ORIGINAL ARTICLE

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Community assembly along a species pool gradient: implications for multiple-scale patterns of species diversity

Abstract Various ecological processes influence patterns of species diversity at multiple spatial scales. One process that is potentially important but rarely considered is community assembly. I assembled model communities using species pools of differing size to examine how the history of community assembly may affect multi-scale diversity patterns. The model contained three scales at which diversity could be measured: local community, metacommunity, and species pool. Local species saturation occurred, as expected from the competition and predation built in the model. However, local communities did not become resistant to invasions except when the species pool was very small. Depending on dispersal rate and trophic level, the larger the species pool, the harder it was to predict which species invades which local community at a given time. Consequently, local-community dissimilarity maintained by assembly history increased linearly with pool size, even though local diversity was decoupled from pool size. These results have two implications for multi-scale diversity patterns. First, assembly history may provide an explanation for scale-dependent relationships between local and regional diversity: assembly causes the relationship to be curvilinear at one scale (local community), while linear at another (metacommunity). Second, assembly history influences how γ-diversity is partitioned into α- and β-diversity: assembly causes the relative contribution of β to increase with pool size. Overall, this study suggests that community assembly history interacts with species pool size to regulate multi-scale patterns of species diversity.

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Introduction

Multiple processes interact to influence patterns of species diversity at different scales. The relative importance of these processes has been a central subject of ecological and evolutionary research (Ricklefs and Schluter 1993; Godfray and Lawton 2001; Noda 2004). One popular approach to examining the relative importance of small- versus large-scale processes has been to plot local versus regional species richness for matching sites, a method originally used by Terborgh and Faaborg (1980) and recently reviewed by Srivastava (1999), Hillebrand and Blenckner (2002), and Shurin and Srivastava (2004) . These plots frequently show a linear pattern without reaching an asymptote, which has been interpreted to mean that local species interactions do not limit membership in ecological communities, that local communities are not "saturated" with species, and that regional processes such as long-distance dispersal and speciation are the main determinants of local richness (Ricklefs 1987; Cornell and Lawton 1992; Cornell and Karlson 1997; Caley and Schluter 1997; Lawton 1999; but see Shurin and Allen 2001). This view necessarily runs counter to the traditional premise in ecology that local richness is strongly governed by local species interactions (e.g., MacArthur 1972).

More recently, however, a number of problems have arisen in using local–regional plots (reviewed in Srivastava 1999; Hillebrand and Blenckner 2002). In particular, it has been argued that local–regional richness relationships are too sensitive to the definition of local and regional scales to adequately detect species saturation (Westoby 1998; Huston 1999; Rosenzweig and Ziv 1999; Loreau 2000; Godfray and Lawton 2001). Consequently, Loreau (2000) and others dismissed the use of

local–regional plots to infer the relative importance of local and regional processes. A more promising question to ask in understanding species diversity across multiple scales, they argue, is how γ-diversity, the total diversity in a given region, is partitioned into α-diversity, the within-community component of diversity, and β-diversity, the between-community component (Loreau 2000; Godfray and Lawton 2001; Veech et al. 2002). This question is actually a revival of an old one (e.g., Whittaker 1972) that has received little attention until it was recently given new conceptual importance (see Veech et al. 2002). The question in its new context has already proven useful in a few recent studies (Fourier and Loreau 2001; Gering and Crist 2002; Crist et al. 2003).

One process that is potentially important but rarely considered with respect to multi-scale diversity patterns is community assembly (Morton and Law 1997). Here I define community assembly as the construction and maintenance of local communities through sequential arrival of potential colonists from an external species pool (Drake 1990; Warren et al. 2003). Note that "viewed in this way, community assembly emphasizes changes in the community state rather than embracing all evidence for pattern in community structure, the broader context in which the term assembly is sometime used" (Warren et al. 2003, p 1001). We know that the history of community assembly can in some cases greatly affect local species diversity (e.g., Drake 1990; Fukami and Morin 2003). If this sequence effect interacts with the size of the species pool to influence diversity, community assembly may have important implications for understanding multi-scale diversity patterns (Wilson 1992; Chase 2003). In practice, however, ecologists usually must regard the dynamics of community assembly as a black box, because it is difficult to control experimentally or to reconstruct in specific detail. For example, in previous studies that used local–regional plots, local scale was often defined so broadly that it probably contained multiple communities that were each undergoing assembly (e.g., Caley and Schluter 1997; Bini et al. 2000).

