

LETTER

Limiting similarity and functional diversity along environmental gradients

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Abstract

Recent developments in community models emphasize the importance of incorporating stochastic processes (e.g. ecological drift) in models of niche-structured community assembly. We constructed a finite, spatially explicit, lottery model to simulate the distribution of species in a one-dimensional landscape with an underlying gradient in environmental conditions. Our framework combines the potential for ecological drift with environmentally-mediated competition for space in a heterogeneous environment. We examined the influence of niche breadth, dispersal distances, community size (total number of individuals) and the breadth of the environmental gradient on levels of species and functional trait diversity (i.e. differences in niche optima). Three novel results emerge from this model: (1) niche differences between adjacent species (e.g. limiting similarity) increase in smaller communities, because of the interaction of competitive effects and finite population sizes; (2) immigration from a regional species pool, stochasticity and niche-assembly generate a bimodal distribution of species residence times ('transient' and 'resident') under a heterogeneous environment; and (3) the magnitude of environmental heterogeneity has a U-shaped effect on diversity, because of shifts in species richness of resident vs. transient species. These predictions illustrate the potential importance of stochastic (although not necessarily neutral) processes in community assembly.

Keywords

Climate, community assembly, diversity, gradients, limiting similarity, neutral theory, stochasticity.

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INTRODUCTION

The maintenance of diversity stands as one of the great theoretical (and empirical) challenges of ecology. The principle of competitive exclusion states that two ecologically identical species cannot coexist indefinitely. Niche theory provided the first solution to the coexistence problem, based on the differentiation in resource use among co-existing species and associated reduction in the intensity of interspecific competition (MacArthur & Levins 1967; MacArthur 1970; Tilman 1980). A variety of other models have been proposed that lead to maintenance of diversity, such as competition-colonization trade-offs, storage effects, and chaotic oscillations (Chesson & Warner 1981; Tilman 1990; Pacala & Rees 1998; Huisman & Weissing 1999). A critical feature shared by all of these models is that the mechanisms of coexistence are based on differences in demographic or ecological attributes of the

species, so they explicitly predict the maintenance of functional diversity (i.e. differences in resource use or niche parameters) in parallel with species diversity.

In contrast, non-niche-based models of diversity have examined the role of stochastic dynamics and intrinsic frequency-dependence, in the absence of explicit differences in species' ecological parameters. Island biogeography theory was an early example of a non-niche-based theory (MacArthur & Wilson 1967). More recently, Hubbell (1979, 1997, 2001) has championed a neutral theory of diversity based on stochastic demographic dynamics in a large meta-community landscape. In Hubbell's neutral theory, speciation in the regional species pool counteracts random demographic extinctions, and migration between communities maintains diversity in the face of random local extirpation. The neutrality assumption is that all species are demographically identical, and therefore species diversity is maintained without any contribution of functional or

demographic diversity among species. This model has reinvigorated a long debate on the role of stochastic and non-equilibrium processes in plant community ecology: processes that can maintain species numbers with unstable turnover of species identity and relative abundance (Loreau & Mouquet 1999; Bell 2000; Hubbell 2001; Chave *et al.* 2002; Chave 2004).

These contrasting models offer very different explanations for diversity, and predictions regarding the factors that will influence diversity levels. The neutral theory explains diversity in terms of the balance of speciation/extinction in the meta-community and immigration/extirpation in the local community. The key attribute of individual communities is their absolute size, in numbers of individuals J , and diversity is a monotonically increasing function of J . Total population size has long been recognized as a key factor in population biology and population genetics, where mutation and drift act as the diversity creating and culling processes analogous to speciation and extinction. Finite population sizes introduce demographic stochasticity and several recent patch-occupancy models have made progress in combining demographic stochasticity and niche theory (Amarasekare & Nisbet 2001; Mouquet & Loreau 2002; Wang *et al.* 2002). Recent work has suggested that demographic stochasticity (ecological drift) can explain limiting similarity and increase realized niche widths (Hurtt & Pacala 1995; Tilman 2004).

Environmental heterogeneity is often invoked as the explanation for coexistence when there is niche-differentiation (Harner & Harper 1976; Grubb 1977; Chesson & Warner 1981; Comins & Noble 1985). This view thus explains higher diversity in terms of greater levels of environmental heterogeneity or a reduction in limiting similarity (closer packing of species along niche axes). For discrete patches, several models have shown that species diversity cannot exceed patch diversity (Chesson & Warner 1981; Pacala & Tilman 1994; Mouquet & Loreau 2002). However, for continuous and stable environments, with infinite community size, there is no theoretical upper limit on diversity, and limiting similarity can approach zero (Abrams 1983, 1996; Chesson 2000). Pacala & Tilman (1994) suggested several processes that avoid this infinite diversity scenario, including temporal heterogeneity in environmental conditions. Unfortunately, much of the debate over limiting similarity has been muddled by a failure to distinguish the theoretical problem of absolute limits to invasion of new species (Abrams 1996) from the observed similarity of species that emerges under different conceptual frameworks, i.e. 'realized limits to similarity' (Pacala & Tilman 1994). We are concerned with the second problem in this paper, which we term 'realized similarity', which is expressed as the mean distance between species niche optima in communities at or near equilibrium.

