

Joint consequences of dispersal and niche overlap on local diversity and resource use

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Summary

1. Several ecological theories predict that species coexist by exploiting different resource niches, and therefore, more diverse communities should have greater resource uptake. Supporting evidence, however, is equivocal. Species with similar competitive abilities are predicted to coexist with little niche differentiation, suggesting that communities containing more functionally redundant species may be more diverse but with little impact on resource use. Likewise, high rates of seed dispersal often increase diversity, but the effect of this diversity on resource uptake is unknown.

2. I incorporate resource competition into a metacommunity model where communities differ in regional diversity and also in the dispersal and niche overlap (functional redundancy) of their constituent species. In this model, each species within the metacommunity is the optimal competitor in one or more patches, and the patches are linked by dispersal.

3. The model predicts that niche overlap and dispersal have similar and synergistic effects on local diversity, but opposite effects on resource use. Increasing niche overlap and dispersal causes an increase in local diversity to a critical point, after which local diversity crashes. However, increasing dispersal invariably decreases resource use, whereas increasing niche overlap increases resource use. Increasing the regional species pool causes the only consistently positive relationship between local diversity and function but becomes saturated at a local species richness of 2–3 species.

4. *Synthesis.* The distinct mechanisms that drive diversity in local communities can have different and even opposing effects on resource use. Understanding how dispersal and niche overlap structure diversity is critical to predicting the relationship between diversity and resource use. Distinguishing between these mechanisms should be a priority when attempting to understand the causes and consequences of diversity.

Key-words: biodiversity, dispersal, ecosystem function, mass effects, metacommunity, neutral model, sink, source, spatial scale

Introduction

Two important debates in ecology focus on the mechanisms that maintain species diversity, such as neutral or stabilizing processes, (Chesson 2000; Hubbell 2001), and the importance of this diversity to ecosystem function (Schwartz *et al.* 2000; Srivastava & Vellend 2005; Cardinale *et al.* 2006). Among the processes that stabilize diversity, community-resource dynamic models (CRDMs) predict that species diversity is maintained by each species being an optimal competitor in a particular environment or set of environmental conditions (Tilman 1980; Chesson 2000). An extension of this prediction is that, in a heterogeneous environment, a large number of species will utilize resources more completely by maximizing resource use in each

species' optimal niche spaces (Tilman, Lehman & Thomson 1997; Cardinale *et al.* 2006). However, this prediction of species complementarity is often based on the assumption that competitive dynamics reflect equilibrium conditions in a closed community (Tilman 1980; Tilman, Lehman & Thomson 1997) or that local competitive dynamics are not influenced by dispersal (Gross & Cardinale 2007). Other CRDMs that avoid this assumption describe general rules for stable coexistence but do not generate explicit predictions for ecological metrics such as alpha diversity or local resource use (Chesson 2000). Indeed, one of the fundamental challenges of CRDMs is that of scale, in particular, linking environmental heterogeneity to species occurrence, dispersal and competition (Snyder & Chesson 2003).

Two areas of field research have challenged the general applicability of CRDMs to ecological communities. First, there has been considerable research on the link between species diversity and ecosystem function (both productivity

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and resource use). Recent meta-analyses have shown that a diverse community is usually no better than the 'best' species in that community, with diverse communities generally decreasing function at the outset of experiments but eventually equaling the dominant competitor after about 5 years (Cardinale *et al.* 2007). In other words, the prediction that a large number of species are beneficial because they exploit more available niches is not supported over short (1–5 year) time frames. However, many of these studies are subject to criticisms of scale as they tend to test the effects of diversity in small, homogenous plots, whereas much of the theory relating diversity to resource use depends on heterogeneous environments (Tilman, Lehman & Thomson 1997). Although niche complementarity is possible at these small scales, it is not guaranteed (Levin 1976; Tilman 1980), and CRDMs predict much stronger diversity–resource use relationships at larger scales where environmental variation is more pronounced (Davies *et al.* 2005).

The second challenge to the applicability of CRDMs comes from field research that uses seed addition experiments to test invasibility of communities. Despite the importance of resource competition in plant communities (HilleRisLambers *et al.* 2004; Harpole & Tilman 2006), studies on species invasions and persistence have indicated that dispersal limitation, or an absence of seeds from potential competitors, is often equally or more limiting to plant establishment than competition for resources (Tilman 1997; Seabloom *et al.* 2003; MacDougall & Turkington 2006). Different dispersal rates of seeds into a patch are also important determinants of alpha diversity (Levine 2000), even when the species dispersing into the community appears to be an inferior competitor (MacDougall & Turkington 2006). Models of closed communities, which ignore dispersal from outside sources, are clearly not appropriate for these systems (Abrams & Wilson 2004).

Together, these discrepancies between experimentation and CRDM predictions suggest that mechanisms that increase local diversity, other than local niche partitioning, need to be considered. The results from seed addition experiments suggest that one important determinant of local diversity is dispersal (Tilman 1997; MacDougall & Turkington 2006). A number of metacommunity models have been developed to address the effects of dispersal on local diversity when dispersal rates are high enough to affect competitive interactions (Amarasekare 2003; Leibold & Miller 2004; Leibold *et al.* 2004). These models often use a lottery or patch occupancy approach and assume that competitive outcomes are a product of both propagule supply and competitive ability (Amarasekare & Nisbet 2001; Mouquet & Loreau 2002, 2003; Snyder & Chesson 2003). Such approaches have generated predictions about species coexistence and the conditions necessary for the persistence of source and sink populations. However, because each individual fills a single space in lottery models, this approach may not be suitable for predicting the effect of resource use on population dynamics and vice versa. For example, Mouquet & Loreau (2003) used a lottery model in which established individuals depleted resources but unused resources did not affect the number of new individuals establishing. Thus, inefficient

resource use by poor competitors could not be offset by new individuals establishing and creating larger population sizes, which is an important component of CRDMs (Tilman 1980).