In this paper, I examine the role of community assembly history in generating multi-scale diversity patterns. For this purpose, I simulated the assembly of communities structured by competition, predation, and dispersal using species pools of differing size. The model was a general Lotka-Volterra system that has been extensively used for studying assembly. However, my model differed from most prior assembly models (e.g., Morton and Law 1997; Mouquet et al. 2003) in one important respect: I assembled not only local communities but also metacommunities consisting of five local communities by allowing dispersal both from the species pool (hereafter called external dispersal) and among local communities (hereafter called internal dispersal) (Fig. 1, see Wilson 1992 for a similar approach). As such, the model contained three ecologically distinct spatial scales at which species diversity could be measured: local community, metacommunity, and species pool.
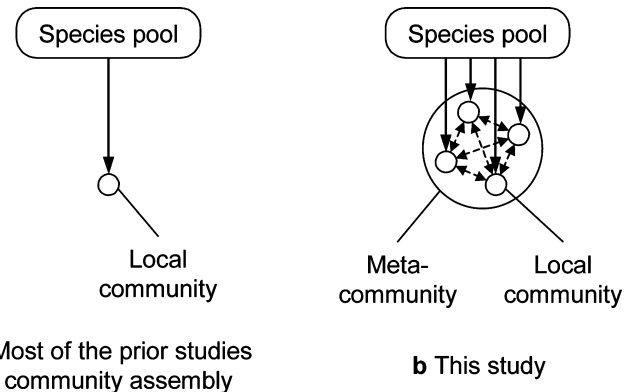

a Most of the prior studies on community assembly

b This study

Fig. 1 Schematic representation of community assembly models. *Solid* and *dashed arrows* indicate external and internal dispersal, respectively

Methods

Constructing species pools

Population dynamics within each local community were governed by general Lotka-Volterra equations defining population growths and intra- and inter-specific interactions:

$$\frac{dx_{ik}}{dt} = x_{ik}\left(b_i + \sum_{j=1}^{m} a_{ij}x_{jk}\right). \tag{1}$$

Here, x_{ik} is the density of species i in local community k, b_i is the per capita intrinsic rate of increase or decrease of species i, and a_{ij} is the per capita effect of species j on species i. Given these equations, a set of m species that are each assigned a value of b_i and those of a_{ij} would define a species pool from which species disperse to local communities.

I created 17 species pools using a method similar to that of Law and Morton (1996) and Morton and Law (1997). For each pool, I divided m species into m_1 basal species and m_2 consumer species (m_1 equaled m_2). A basal species did not eat other species and could grow alone. A consumer species ate some of the species from the pool and could not sustain its population in local communities without them. The 17 pools differed in the number of species. The smallest pool had $m_1 = 2$ and $m_2 = 2$ species, and the largest $m_1 = 50$ and $m_2 = 50$ species. I created these pools independently to avoid pseudoreplication (Srivastava 1999; Fox et al. 2000). However, the results presented here qualitatively hold for pools created non-independently as follows: first make a pool with $m_1 = 50$ and $m_2 = 50$ species and then progressively remove $m_1 = 3$ and $m_2 = 3$ species randomly chosen from the remaining species in the pool.

For each pool, I first assigned a body size, s_i, to each species i. I drew the logarithm of body size of species i, $\log_{10}(s_i)$, at random from a uniform distribution over the range $[-2, -1]$ for basal species and $[-1, 1]$ for consumer species. Body sizes are typically distributed lognormally in

natural systems (e.g., Cohen et al. 1993). The unit for s_i is g. I assumed that, if $s_i < s_j$, species i may be eaten by species j, but not vice versa.