Our model combines the deterministic features of niche differentiation models with the demographic stochasticity and immigration from a regional species pool that characterize Hubbell's neutral model. The primary objectives of our model are twofold: first, we address the contribution of community size (number of individuals) to equilibrium diversity levels. We hypothesize that demographic stochasticity may provide a solution to the problem of limiting similarity in light of recent theoretical work (Hurtt & Pacala 1995; Chesson 2000; Tilman 2004) and that realized niche widths should increase, and diversity decrease, as community size decreases. Second, we explore a continuum of models from full neutrality to strong niche differentiation and examine the consequences for overall diversity and realized similarity. Environmental structure should provide 'safe sites' for species and therefore increasing the breadth of the environmental gradient should increase diversity at a given community size. The model is presented primarily through simulations with an extensive exploration of the parameter space, coupled with analysis of the deterministic invisibility criterion implicit in our simulations.

MODEL PRESENTATION

Our model consists of a one-dimensional lattice landscape with a simple monotonic environmental gradient. Monotonic gradients on small spatial scales may only be observed in certain habitats (e.g. lake and ocean shores, vernal pools, steep elevation gradients). In complex models, it is critical to start with simple patterns to be certain we understand the mechanisms driving the results. Additionally, our model acts as a microcosm for large scale patterns on latitudinal and climatic gradients.

Each cell on the lattice landscape can be inhabited by a single plant. The total number of individuals in the local community is J . An environmental function maps each location on the landscape to a value of the environmental condition, E (for notation see Table 1). The environmental units are relative and arbitrary. For all results we present, this environmental value (E) is a linear function of location on the landscape ranging from $E_{\min} = 0$ to a variable maximum, E_{range} :

$$E_x = E_{\min} + \frac{x}{J} E_{\text{range}} \quad (1)$$

In our model, unlike in resource-drawdown models (Chase & Leibold 2003), plants have no feedback effects on the gradient. Individual death and recruitment follow the framework of Hurtt & Pacala (1995): sites are vacated by the random death of plants and vacant sites become occupied as the result of competition among seedlings.

Species (and their constituent individuals) have two traits, a fitness response curve and a dispersal curve (or kernel),

Table 1 Model notation

Parameter	Symbol
Range of environmental gradient	E_{range}
Niche optimum of species s	E_s^*
Community size	J
Diversity of regional species pool	M
Immigration rate	m
Niche breadth	ϵ
Dispersal breadth	σ
Distance between species niche optima	L^*
Position of gap cell	x
Position of potential parent	y

both modelled as Gaussian probability distributions. The fitness function ($F_{s,x}$) for species s at location x is described by two parameters: a niche mean (E^*) and a niche breadth (ϵ), both in units of the environmental resource. This function takes the form of a normal curve:

$$F_{s,x} = \frac{1}{\epsilon_s \sqrt{2\pi}} e^{-\frac{1}{2} \left(\frac{E_x - E_s^*}{\epsilon_s} \right)^2} \quad (2)$$

where E_x denotes the value of the environment at the gap location x , E_s^* is the niche optimum of species s , and ϵ_s is the niche breadth of species s . For all results shown here, all species niche breadths are the same ($\epsilon_s = \epsilon$ for all s).

The dispersal function, D , is described by a single parameter, dispersal breadth, σ_s , and is always centred on the parent plant at position y :

$$D_{y,x} = \frac{1}{\sigma_s \sqrt{2\pi}} e^{-\frac{1}{2} \left(\frac{x-y}{\sigma_s} \right)^2} \quad (3)$$

where x is the position of a gap available for colonization and y is the position of the potential parent. For all results shown, all individuals and species had equal dispersal breadths ($\sigma_s = \sigma$ for all s). For all runs, dispersal distance, σ , was scaled relative to J . This allowed us to isolate the stochastic effects of community size from the interaction of dispersal with the spatial environmental gradient. As J increased, σ increased so that dispersal covered a constant proportion of the environmental gradient. Increasing J , therefore, did not increase the degree of dispersal limitation relative to the environmental gradient across the landscape.