A second important mechanism for maintaining diversity is the degree to which species in a community are functionally similar or, alternatively, show strong competitive differences and niche differentiation (Gravel *et al.* 2006; Adler, HilleRisLambers & Levine 2007). The two extreme cases of functional differentiation are described by neutral models, in which competitive differences and niche differences do not affect species' distributions (Hubbell 2001), and equilibrium CRDMs, in which both of these factors determine species' distributions (Tilman 1980; Chesson 2000). Between these two extremes, functional differences may have variable effects on diversity and ecosystem function. For example, functionally similar species are more likely to persist in sink populations, potentially causing a negative diversity–function relationship (Mouquet & Loreau 2003). However, broad niche overlap can also decrease the unexploited niche space between neighbouring species, creating a positive diversity–function relationship (Tilman 1997).

Here, I introduce a metacommunity CRDM that is designed to model an interaction between competitive dynamics and dispersal. The environment is modelled as locally homogenous (within patches) but heterogeneous across patches, an approach commonly used in metacommunity models (Amarasekare *et al.* 2004; Leibold *et al.* 2004). I develop a weighted competition model in which a species' local success is dependent on the number of seeds in the patch, resource availability and its response to local environmental conditions. Patches within the metacommunity are connected through seed dispersal. Species interactions are placed on a continuum so that the metacommunity can range from strongly niche-based to neutral. I then use the model to test the degree to which dispersal, niche overlap among species and the regional species pool can augment local diversity and thereby change resource use and productivity. This approach is novel in that it explicitly incorporates resource dynamics into a metacommunity framework and allows both niche differentiation and the effect of dispersal on competitive outcomes to vary among communities.

The model

I use a model in which species demographic attributes are identical (e.g. adult mortality rates, seed production rates and average competitive ability) and vary only those model parameters that affect local diversity and ecosystem function (dispersal, niche width and regional diversity). This allows the model to become a neutral model when species have complete niche overlap as species are then competitively equal and functionally redundant. The model is written as a plant model with seed dispersal but can represent any metacommunity of sessile organisms that have dispersing propagules and are limited by a consumable resource. Dispersal is global, and all sites are therefore equally likely to receive seeds that have dispersed out of the site of the parent plant.

The model progresses with mature plants first competing for a limiting resource (R), which they use to produce seeds (q). A species' ability to compete in a patch depends on its relative abundance and its species-specific environmental response to that patch (E , described below). Seeds either stay in the locality of the adult plant or disperse to a global pool that is then distributed evenly among patches. For a given patch, the number of surviving offspring (f) of each species depends on its relative seed abundance and its potential reproductive success (g), which is also a function of its environmental response to that patch (E) and the resources left unused by adult plants (R').

The model can be written in matrix form by tracking the change in the population (X) of species i in patch j , which depends on adult mortality (m), and the competitive success of all species locally and in other patches:

$$\Delta X_{ij} = f_{ij}(\bar{q}_j(\mathbf{X}, \mathbf{E}, \bar{R}), g_{ij}(R'_j, E_{ij})) - mX_{ij} \quad \text{eqn 1a}$$

The vector \bar{q} denotes values for all species at site j . The vector for resource levels (R) is for all sites, and the matrix of populations (\mathbf{X}) and environmental responses (\mathbf{E}) are for all species at all sites. The change in resource availability is in turn given as

$$\begin{aligned} \Delta R_j = & - \sum_{i=1}^S h_{ij}(X_{ij}, R_j) - \sum_{i=1}^S c f_{ij}(\bar{q}_j(\mathbf{X}, \mathbf{E}, \bar{R}), g_{ij}(R'_j, E_{ij})) \\ & + p(R_j - \sum_{i=1}^S h_{ij}(\dots) - \sum_{i=1}^S c f_{ij}(\dots)) \end{aligned} \quad \text{eqn 1b}$$

Here, h is the amount of resource used by mature plants for maintenance growth and reproduction, and c is the per capita resource cost of producing a new plant. The supply function, p , describes the amount of the resource that is replenished from external sources. I set p to be proportional to the difference in resources from the resource availability in a site at equilibrium with no species present (R_{0j}) so that $p(R_j) = \zeta(R_{0j} - R_j)$, and ζ is bounded between 0 and 1 (Tilman 1980).

Each time step begins with resource uptake by mature plants:

$$h_{ij} = \text{Min} \left[\begin{array}{l} X_{ij} a E_{ij}, \\ R_j X_{ij} a E_{ij} / \sum_{i=1}^S X_{ij} a E_{ij} \end{array} \right] \quad \text{eqn 2}$$

Equation 2 allows all species to uptake their maximum level of resources unless the sum total for all species exceeds the available resources at the site, in which case a species receives an amount proportional to its relative abundance and its per capita resource uptake rate (the lower portion of eqn 2).

