under low dispersal. Had survival and seedling carrying capacity been sufficiently low, there would be many unoccupied patches, especially in small reserves having a higher risk of stochastic extinction (Ovaskainen 2002). As a result, the best local competitor might rarely be present in small reserves, and environment would play a reduced role in community composition (Horn and MacArthur 1972). While smaller reserves in our study maintained greater γ richness, real forested landscapes may suffer from more frequent disturbance at fragment edges that could change our results (Laurance et al. 1998). High temporal frequency disturbances can eliminate the gains in γ diversity in fragmented landscapes (Roy et al. 2004).

Increased dispersal across environmental gradients in large reserves and intact landscapes caused homogenization of communities, as evidenced by the reduced importance of environment in explaining community variation compared to small reserves (Mouquet and Loreau 2003; Schwilk and Ackerly 2005; Gravel et al. 2006; Mouquet et al. 2006). At all but the largest dispersal scales, communities in small reserves tended to have composition determined by environmental conditions. Our results are consistent with findings from fragmentation experiments that (1) β diversity in old fields was greater among small fragments compared to within large fragments (Cook et al. 2005) and (2) the distributions of common understory plant species became more aggregated over time within small forest fragments relative to distributions in continuous forest (Morgan and Farmilo 2012). In our study, temporal community turnover was greater in large reserves, albeit under limited conditions. Similarly, in a metacommunity of larval amphibians, ponds with greater connectivity to other ponds showed greater temporal community turnover, suggesting a role for landscape structure in controlling dispersal and thus community stochasticity (Werner et al. 2007). To the contrary, the old field experiment of Cook et al. (2005) showed the greatest temporal turnover in small patches, which the authors attributed to greater stochastic extinction due to low population sizes in small patches. However, dispersal distances in the study by Cook et al. (2005) may have been sufficiently large to overcome distances between patches, which would reduce the effects of patch area.

The changing importance of deterministic environmental constraints versus stochastic dispersal limitation and the sustainability of sink populations are rarely quantified in assessments of anthropogenic impacts. However, sink populations maintained by dispersal may have an important conservation value. Source-sink dynamics are likely common in sessile organisms with passive dispersal, such as trees, because they have a limited ability to disperse to optimal environments (Eriksson 1996). Sink populations may promote metapopulation persistence under temporal disturbance regimes (Falcy and Danielson 2011). Additionally, stochastic dispersal that maintains α diversity in one functional group, such as trees, may be important to diversity conservation of a functional group that interacts with trees (Kissling et al. 2007). For example, if a pollinator community depends on year-round floral resources from a diverse forest community, breaking a landscape into small forest reserves may change the distribution of plant diversity compared to diversity in large reserves and hence the spatiotemporal distribution of floral resources.

Here, we have shown how the decision to create large reserves (Diamond 1975) versus small reserves can affect the distance between environments dominated by different species and have cascading effects via source-sink dynamics. Communities in which local coexistence is dominated by source-sink dynamics may be more sensitive to reserve size compared to communities in which local coexistence is due to local niche partitioning. Factors that reduce source-sink dynamics, such as directed dispersal to optimal environments, may reduce the reserve size effects we observed. However, the empirical importance of source-sink dynamics and their role in driving diversity patterns is poorly known. Scientists' limited understanding of the importance of dispersal in community assembly represents a major challenge to land-use planning because dispersal is strongly affected by landscape change (Economo 2011).

The increased importance of source-sink dynamics in large reserves was responsible for decreased productivity. In community models with high occupancy where species niches are differentiated spatially across environments (as opposed to locally within environments), increasing local diversity tends to decrease productivity because additional species are sink populations of inferior competitors (Mouquet and Loreau 2003). This negative diversity-productivity relationship is known as a negative selection effect (Loreau 2010). Our results show that the negative selection effect decreased in smaller reserves. When species niches are differentiated locally within an environment, more diverse communities tend to be more productive, partly because species limit themselves more than each other, causing overyielding (MacArthur and Levins 1967). Additionally, temporal environmental variation can cause positive diversity-productivity relationships when dispersal provides spatial community "insurance" across different temporal environmental fluctuations (Loreau et al. 2003; Gonzalez et al. 2009). The degree to which spatial niche differentiation across environments versus local niche differentiation explains species coexistence will partly determine the strength of reserve size effects on productivity. The cascading effects of landscape change on community assembly and properties such as productivity merit further investigation because of the possible dependence on axes of niche partitioning. Finally, had we begun simulations with species located far from their optimal positions on the environmental gradient, low dispersal between small reserves might have left small reserves stuck with suboptimal species of low productivity.