A critical feature of our model was the scaling of niche diversity in the regional species pool relative to the extent of environmental heterogeneity in the local community. This was approached in two ways. In model A, the distribution of niche optima in the regional species pool was evenly spaced across the range of available environments. For species numbered 1 to M , the niche optimum of species s (E_s^*) was

$$E_s^* = \frac{(s-1)E_{\text{range}}}{M} + \frac{1}{2M} \quad (4)$$

For example, if $E_{\text{range}} = 1.0$ and the regional pool had 100 species, then the niche optima would be set at 0.005, 0.015, 0.025, ..., 0.985, 0.995. As E_{range} was decreased or increased, species would become more or less similar in their niche optima, respectively. By setting E_{range} to 0, species niche optima become identical and the model converges to a neutral model with dispersal limitation. Model A allows us to isolate the effect of E_{range} and J from the effect of regional species pool size: it corresponds to a scenario under which species niche optima have evolved in the context of the distribution of environments represented in the local landscape.

In another set of simulations (designated model B), the spacing of niche optima in the regional pool was maintained constant while E_{range} was varied. This would correspond to a situation in which local communities occupied more or less heterogeneous environments, and were assembled from a regional species pool with a fixed level of ecological diversity. In this set of runs, the position of the local environmental gradient was centred in the range of regional niche optima as E_{range} was varied. Model B corresponds to a scenario in which multiple local communities of limited environmental heterogeneity share a regional species pool.

Selection occurs during seedling establishment in a weighted-lottery competition for space. Mortality is imposed with uniform probability across all phenotypes/species, but recruitment into the vacated cell depends upon the distance of potential parents from the gap and the potential seedling's fitness with regard to the environmental value at that location. At the start of each simulation run, the landscape is seeded with species drawn from a regional species pool. Our regional pool plays the role of the metacommunity in Hubbell's local models (e.g. Hubbell 1979), but because our metacommunity is static, we refer to it as a regional species pool (Etienne & Olf 2004). When the number of species in the pool (M) meets or exceeds the size of the community, there is at least one species 'perfectly suited' to each position on the landscape (there is a species such that $E_s^* = E_x$ exists for all x). For all results represented, species in the regional pool have a log-series abundance distribution in which each species' phenotype is random with respect to its abundance. In other words, we assume that abundances in the regional pool are shaped by neutral processes independent of niche optima and are not shaped by processes in local communities (Hubbell (2001), but see Alonso & McKane (2004) for abundance distribution expectations in species-poor metacommunities). Runs in which the regional pool species have a uniform abundance showed qualitatively similar results (results not shown). During the run, species from the pool can immigrate into the landscape with low probability, m . Our

immigration parameter is not quantitatively equivalent to Hubbell's, however, because a potential immigrant's fitness is tested before a successful recruitment event occurs.

Our simulation model follows an asynchronous scheme, where one gap develops at each time step. During each time step:

- (1) A plant is selected at random for replacement (probability for mortality is uniform).
- (2) Candidate seedlings from each parent plant on the landscape are created. A random seedling from the regional species pool (chosen weighted by abundance in the pool) may immigrate to become a candidate with probability m per recruitment event. For such an immigrant, given successful immigration, $D = 1$.
- (3) A winning seed is chosen from among all candidates (which may include an immigrant) according to a weighted lottery function. The probability that gap site x is occupied by species s during each time step is determined by a weighting function:

$$R_{s,x} = \frac{\sum_{y \neq x} \phi_{s,x,y}}{\sum_{k=1}^M \sum_{y \neq x} \phi_{k,x,y}} \quad (5)$$

where $\phi_{s,x,y} = F_{s,x} \times D_{y,x}$ if position y contains species s , otherwise $\phi_{s,x,y} = 0$. The denominator in eqn 5 normalizes over all species. Seedlings are selected after mortality, therefore a plant cannot replace itself (i.e. no seed bank).

The landscape was run for 5000 epochs (one epoch = J time steps; on average this is one complete turnover of the population). This number of time steps was determined to be sufficient for asymptotic behaviour to develop. For non-neutral runs this resulted in stabilization of species richness with an average change of less than 0.01% over 10 consecutive, non-overlapping running averages of 10 epochs. Neutral runs showed more stochasticity, but simulations run to 15 000 epochs showed no directional tendency in diversity. The C++ code is available at <http://www.schwilk.org/research/data.html>.

For each simulation the following output parameters were calculated: species diversity (richness) and mean realized similarity (L^*). Mean realized similarity was calculated by determining the realized niche mode of each species on the final landscape (average value of E at sites occupied), ordering these means and calculating the average distance between adjacent species. For a subset of runs we also calculated the residence time of each species in the final landscape (epochs since invasion) and the abundance of each species.