The per capita resource uptake rate is dependent on the functional form of resource uptake, a , and the species-specific environmental response (E_{ij}). I use a Monod function as the resource uptake function, so that $a = bR/(R + K)$, with b acting as a scalar that sets the maximum uptake per individual. Environmental responses are modelled as a Gaussian

function, with $E_{ij} = e^{-(E_{\text{opt}_i} - E_j)^2 / \sigma^2}$, where E_{opt_i} is the niche optima of species i and E is the niche value of site j . The environmental response of each species therefore depends on two aspects of the niche: the distance of a species' optimal niche from the site's environment ($E_{\text{opt}_i} - E_j$) and the niche width of the species (σ ; Fig. 1a).

Seed production (q) is a linear function of resource uptake, with the proportion of seeds that are globally dispersed to all L

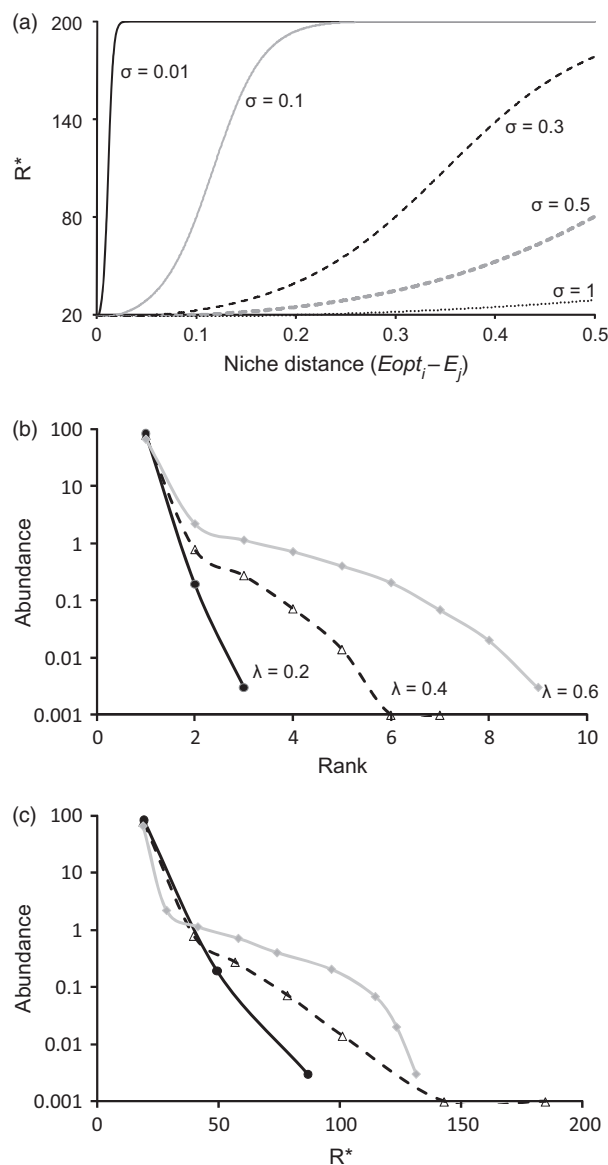


Fig. 1. Species R^* values and their relationship with local abundance. (a) R^* depends on a species environmental response ($E_{\text{opt}_i} - E_j$) and niche width (σ). (b) The resulting rank–abundance curve within a site depends on dispersal among sites (λ). (c) The relative abundances of species are negatively correlated with their R^* values (c; curves have the same λ values as in b). R^* values in (a) were solved numerically with $R_0 = 200$, $\zeta = 0.3$, $m = 0.3$, $S = 50$, $k = 2$, $c = 0.5$, $b = 0.5$, $\varphi = 1$. Values for (b) and (c) are averages over 1000 patches within simulations with the above parameter values and $\sigma = 0.1$. Abundance values of < 1 indicate that only some patches in a simulation were occupied by species of a given rank (b) or R^* (c). In (c), R^* values were averaged over all species of a given rank.

patches equal to λ . The number of seeds of species i in patch j is then

$$q_{ij} = (1 - \lambda)uh_{ij} + \frac{1}{L} \sum_{j=1}^L \lambda u h_{ij} = (1 - \lambda)uh_{ij} + \lambda u \bar{h}_i \quad \text{eqn 3}$$

where u is the mean number of seeds per unit resource used. Although seed production in real communities varies among species, I constrain u to be equal for all species to allow the model to become neutral as niche differences are removed.

In many communities, mature plants produce many more viable seeds than could possibly survive to reproductive maturity (Seabloom *et al.* 2003; Tilman 2004). Indeed, even though individual species may be seed-limited, a community is not seed-limited when per capita seed production rates exceed mature plant mortality rates. In such communities that are not seed-limited, there are two processes that determine the number of successful offspring of a species. First, species have different potential reproductive success (g), with this value indicating the maximum number of surviving seedlings when seeds are not limiting. Second, each seedling must compete with other seedlings for resources, and therefore, each species realizes only a portion of its potential reproductive success.