In determining the strength of the interaction between a consumer and a victim, I assumed an optimal ratio of body size between a consumer and a victim that gives the maximum interaction strength possible (cf. Cohen et al. 1993). Thus, the mean effect of an encounter between a consumer j and victim i on the per capita rate of increase of the victim was given as:

$$\bar{a}_{ij} = -0.1 \times \exp\left\{-\left(\log_{10}(10 \times s_i/s_j) \times c_1\right)^2\right\} \quad s_i < s_j$$
$$a_{ij} = 0 \quad s_i \geq s_j. \tag{2}$$

Here the maximum interaction strength is 0.1, and the optimal body size ratio is 10. The parameter c_1 measures the degree of specialization of the consumers around the optimal ratio. I used $c_1 = 10$. Conversely, taking into account energetic constraints so that the loss of victim density is balanced against the gain in consumer density, the mean effect on the per capita rate of increase of the consumer was given as:

$$\bar{a}_{ji} = -\bar{a}_{ij} \times c_2 \times s_i/s_j \quad s_i < s_j$$
$$a_{ji} = 0 \quad s_i \geq s_j. \tag{3}$$

The parameter c_2 measures conversion efficiency. I used $c_2 = 0.05$, which lies within the biologically feasible range (Humphreys 1979). Note that both basal and consumer species can be victims of other consumer species, depending on their body size.

I assumed an upper limit to total biomass, or the carrying capacity K_i, of basal species within a local community. Assuming $K_i = 100$ biomass units for each basal species i, the self-limitation term for basal species i is:

$$\bar{a}_{ii} = -b_i \times \frac{s_i}{100}. \tag{4}$$

When different basal species occur together in the same local community, they compete for limited resources such that the mean effect of basal species j on basal species i is:

$$\bar{a}_{ij} = -c_3 \times b_i \times \frac{s_j}{100}. \tag{5}$$

The dimensionless parameter c_3 measures the similarity of the basal species in their resource use. Species do not affect each other if $c_3 = 0$; they are identical if $c_3 = 1$. I let $c_3 = 0.9$ as in Morton and Law (1997). Consumers are limited only by victim density, and their self-limitation term is 0.

Based on an empirical relationship between body size and b_i of basal species (Fenchel 1974; Blueweiss et al. 1978), I assumed, with units of day^{-1}, that:

$$\log_{10} \bar{b}_i = -1 - 0.25 \times \log_{10} s_i. \tag{6}$$

It is less clear how b_i of consumers should be scaled with body size. Following Morton and Law (1997), I assumed:

$$\bar{b}_i = -0.1 . \tag{7}$$

In nature, it is unlikely that a_{ij} and b_i are determined solely by body size. Morton and Law (1997) assume that there are random variables with mean values set by Eqs. 2–7, and I follow this approach. Thus, if $\bar{p}$ = the mean value of a parameter from Eqs 2 to 7, p itself was taken as a random variable from a normal distribution $N(\bar{p}, 0.1 \times \bar{p})$, with the distribution truncated to ensure that p has the same sign as $\bar{p}$.

Because of the specific assumptions made regarding body sizes and interaction strengths, these methods for constructing species pools do not apply to every real community possible. However, the methods give values of a_{ij} and b_i more consistent with the skewed distributions of interaction strengths found in natural communities (Paine 1992; Berlow et al. 1999; McCann 2000, but see Abrams 2001; Sala and Graham 2002) than do methods that assume that a_{ij} and b_i are distributed uniform randomly (Post and Pimm 1983; Case 1990; Drake 1990; Lockwood et al. 1997; Lundberg et al. 2000; Wilmers et al. 2002).

Assembling communities

With each of the 17 species pools created, I simulated the assembly of a single metacommunity consisting of five local communities. I initiated the simulations by randomly choosing, for each local community in the metacommunity, a species from the species pool and introducing it to the corresponding local community (external dispersal). After a predetermined period of time passed, I chose a second species randomly from the pool for each local community and introduced it to the corresponding community. I repeated this process for a million days. For each pool, I used two rates of external dispersal: once in 10 days and once in 100 days. I introduced species with a low abundance ($x_{ik} = 1.0 \times 10^{-3}$). This initial abundance was several orders of magnitude lower than the carrying capacities of basal species in a local community, which ranged from 9.09×10^3 [i.e., 100 biomass units divided by the maximum body size possible = $100/(0.1 \times 1.1)$] to 1.11×10^4 [i.e., 100 biomass units divided by the minimum body size possible = $100/(0.01 \times 0.9)$]. I did not allow the species present in a local community at a given time to be chosen as the newly invading species for that community at that time; although this approach may increase external dispersal rate with local species richness, the approach follows previous assembly modeling (e.g., Law and Morton 1996; Morton and Law 1997) and makes results comparable.