INVASION CRITERION

To better understand the behaviour of our simulation model, we constructed a deterministic numerical model that approximates the invasion probability of an immigrant into

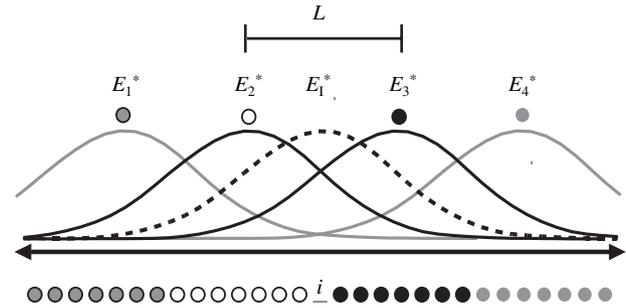


Figure 1 Illustration of niche optima and non-overlapping species distributions for deterministic invasion model. Four resident species are depicted; individuals are represented by circles. The normal curves above show the fitness kernels for each of the resident phenotypes and the kernel of the potential invader. These probability distributions are shown in landscape units, although they are a result of the underlying environmental gradient. The niche optima of four residents and the invader are labelled E_1^* , E_2^* , E_3^* , E_4^* and E_i^* , respectively. Realized similarity (L^*) is the environmental distance between adjacent residents that just prevents invasion.

a saturated community. Unlike the simulation model, this numerical model assumes non-overlapping species distributions (Fig. 1). The invader, I , is assumed to have established at an optimal location, i , given its niche optimum (where $E_i^* = E_i$), and at a cell in the centre of the gradient and exactly equidistant from the niche optima of the established species on either side. With random immigration we assume that some immigrants will eventually land at their E^* and equidistant from competitors. Given this configuration of species arrangements, this is the most favourable position for invasion and we then calculate the probability that the invader population increases before the immigrant's expected time to mortality according to J , E_{range} , L , E , ϵ and σ . We can calculate realized similarity, L^* , by setting all other variables and finding the L at which the invader is likely to establish offspring before dying.

Given non-overlapping, evenly-spaced species distributions with each distribution centred on the E^* of that species and with species' niche optima spaced L apart (Fig. 1), the number of resident species is $\left\lfloor \frac{E_{range}}{L} + 1 \right\rfloor$. If E_{range} is not evenly divisible by L , the species at the end of the landscape will have truncated distributions. The E^* of each species is the environment at the centre of its distribution (Fig. 1). The immigrant's E^* is defined as $E_{J/2}$ and the invader's position, i , is $\frac{J}{2}$. Substituting the invader's E^* , ϵ and σ into eqn 5, we calculate $R_{I,i}$, the invader's probability of establishment per time step.

The invader succeeds when the probability of establishment per time step ($R_{I,i}$) is greater than the per time step probability of the invader's death ($1/J$). This model predicts

invasion according to J , E_{range} , L , ϵ and σ . We wrote a short C program to solve for the values of L at which the invader succeeds – this is the limiting similarity, L^* . The code is available at <http://www.schwilk.org/research/data.html>.

PARAMETER EXPLORATION

The effects of two parameters on stable diversity were explored in depth: community size (J) and the range of the environmental gradient (E_{range}). Two additional parameters were explored in a smaller set of runs in order to verify the model's expected behaviour: niche breadth (ϵ) and dispersal distance (σ) (Table 2). These parameters were explored in two sets of simulation runs, the first explored combinations of E_{range} and J over three immigration rates while holding all other parameters constant. The second explored values of ϵ and σ while holding all other parameters constant. All

Table 2 Model parameters explored in simulation runs

Parameter	Values explored	Constant value
E_{range}	0–2.5	1.0
J	100–3000	1000
M	–	2500
m	0.05–0.2	0.1
ϵ	0.01 and 0.1	0.05
σ	10 and 50	$\frac{J}{20}$

The constant value column gives the value used in explorations where this parameter did not vary.

parameter explorations included at least 50 replicate runs over each set of parameter values. The effects of E_{range} and J on realized similarity were also explored using the invasion criterion model.

RESULTS

When the landscape has environmental heterogeneity ($E_{\text{range}} > 0$), species sort out on the landscape according to their niche optima and a relatively even spacing emerges between coexisting species (Fig. 2). The distance between adjacent niche optima is more even when species have uniform abundances in the regional pool (results not shown). This suggests that the log-series distribution of species in the regional pool contributes to some species which are highly abundant in the pool being maintained in the local community by immigration. The edges of the local landscape also contribute to some forcing effects because populations at the landscape edge face less competition from neighbouring species: edge species have slightly elevated population sizes. Diversity decreases with increasing niche breadth, ϵ , and dispersal breadth, σ (Table 3).