In this model, the potential reproductive success (g) of each species represents its maximum number of offspring for a given resource availability in the absence of interspecific competition when seeds are not limiting. It is a function of a species' environmental response (E) and its functional response to available resources. I use the Monod function to model the functional

$$f_{ij} = \varphi E_{ij} \left[\frac{R'_j [(1 - \lambda)h_{ij} + \lambda \bar{h}_i]}{\sum_{i=1}^S [(1 - \lambda)h_{ij} + \lambda \bar{h}_i]} - k \log \left(k + \frac{R'_j [(1 - \lambda)h_{ij} + \lambda \bar{h}_i]}{\sum_{i=1}^S [(1 - \lambda)h_{ij} + \lambda \bar{h}_i]} \right) + k \log(k) \right] \quad \text{eqn 6}$$

response to resource availability. I assume that the offspring respond to the remaining available resources as they are depleted and that they deplete these resources to the lowest level possible over the remainder of the growing season. Competition for resources as they are depleted is modelled using the integral of the Monod function, as this integral incorporates the total response curve as the resource is depleted. Potential reproductive success is

$$g_{ij} = \varphi E_{ij} \int_0^R \frac{R}{R + k} dR \quad \text{eqn 4}$$

where φ is a scalar for the number of offspring per unit area of resource uptake. In the absence of interspecific competition, the integral would range from 0 to R'_j , with R'_j being the amount of resource left unused by mature plants. Competition among species is also important, however, and limits the amount of resource available for each

species. If a species' access to resources is proportional to the number of seeds produced, then the amount of resource that each species will have available for reproduction will be $R'_j q_{ij} / \sum q_{ij}$, with the denominator summed across all species. Species-specific establishment (f) is therefore

$$f_{ij} = \varphi E_{ij} \int_0^{R'_j q_{ij} / \sum q_{ij}} \frac{R}{R + k} dR \quad \text{eqn 5}$$

Recruitment competition in a community with multiple species is modelled in eqn 5, in which each species' resource access is proportional to the relative amount of seed. This model for reproduction makes three important assumptions. First, species have different maximum recruitment abilities, even when no competing species are present. Thus, in the absence of dispersal, this model works as an R^* model with species having different equilibrium populations and reducing resources to different levels if their environmental responses vary (Tilman 2004). Second, seeds of one species will inhibit those of other species through resource competition, even if the first species has a lower reproductive growth potential. In other words, a species can limit the resource uptake of other species, even beyond what it is able to use for producing viable offspring, as occurs in nature when species produce seedlings that do not survive to reproductive age. Third, it assumes that resources are depleted over the course of the growing season and not replenished until the following growing season.

Equation 3 can be incorporated into eqn 5 and simplified to determine seedling establishment in a given patch (eqn 6):

SIMULATIONS

I used simulations to determine the effects of model parameters on local and regional diversity, productivity and resource use. I present those sets of conditions that illustrate the effect of a particular parameter on species richness, productivity and resource use. Varying other parameters (i.e. k , R_0 , a , etc.) does not alter the qualitative results presented here.

Simulations were initiated with all species equally present in the global seed pool, and the number of patches in the community was held constant at 2000. As with any such simulation model, the long-term equilibrium solution is for all species to go extinct as there is no mechanism for reinvasion from the regional species pool. I initially ran simulations of communities for 5000 time steps to determine what transient effects were present and how long they persisted. Most parameter conditions produced relatively short transient effects that disappeared within 20 time steps. However, parameter combinations that caused a collapse in regional

diversity took variable amounts of time for stochastic effects to cause the collapse and also to reach a semi-stable state afterwards. Nonetheless, even in these communities, trends in species loss emerged within 400 time steps. Based on these results, I ran all simulations for 500 time steps unless otherwise stated.

For all simulations, I designed the model so that it became more neutral as niche overlap increased (i.e. as σ^2 became large). This condition required that species' niche optima ($E_{opt,i}$) and sites' niche values (E_j) were uniformly distributed and also that the niche axis was circular (wrapped so that 0 = 1) so that all species' niche optima were equidistant on average from all site niche values. Stochasticity was introduced into the model by treating mortality (m) as a binomially distributed random variable and establishment (f) as a poisson-distributed random variable. The ranges of the three model parameters explored were regional diversity (1–100 species), niche overlap (σ , 0.001–10) and dispersal (λ , 0–1).

Results

The model predicted varying relationships between local diversity, productivity and resource use depending on the underlying mechanism that increased diversity. I define each of these terms as follows. Local diversity refers to species richness within a patch and also to a number of commonly accepted diversity indices (Shannon Weiner index, Fisher's alpha, 1-Simpson's index), as these indices are all positively correlated with species richness in the model output (smallest $r_s = 0.98$). Resource use refers to the proportion of resources used over the course of a time step ($1 - R_f/R_0$). Productivity is defined as the function h , which describes seed production by mature plants in a patch. However, because productivity and resource use were strongly correlated ($r = 0.99$), only resource use is shown in figures. Each figure holds all variables constant except those indicated to show their effects on model output.

Competitive outcomes within patches depended on the R^* values of species present and the degree of dispersal among patches (Fig. 1), with the R^* defined as the resource level that would support a monoculture at equilibrium in the absence of dispersal. Changing niche width values altered the competitive relationships (R^*) between species (Fig. 1a), whereas altering dispersal did not change the R^* but did change the competitive outcomes (Fig. 1b,c). For low to intermediate levels of dispersal, increased dispersal caused more evenly distributed abundances within communities by flattening the slope of the relationship between local abundance and resource-use efficiency (Fig. 1c). This flattened slope occurred in part because the best competitor (lowest R^* species) devoted a lower proportion of its seed production to the local community ($1 - \lambda$; eqn 6) and in part because higher dispersal caused more seeds from other species to arrive in the community, thus increasing the chance that they would also establish. However, dispersal did not alter the direction of the relationship between com-