We acknowledge that model simplification may prevent our simulation from capturing many aspects of real landscapes, such as increased disturbance at forest edges and the persistence of trees in the matrix. The demographic parameters used in our model are not representative of any specific community, thus the strength of reserve size effects will change among systems. Additionally, the amount of habitat lost can also affect which reserve size strategies are optimal for a given metapopulation (Ovaskainen 2002).

Conclusions

Our model provides novel results about potential impacts on community structure and assembly of a large versus small reserve size strategy. Our results shed light on previously understudied aspects of reserve size variation but are not intended to determine a single, universally applicable reserve size strategy (Ovaskainen 2002). Overall, our results indicate trade-offs in community patterns if a large reserve size strategy is adopted, with α richness and community stochasticity enhanced in large reserves and γ richness, productivity, and environmental constraints enhanced in small reserves. We demonstrated that reserve size, fragmentation, and the scale of habitat loss impact many characteristics of communities and their assembly mechanisms. These impacts should be considered in evaluations of anthropogenic landscapes. Communities where diversity is most strongly influenced by dispersal are likely to be most sensitive to reserve size variation.

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APPENDIX

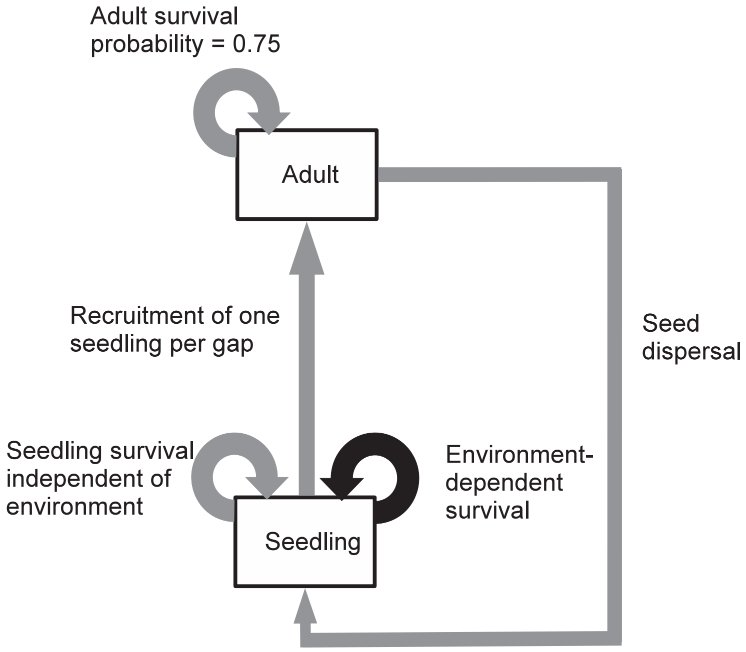

Figure A1: Life cycle of simulated trees. Processes described by gray arrows were neutral with respect to species identity. The black arrow indicates seedling survival, which was the only process that varied depending on species identity and the local environment.