Effect of community size on realized similarity and diversity

Realized similarity narrows (L^* decreases) with community size (Fig. 3), while stable diversity increases (Fig. 4). This result holds over all values of E_{range} and m , but diversity rises with increasing community size (J) more rapidly under

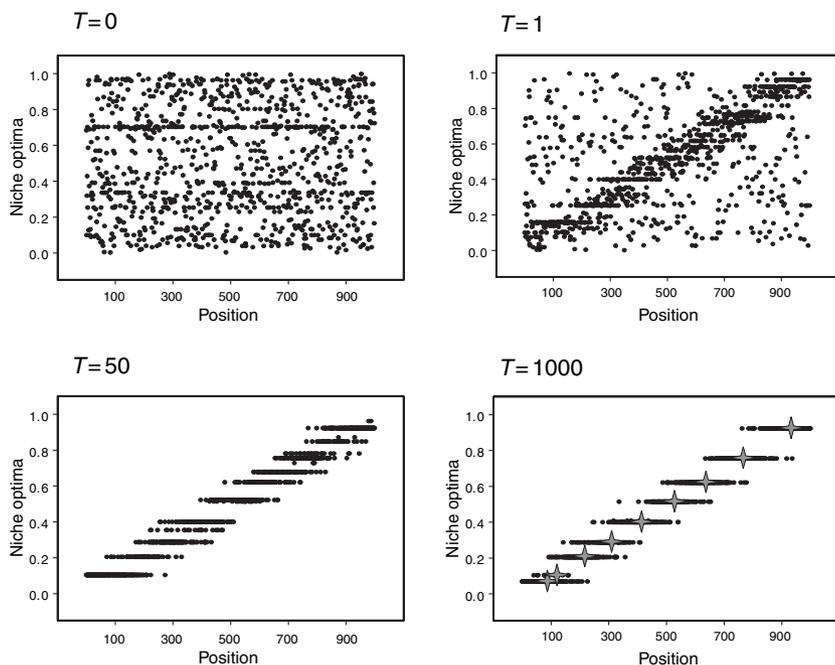


Figure 2 Niche optima of all individuals on the landscape at four time points (cycles) during an example run. For this run $E_{\text{range}} = 1.0$, $J = 1000$ and $m = 0.1$. The grey stars in the $T = 1000$ panel indicate the position at which each population is at its optimum environmental value. We calculate realized similarity for a landscape as the mean vertical distance between adjacent stars. Initial seeding of the landscape is random. The differential abundance of species in the regional pool can be seen in the relative abundance of local species lined up in horizontal rows.

Table 3 Effect of niche breadth (ϵ) and dispersal breadth (σ) on diversity

	$\epsilon = 0.01$	$\epsilon = 0.1$
$\sigma = 10$	32.5 ± 1.5	15.7 ± 2.2
$\sigma = 100$	26.20 ± 1.5	5.9 ± 1.15
Uniform dispersal (no dispersal limitation)	25.7 ± 1.3	4.1 ± 0.9

Table shows mean diversity \pm SD for six parameter values over 50 replicate runs. For these runs, $E_{\text{range}} = 1.0$ and $J = 1000$.

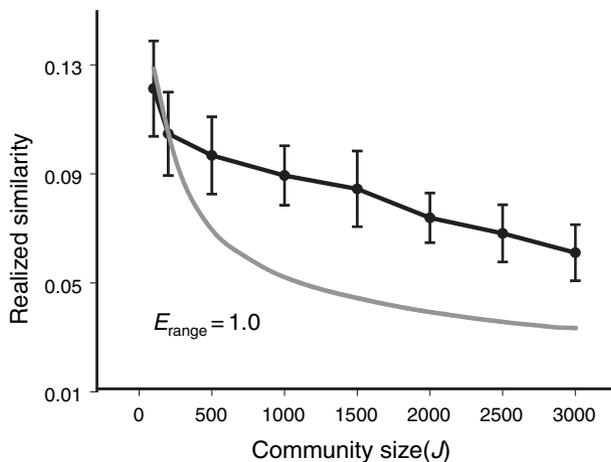


Figure 3 Effect of J on realized similarity (L^*) for simulation runs (black circles and line) and deterministic invasion criterion model (grey line). In all runs, $E_{\text{range}} = 1.0$. Simulation runs show mean and SD of 50 replicates. Deterministic model results show smoothed line for clarity (step changes in diversity lead to a sawtooth pattern for L^*).

environmental structure than on neutral landscapes (Fig. 4a vs. b, respectively). As community size increases, population sizes of each species remain relatively constant, but more species coexist on the larger landscape and niche optima of adjacent species are closer together (L^* decreases). L^* is slightly lower in the deterministic model where the effects of immigration are removed (Fig. 3).