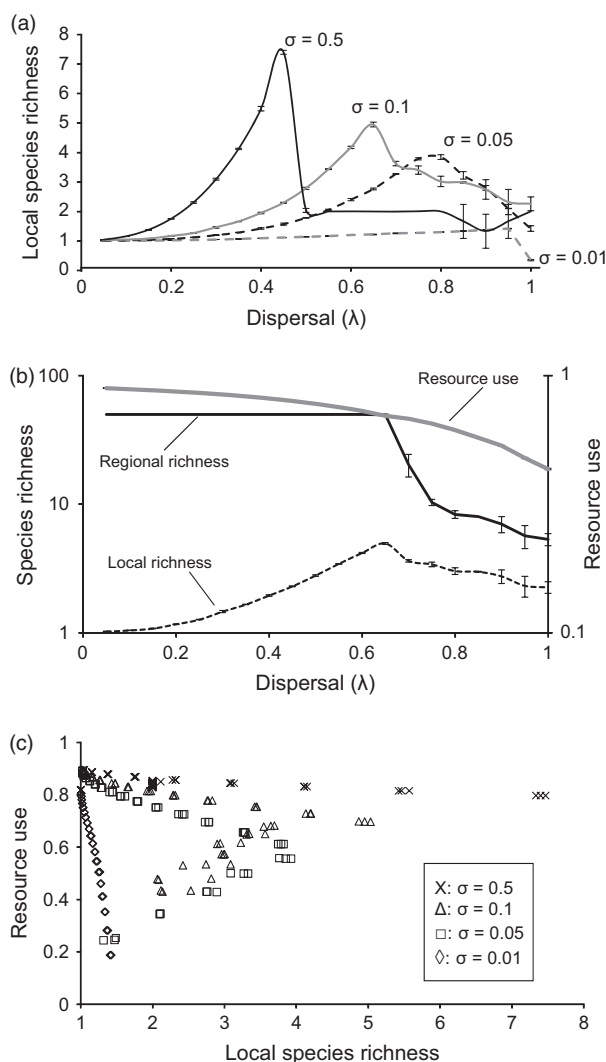


Fig. 2. (a) The relationship between dispersal and local species richness at different levels of niche overlap. (b) The resulting relationship between local species richness (dashed line), regional richness (solid black line) and resource use (grey line; $\sigma = 0.1$ for all lines). (c) When considered across different levels of dispersal and niche overlap, the relationship between local richness and resource use is highly variable at low species richness and less variable at high species richness. Parameter values are $R_0 = 200$, $\zeta = 0.3$, $m = 0.3$, $S = 50$, $k = 2$, $c = 0.5$, $b = 0.5$, $\phi = 1$. Error bars represent standard deviations.

petitive ability and species' abundances; dispersal decreased the relative abundance of the dominant competitor but did not change its rank (Fig. 1c).

Increasing dispersal among patches caused an increase in local diversity at low levels, followed by a crash that mirrored a crash in regional diversity (Fig. 2a,b). Both the increase in diversity at lower levels of dispersal and the subsequent crash at higher levels depended on the degree of niche overlap among species. Communities with functionally redundant species, marked by high niche overlap, had higher local diversity at low dispersal but also crashed at lower levels of dispersal (Fig. 2a). Resource use and productivity were negatively related to dispersal, regardless of whether increasing dispersal increased

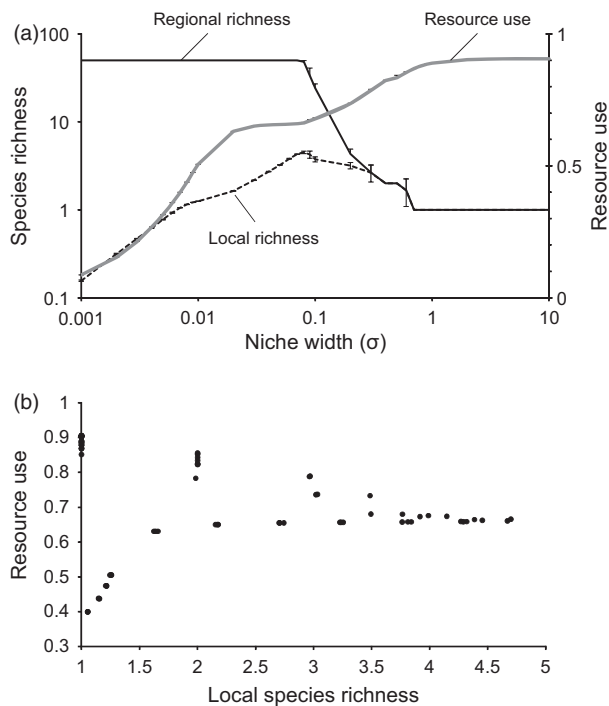


Fig. 3. (a) The effect of species' niche widths (σ) on local species richness (dashed black line), regional richness (solid black line) and resource use (grey line). Error bars show standard deviations, and model parameters are $R_0 = 200$, $\zeta = 0.3$, $m = 0.3$, $S = 50$, $k = 2$, $c = 0.5$, $b = 0.5$, $\phi = 1$, $\lambda = 0.7$. (b) When considered across communities with different levels of neutrality, resource use is less variable at high levels of local species richness.

or decreased local diversity (Fig. 2b). This occurs because low dispersal allows species to accumulate seeds in locally favourable sites, whereas high dispersal causes species to disperse their seeds across both favourable and unfavourable sites. When considered across communities with differing degrees of dispersal, resource use was negatively related to local diversity for a given niche width (comparing with σ , Fig. 2c) but tended to show a more variable level of resource use at low diversity levels when considered across communities with differing niche widths.