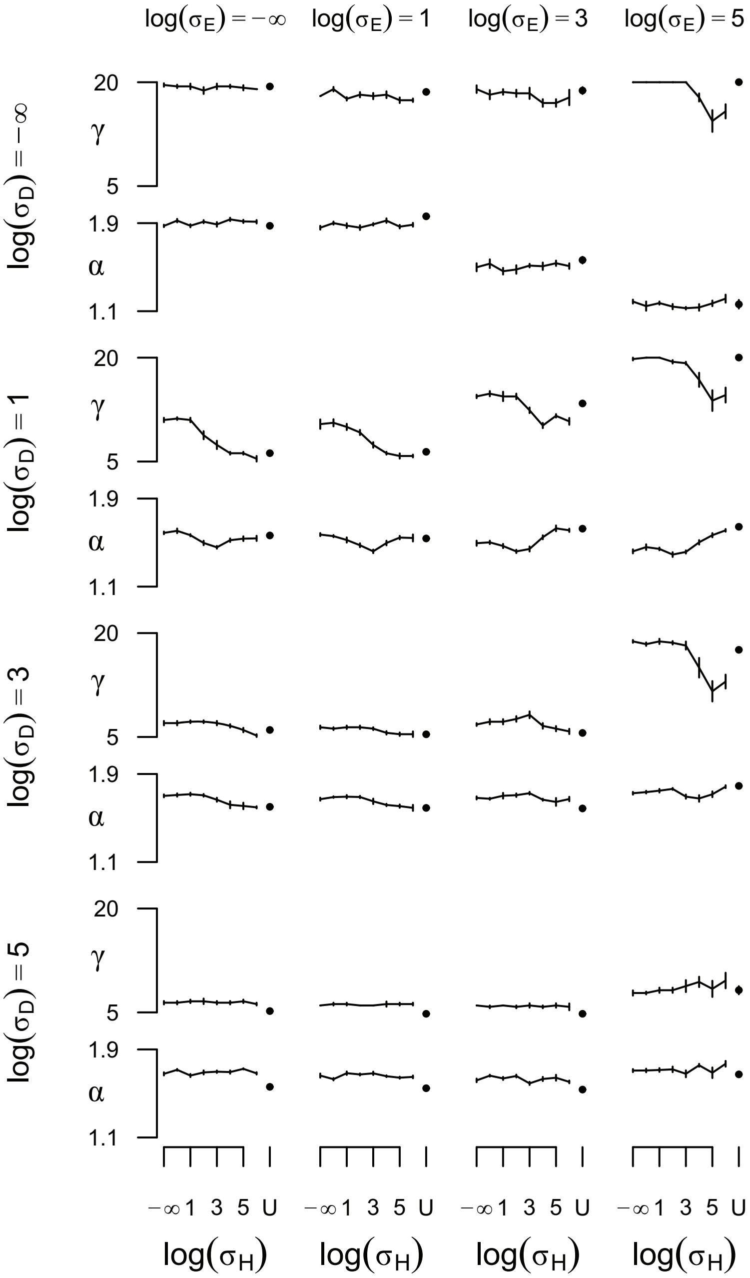

Figure A2: Changes in α and γ species richness as a function of reserve size, under different scales of dispersal and environmental spatial autocorrelation. Note that scales are absolute and not relative as in main text figures. Vertical bars show standard errors. The letter *U* and circles indicate results from unfragmented, intact landscapes. A reduced set of values (i.e., only odd integers) for σ_E and σ_D is shown to reduce plotting area. Also note that in all simulations of reserve size, the proportion of habitat preserved was fixed at 0.25.

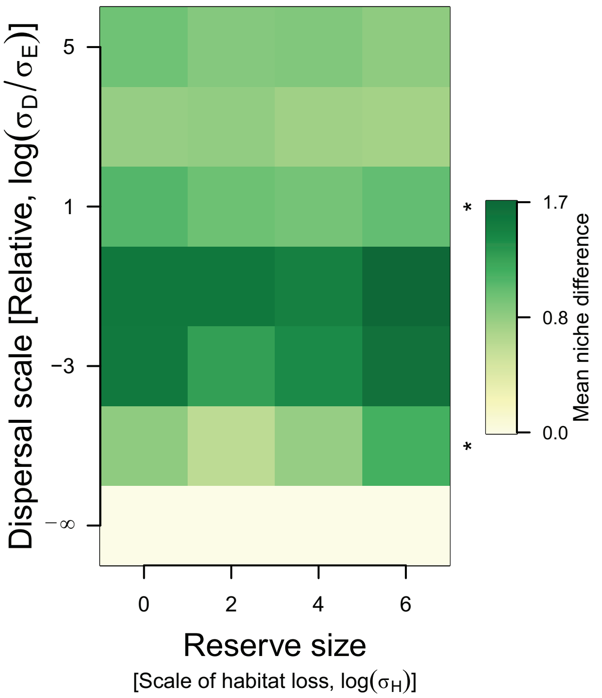

Figure A3: Change in temporal community stochasticity across landscapes of varying reserve size (scales of habitat loss, *X*-axes) and relative scales of dispersal (*Y*-axes). Temporal turnover is measured as average change in species niche between adults occupying the same cell in successive generations ($l = 1$) across the last eight generations of simulations. Note that in all simulations of reserve size, the proportion of habitat preserved was fixed at 0.25. Asterisks indicate the significance of the reserve size effect for a given level of relative dispersal, that is, the correlation between temporal turnover and the scale of habitat loss (linear mixed-effects model; asterisk, $P < .05$).

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