Effect of environmental heterogeneity on realized similarity and diversity

Landscapes with environmental structure have more even abundance distributions than do neutral landscapes (Fig. 5). Under model A, realized similarity widens with increasing environmental range (Fig. 6): species niche optima become further apart. As before, L^* under the deterministic model is slightly lower. E_{range} has a non-monotonic effect on diversity (Fig. 7). As E_{range} increases from a neutral

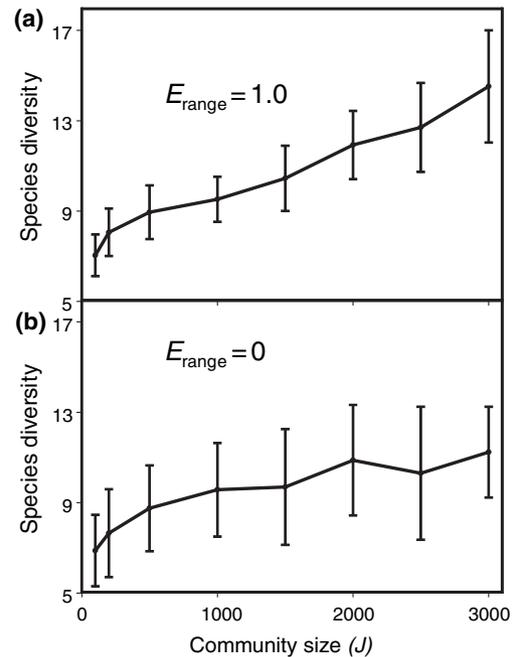


Figure 4 Diversity rises with increasing community size (J) more rapidly under environmental structure (a) than on neutral landscapes (b). Error bars indicate SD over 50 replicate runs. Both panels show results when the niche optima in the regional species pool are scaled relative to the available environments in the local community (model A).

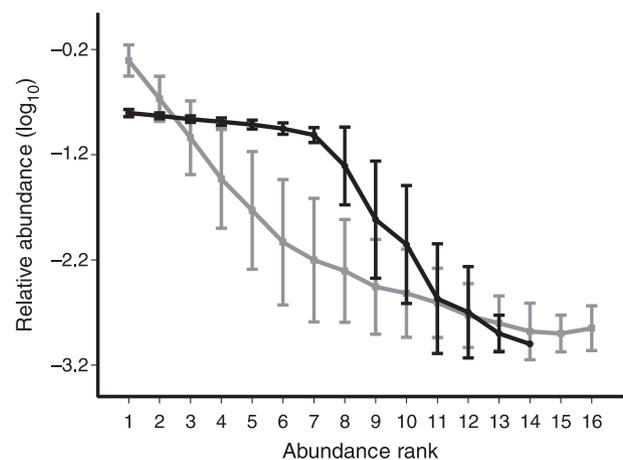


Figure 5 Rank-abundance curves for landscapes with environmental structure ($E_{\text{range}} = 1$, black symbols and line) and for neutral landscapes ($E_{\text{range}} = 0$, grey symbols and line). Error bars show SDs over 50 replicate runs. For all runs shown $J = 1000$.

landscape to steeper and steeper gradients, diversity first decreases and then begins to increase. As E_{range} increases, species niche optima become less similar (Fig. 6) – this increase in L^* , however, is not proportional to the increase in E_{range} and, as a result, diversity increases as well (Fig. 7).

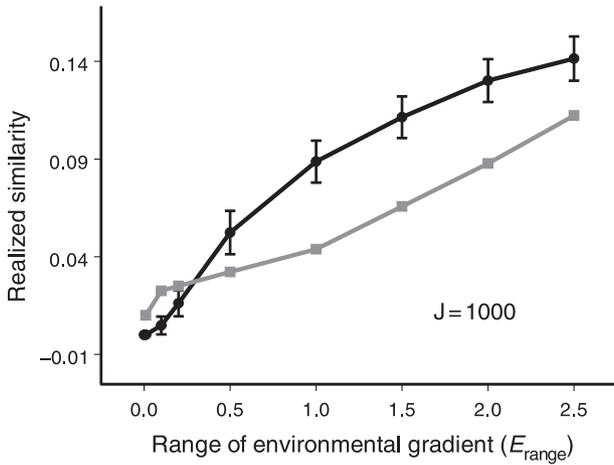


Figure 6 Effect of E_{range} on realized similarity for simulation runs (black circles) and deterministic invasion criterion model (grey squares) for model A. In all runs, $J = 1000$. Simulation results show mean and SD of 50 replicates.