Niche width and dispersal had similar effects on local and regional species richness but opposite effects on resource use (Figs 2b and 3a). Communities with broader niche widths invariably used more resources as 'gaps' between niches disappeared in these communities (Figs 1a and 3a). However, the elimination of these gaps caused species to become redundant, which in turn caused stochastic processes to dominate population regulation and resulted in many species going extinct (Fig. 3a, $\sigma > 0.1$). The resulting hump-shaped relationship between niche overlap and local richness caused a variable relationship between local richness and resource use when trends in local richness were driven by differences in niche width (Fig. 3b). In particular, low local diversity could be caused by large or small niche widths, resulting in high or low resource use, respectively.

Increasing the species pool (regional richness at the outset of the simulation) also increased local diversity, although local

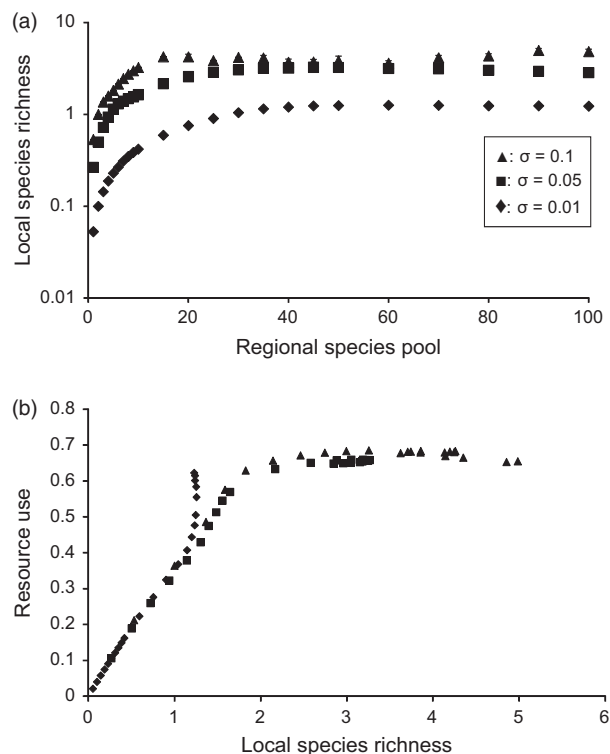


Fig. 4. (a) The effect of species pool (initial regional species richness) on local species richness at various niche widths (σ). (b) The effect of local richness on resource use when local richness is caused by regional richness. Error bars in (a) show standard deviations, and model parameters are $R_0 = 200$, $\zeta = 0.3$, $m = 0.3$, $S = 50$, $k = 2$, $c = 0.5$, $b = 0.5$, $\phi = 1$, $\lambda = 0.7$.

diversity saturated at relatively small species pools of 20–40 species (Fig. 4a). The increase in local diversity created consistent and positive diversity–resource use relationships at relatively low levels of niche overlap (σ). However, this positive diversity–resource use relationship typically saturated at a local species richness of 2 or 3 species (Fig. 4b). At high levels of neutrality (high σ , not shown), regional diversity has no impact on resource use, as local and regional diversity collapsed to a single species (Fig. 3a).

Discussion

By incorporating community–resource dynamics into a meta-community framework, the model predicts two important trends that are novel to our understanding of plant communities. First, increases in local diversity beyond that supported by local environmental heterogeneity can increase or decrease average ecosystem functioning, depending on the underlying mechanism. Mechanisms that increase diversity by saturating regional niches (increasing niche width, increasing regional diversity) also increase local resource use, whereas increasing diversity without altering regional niche use (i.e. by increasing dispersal) causes a decrease in resource use. Most CRDMs do not allow for such variable outcomes of local dynamics except in transitory states (Tilman 2004), and previous metacommunity models with similar assumptions predicted that, for a

given regional diversity, increasing local diversity beyond a single, optimal competitor would cause function to decrease (Mouquet & Loreau 2003). The current model predicts instead that a number of factors can determine local levels of diversity (Levin 1976; Shmida & Wilson 1985) and that the effects of this local diversity on resource uptake and productivity can only be predicted when these underlying factors are known (Bond & Chase 2002). Second, despite the common metacommunity prediction that low dispersal rates increase diversity but that high rates reduce diversity (Mouquet & Loreau 2003; Leibold & Miller 2004; Leibold *et al.* 2004), the current model predicts that the effect of dispersal on diversity depends critically on the degree of neutrality (versus niche differentiation) in the community. In communities with high levels of immigration and emigration, the interplay between dispersal and niche dynamics may be much more important than previously suggested by both niche models (Tilman, Lehman & Thomson 1997) and metacommunity models (Hubbell 2001; Mouquet & Loreau 2003). Together, these two broad results suggest that the disparate effects of diversity on ecological processes such as resource uptake and invasibility may be resolved through understanding the interplay of dispersal and niche dynamics in natural communities.

DISPERSAL, NICHES AND DIVERSITY

The prediction that diversity peaks at an intermediate level of dispersal is common to many metacommunity models (reviewed in Leibold *et al.* 2004). For example, in a metacommunity model with similar assumptions about regional environmental heterogeneity, Mouquet & Loreau (2002, 2003) showed that local diversity peaks when *c.* 30% of seeds are globally dispersed; however, this scenario is actually a special case among a number of competition models that range from close to neutral to strongly niche-based (Fig. 2a). Indeed, it is the level of niche overlap among species that determines whether a given level of dispersal will increase diversity through source–sink dynamics or cause regional diversity to quickly crash because of stochastic fluctuations.