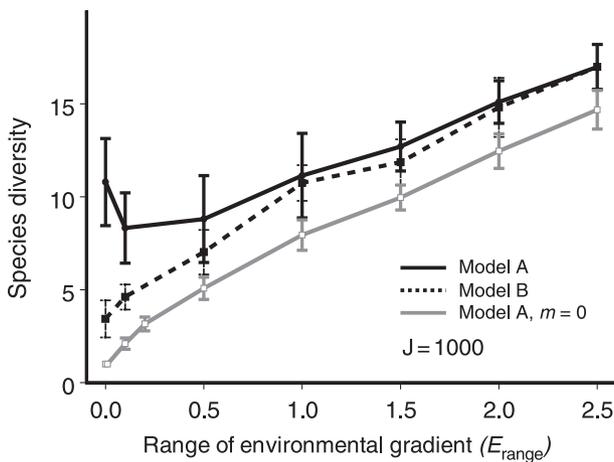


Figure 7 Environmental heterogeneity (E_{range}) has a non-monotonic effect on diversity. The solid line shows the effect of E_{range} when the distribution of niche optima in the regional species pool is scaled relative to the local environmental range (model A). The grey line indicates the effect of E_{range} under model A when there is no immigration from the regional pool ($m = 0$) – effectively limiting the community to resident species. The dashed line shows mean diversity when the distribution of niche optima in the regional pool remains constant and distributed over the range 0–2.5 (model B). Error bars indicate SDs over 50 replicate runs.

The minimum point in this curve (Fig. 7) occurs at increasing values of E as community size, J , increases (results not shown).

Under model B, where niche diversity of the regional species pool is constant, E_{range} has a monotonic effect on diversity (Fig. 7). As E_{range} collapses to zero, one species is

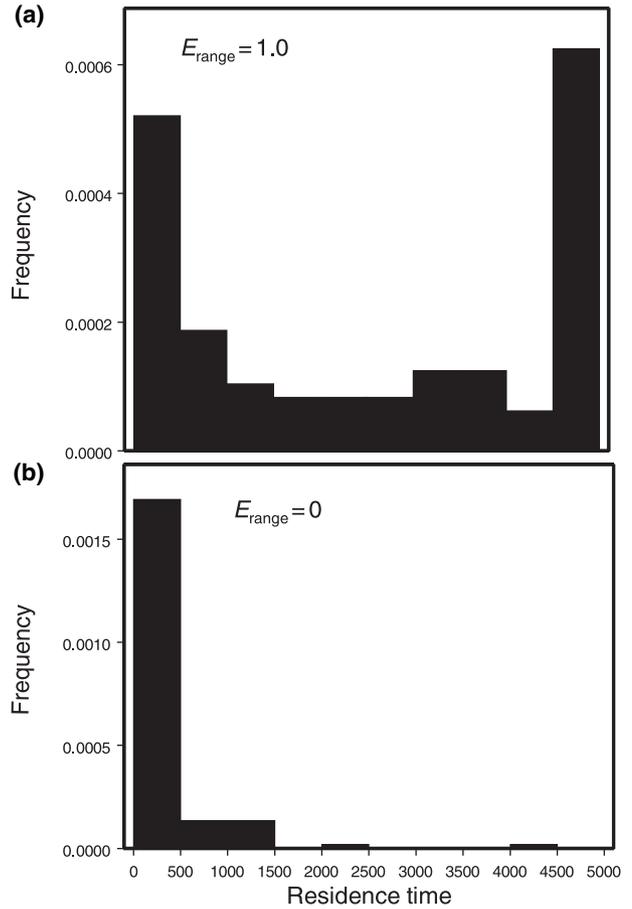


Figure 8 Frequency distributions of species residence times in epochs for an environmentally structured landscape (top panel, a), and for a neutral landscape (b). Each figure represents the distribution of residence times for species in the final landscape averaged over 10 simulation runs. For these runs $E_{range} = 1.0$, $J = 1000$.

favoured as its E^* matches the environment value on the landscape. This species dominates, along with a few transients with niche optima less perfectly suited to the local landscape.

Examination of the dynamics of species turnover (number of epochs between immigration and extirpation) reveals a bimodal distribution of residence times – with species falling into two natural categories: residents and transients (Fig. 8). In the neutral model (when $E_{range} = 0$), all species are transients. Increasing E_{range} results in a loss of transient species and a gain in residents. The dip in species diversity results from the interaction of these two effects. Line showing the effect of E_{range} when immigration is zero (Fig. 7) shows the diversity of residents only. The difference between this grey line and the solid black line shows the diversity of transients as a function of E_{range} .

DISCUSSION

This model has yielded three important results (1) In finite communities, realized similarity of coexisting species arises from the interaction of niche-based community assembly and stochastic demographic processes; (2) the interaction of immigration, stochasticity and niche-assembly generates two species groups within communities: residents and transients, with a bimodal distribution of residence times; (3) the magnitude of environmental heterogeneity has a non-monotonic effect on diversity, because of shifts in abundance of resident vs. transient species.

The model provides a solution to the dilemma of infinitely close limiting similarity, as limits on diversity arise because of fixed community size, finite population sizes and demographic stochasticity. Along the environmental gradient, species sort into evenly-spaced distributions according to their niche optima. As the number of individuals in the community (J) increases, with a fixed environmental gradient, average population size does not grow in proportion to J , so diversity increases and the distance between niche optima (realized similarity) narrows. This pattern is consistent with observations of expanded niche breadth for species occupying small islands where the total number of individuals for a given guild would necessarily be small (Crowell 1962; MacArthur *et al.* 1972). The potential for demographic stochasticity to affect niche similarity as a result of extinction of small populations has been predicted for some time (Turelli 1980; Hurtt & Pacala 1995; Chesson 2000). Tilman's recent incorporation of stochasticity into resource-based niche theory has also shown that stochasticity can promote limiting similarity and increase niche differences among species (Tilman 2004). Our spatial model supports his result and provides further theoretical support that zero-sum dynamics and demographic stochasticity can reduce the similarity of competing species.

Diversity rises with greater environmental heterogeneity, but, surprisingly, this relationship is not monotonic: with non-zero immigration from the regional species pool, diversity in a neutral community is higher than the diversity of a weakly heterogeneous landscape (Fig. 7, model A). As the community converges on the neutrality condition, the initial dip and then rise in diversity results from the fates of immigrants from the pool. In a neutral or weakly heterogeneous landscape, immigrants are as likely to succeed in a gap, given their arrival, as are offspring of species currently in the community. This leads to many transient species represented by one or a few individuals (Fig. 8B). As environmental heterogeneity increases, a group of resident species becomes established in the community, spatially distributed along the gradient according to their phenotypes (niche optima). Offspring of resident species will usually disperse to locations where they have relatively high fitness

(because of the monotonic environmental gradient), and immigrants face a greater average fitness disadvantage as they are unlikely to land near their optimum niche value.

This U-shaped effect depends upon immigration from the regional species pool. When the effective size of the pool is reduced (model B) or immigration is zero, diversity is reduced and the relationship between E_{range} and diversity is monotonic (Fig. 7). We find that the decline in number of transient species with increasing E_{range} initially outpaces the increase in resident species, leading to the dip in total diversity. The bimodal distribution of residence times (Fig. 8) and abundance distributions (Fig. 5) are consistent with results of Bell's (2000) neutral model simulations and the abundance distributions predicted by the core-satellite hypothesis of meta-population dynamics (e.g. Hanski 1982; Collins & Glenn 1990, 1991). In analysis of 21 years of fish community data, Magurran & Henderson (2003) found that communities were also comprised of resident and transient species. Magurran & Henderson (2003) found that the abundance distribution of transients matched neutral model predictions (log series), while residents had more even abundance distributions (log normal) that was not predicted by neutral processes.

Our results suggest that bimodal residence time patterns that Magurran & Henderson (2003) report is predicted whenever there is immigration to the local community from a regional pool as well as habitat heterogeneity. The diversity of transients in these communities should be highly dependent upon the diversity of the regional pool (Ricklefs 1987) and on immigration rates. The diversity of residents, however, should depend more strongly upon habitat heterogeneity. Our model predicts that diversity should increase in larger communities (islands, patches, etc.) that have similar levels of environmental heterogeneity, or in patches of the similar size that have greater heterogeneity. Separating the effects of habitats and area has been a goal of much diversity research (e.g. Simberloff 1976; Nilsson *et al.* 1988).

Our model only examines a simple monotonic environmental gradient, but preliminary explorations of patchy environments exhibit qualitatively similar behaviour (results not shown), therefore, these empirical predictions do not have to be tested only on simple gradient systems. We do not yet know if these results will qualitatively change in a two-dimensional or higher model. The structure of patches (as distinct from the distribution of environmental states) deserves greater study as the potential effects of patchiness on diversity could be variable. A patchy environment with relatively large patches would likely support a more diverse local community as species in spatially disjunct patches might be protected from competition with one another even if their niche optima were similar. On the other hand, increased patchiness in a limited area could decrease

effective population sizes and increase demographic stochasticity. Our future plans include using this model to explore evolutionary dynamics on environmental gradients and the role of community assembly as a factor promoting niche conservatism (Ackerly 2003).

Demographic stochasticity has strong effects on diversity and realized similarity in our model, even in the presence of environmental structure and niche differentiation. Hubbell's (2001) neutral theory brought together neutral speciation and neutral stochastic zero-sum dynamics. Although much attention has been paid to the neutrality contribution of Hubbell's theory, our results highlight the potential importance of stochasticity in non-neutral dynamics.

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