The degree to which species coexist through strong niche differentiation versus equalizing processes (*sensu* Chesson 2000) is currently an important debate in ecology (Adler, HilleRisLambers & Levine 2007). The model presented here represents a completely equalized community, as all species have identical distributions of optimal environments, equal seed production per unit resource consumed and symmetric competition. It is nonetheless apparent that weak niche differentiation (large σ) can lead to a fast collapse in diversity, especially when dispersal is high (Figs 2a and 3a). However, it is unclear how applicable this scenario is to natural settings; is niche differentiation in natural communities strong enough for most species to persist in the face of high dispersal? A recent meta-analysis of seed limitation indicated that experimental levels of seed addition have been insufficient to displace competitive dominants with inferior competitors (Clark *et al.* 2007). In addition, recent experimental work has shown that niche differentiation, at least among grassland species, is considerable (Levine &

HilleRisLambers 2009). These strong niche differences exist even in a community that lacks large competitive differences (Adler, Ellner & Levine 2010), suggesting that extremely high levels of dispersal would be required to see the species loss predicted by the model (Fig. 2a,b). However, factors such as small community size are predicted to increase the importance of stochastic loss of species, suggesting that relatively small communities are more prone to the collapse in diversity seen here (Fig. 2; Orrock & Flethcher 2005).

A more common observation in natural communities is that dispersal increases local diversity through source–sink populations, which have long been predicted to affect community properties such as species–area relationships and beta-diversity (MacArthur & Wilson 1967; Shmida & Wilson 1985; Pulliam 2000; Amarasekare & Nisbet 2001). The positive effect of experimental seed addition on local diversity suggests that sink populations may augment diversity (Clark *et al.* 2007; Myers & Harms 2009), but these experiments rarely follow communities long enough to determine whether newly established populations are in fact sinks. Most source–sink studies follow the demography of single species (reviewed in Pulliam 2000), making the relative importance of sink populations for diversity unknown. Nonetheless, results from experiments and sampling suggest that sink populations are important to include in both theoretical and applied models of species distributions (Pulliam 2000; Clark *et al.* 2007; Allouche *et al.* 2008).

DIVERSITY AND ECOSYSTEM FUNCTION

Although it is generally accepted that numerous mechanisms can alter diversity (Levine 2000), the effect of diversity on ecosystem functioning remains controversial (Srivastava & Vellend 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2006, 2007). At first glance, the model presented here appears to add further complexity to the debate. If a simple model of regional heterogeneity causes opposing relationships between local diversity and ecosystem function, how can these relationships be predicted or interpreted? The variety of results from research on diversity and ecosystem function emphasize this question. Meta-analyses show that although average trends exist, communities show both positive and negative relationships between diversity and ecosystem function when compared to the performance of the most productive species (for example, 12% positive vs. 25% negative in the study of Cardinale *et al.* (2007)). Indeed, it may well be that differences among communities in their diversity–ecosystem function relationships will further our understanding of ecological dynamics more than their mean effects.

The model presented here predicts three distinct trends that can help to frame the debate on diversity and ecosystem function. The first trend predicted by the model is that species' relative abundance should reflect their competitive abilities in communities where regional richness does not collapse (Fig. 1b,c). Plant community studies support this prediction by showing a negative correlation between species' abundance and their R^* s (HilleRisLambers *et al.* 2004; Harpole & Tilman 2006). In addition, several studies that compare the role of

dominant and rare species in plant communities have shown that dominant species often have the most influence on resource uptake (Smith & Knapp 2003; Emery & Gross 2007), although this pattern varies across species and communities (Cardinale *et al.* 2007; Gilbert, Turkington & Srivastava 2009). Further studies that contrast the role of species dominance and diversity will shed light on the importance of such competitive hierarchies.

The second prediction is that the effect of dispersal on productivity is mediated by niche overlap among species. For example, the negative effects of sink populations which are apparent when niche overlap is low virtually disappear when niche overlap is high (Fig. 2c, $\sigma = 0.01$ vs. $\sigma = 0.5$). Although other studies have not explicitly tested the effects of neutral versus niche interactions on productivity, different predictions about the effect of dispersal have arisen in part from differing assumptions about species niches. For example, when the best competitor wins at a site by default, increasing dispersal invariably increases productivity (Mouquet, Moore & Loreau 2002). This result, which is contrary to the one presented here, arises because sink populations in these models do not result from high dispersal rates (Hurtt & Pacala 1995). Similarly, in homogenous environments that contain a single best competitor, it has been shown that increasing the dispersal of the best competitor increases productivity (Loreau & Mouquet 1999; Mouquet, Moore & Loreau 2002). This result differs from those presented here (Fig. 2b,c) because neither niche-based nor neutral communities ever have a single best competitor (Fig. 1). These differences in predictions from various models suggest that understanding the degree of niche overlap among species is essential for untangling the relationship between dispersal, diversity and productivity. The role of niche overlap can be empirically tested in studies designed to disentangle the importance of niche differences from equalizing processes (Adler, HilleRisLambers & Levine 2007).

The third trend predicted by the model is that an increase in local diversity should correlate with a decrease in ecosystem function when this diversity is comprised of sink populations formed by increased immigration (Fig. 2a). This prediction is analogous to the effect of high dispersal levels in population genetics: immigration can dilute selection in local populations (Spieth 1974), resulting in a higher genetic load and persistence of less fit genotypes in a patch (Levene 1953; Wiens 1976). The presence of sink populations in spatially structured communities has long been noted theoretically and empirically (Levin 1976; Wiens 1976; Shmida & Wilson 1985; Mouquet & Loreau 2003), although the relevance to resource use has not been explored in recruitment models that depend on resources. The model presented here does depend on resources for population regulation and has a positive feedback between resource availability and recruitment of new individuals (eqn 5), which is common to all CRDMs. Given this feedback, why do communities with more unused resources not then recruit more individuals, eliminating the effects of the sink populations? The answer is twofold. First, poorly adapted species still compete for limiting resources, whether or not they are able to utilize

these resources fully. Second, the best-adapted species for a given patch have lower seed densities than in a closed model because some seeds disperse out of the patch, limiting the uptake of resources.

If sink populations increase local diversity and thereby decrease resource use and productivity, we would expect to see these trends in experiments that manipulate species diversity. Although biodiversity–ecosystem function experiments do test this possibility, these experiments alter the ‘regional pool’ of seeds and manipulate both the probability of including the best-adapted competitor and the probability of including sink populations. These different mechanisms should produce opposite diversity–functioning relationships (Figs 2 and 4), and it is not clear whether the net result should be positive or negative. Testing the role of dispersal in creating diversity, and its successive role in ecosystem function, would be a more direct way of testing the effects of sink populations.

ENVIRONMENTAL HETEROGENEITY

Although the model presented here is simple, it nonetheless represents important dynamics that may drive species diversity in natural systems. A number of ecosystems have distinct environmental ‘patches’ that are semi-permanent structures on the landscape (Harrison 1997; Davies *et al.* 2005). The temporally static structure of the environment in this model is a good approximation of such ecosystems.

Despite the importance of spatially structured environmental heterogeneity, the dynamics described by the model, and in particular the importance of sink populations, result in part from the underlying assumption that niche complementarity is not possible within a patch. In reality, complementarity may be present at small scales and even in homogenous environments, as can occur when species that partition resources spatially or temporally are present in a locality (McKane *et al.* 2002; Cardinale *et al.* 2007) or when more than one resource is limiting (Levin 1976; Tilman 1980). For example, McKane *et al.* (2002) demonstrated differential resource use by co-occurring plants that differed in rooting depth and phenology. Niche complementarity within patches would partially alter model predictions by producing positive correlations between local diversity and resource use (Tilman, Lehman & Thomson 1997). However, the presence of niche complementarity, as with facilitation or other processes not included in this model, would not negate the role of sink populations but rather determine their relative importance to overall ecosystem function.

Niche complementarity can be evaluated in the model presented here by considering the effect of regional diversity on average ecosystem function. The positive effect of regional richness on resource use observed in the model output is a result of species occupying distinct niches in the region (Fig. 4). Mouquet & Loreau (2003) showed a decrease in productivity with a decrease in regional diversity that was due to the vacating of ‘niche spaces’ that occurred when species went regionally extinct. Similarly, Bond & Chase (2002) proposed that productivity increases linearly with increased regional

richness. The model presented here shows a different trend: adding species into a variable region only increases ecosystem function when a small number of species are present (Fig. 4b). The flat trend at higher levels of diversity is likely caused by a trade-off between greater saturation of the regional environmental niche space (causing a positive relationship), the increased number of sink populations (causing a negative relationship) and the increased degree of niche overlap that occurs with greater species packing, which makes each species more redundant on average. Overall, even when niche complementarity is built into a metapopulation model, the positive effects of diversity on ecosystem function plateau at relatively low levels of local diversity (2–4 species; Fig. 4), a trend also seen in numerous studies (Schwartz *et al.* 2000; Cardinale *et al.* 2006).

Summary

As with all models, the validity of trends predicted here must be tested with empirical studies. A number of such tests are possible. For example, invasion studies have tested the role of increasing propagule pressure on invasion and local diversity (Levine 2000; MacDougall & Turkington 2006), and similar approaches could be used to test the effects of this increased diversity on resource use and productivity. In addition, the degree to which species coexist because of strong niche differentiation (versus competitive similarity) could be tested in a metacommunity framework by altering the propagule pressure of select species to determine the stability of the community (Levine & Murrell 2003; Adler, HilleRisLambers & Levine 2007). Undertaking such tests will quantify the importance of spatial dynamics in natural systems and elucidate the causes and consequences of diversity.

Understanding how dispersal- and niche-based mechanisms generate local diversity may resolve debates on the importance of diversity in ecosystem function at different scales, as well as related issues such as the role of diversity in preventing invasive species from establishing (Raffaelli *et al.* 2005; Fridley *et al.* 2007). Many studies on diversity effects manipulate the 'regional' species pool and simultaneously limit habitat heterogeneity by creating homogenous and identical plots, effectively removing much of the potential variation of species responses to the environment that underlie theories of diversity and resource use. This approach has been criticized for its lack of applicability to conservation (Srivastava & Vellend 2005) and should also be scrutinized for its inconsistency with theory. Devising methods to test the relationship between diversity and ecosystem properties at a scale that captures environmental heterogeneity is a priority for both conservation and theoretical ecology.

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