I also allowed species to disperse among local communities within the metacommunity (internal dispersal). Once in 10 days, I measured total abundance summed over local communities for each species. For each species and local community, I determined whether the species dispersed to the community probabilistically as a linear function of its total abundance in the metacommunity.

For basal species, the dispersal probability was set such that a species that had the maximum total abundance possible would have a probability of 1. The maximum total abundance possible was calculated as follows: the number of local communities in a metacommunity (5) × the maximum biomass units possible in a local community (100)/the minimum body size possible (0.01×0.9) = 5.556×10^4. For consumer species, the dispersal probability was set such that a species that had 5% of the maximum total abundance possible for basal species would have a probability of 1. I placed 5% (note that it is the same as c_2) here so that consumers were better able to disperse between local communities than basal species were. I introduced species with $x_{ik} = 1.0×10^{-3}$. I used two rates of internal dispersal: potential dispersal of species once in 10 days and once in 100 days subject to the dispersal probabilities.

Throughout the simulation, I calculated the abundance of each species in each local community by numerically integrating Eq. 1 using the commercially available algorithm, "d02ejc" (Numerical Algorithm Group 2002), which implements backward differentiation formulae (see Hall and Watt 1976). This method more closely approximates dynamics of the Lotka-Volterra equations than methods used in earlier assembly studies, including local asymptotic stability (Post and Pimm 1983; Drake 1990), Euler integration approximation (Law and Morton 1996; Lockwood et al. 1997; Wilmers et al. 2002), and permanence theory (Law and Morton 1996; Morton and Law 1997) (see also Morton et al. 1996). Species went extinct if their abundance fell below a threshold, $x_{ik} = 1.0×10^{-3}$.

Measurements and analyses

For each metacommunity, I obtained the following richness measures at the end of the simulation: (1) mean number of basal species in a local community, averaged over the five local communities, (2) number of basal species in the metacommunity, (3) local community dissimilarity in basal species composition (i.e., (3) = (2)−(1); used as an index of dissimilarity), (4) mean number of consumer species in a local community, averaged over the five local communities, (5) number of consumer species in the metacommunity, and (6) local community dissimilarity in consumer species composition (i.e., (6) = (5)−(4); used as an index of dissimilarity).

At the end of the simulation, I also measured the mean number of potentially colonizing species, averaged over the five local communities. Potentially colonizing species are species that are absent from the local community but present in the species pool and that would remain in the local community without ever reaching a density below $1.0×10^{-3}$ for at least $1.0×10^3$ days if introduced to the community at the end of the simulation. To obtain this number, I first introduced one of the species absent from the local community to that community, followed community dynamics using the same numerical integration algorithm and extinction criterion as specified above for $1.0×10^3$ days without introducing any more species, and determined if the introduced species had a density greater than the threshold, $1.0×10^{-3}$. If it did, I counted this species as a potential colonizer. I then introduced a second species from the species pool to the community of original species composition and abundance at the end of the simulation and determined if this species was a potential colonizer. I repeated this process for all species in the pool to obtain the total number of potential colonizers. The greater the number of potential colonizers, the less resistant the local community is to invasion by species in the pool. I obtained the richness and resistance measures separately for basal and consumer species.

I used linear regressions to examine the relationships between the size of species pool and each of the above measures of richness and resistance. I examined curvilinearity of the relationships by testing for a significant contribution of the quadratic term to the linear regression (Caley and Schluter 1997; Karlson and Connell 1998; Shurin et al. 2000). If there was a significant linear relation ($P < 0.05$ for the linear term) and if the quadratic term significantly contributed to explain the relationship ($P < 0.05$ for the quadratic term), I concluded that the relationship was curvilinear. If there was a significant linear relation, but if the quadratic term did not significantly contribute, I concluded that the relationship was linear. I used SYSTAT version 10 (SPSS 2000) for all analyses.

Results

Under infrequent external dispersal, species richness showed no overall trends of temporal increase or decrease except during the initial build-up (Fig. 2). Species richness varied greatly over time in both local communities and metacommunities when the species pool had more than 40 species (Fig. 2c–f). Basal species richness in metacommunities increased linearly with the size of species pool (Fig. 3a, Table 1). In contrast, basal species richness in local communities increased curvilinearly with the size of species pool (Fig. 3b, Table 1). Local community dissimilarity increased linearly with pool size, starting from the pool containing 14 species (Fig. 3c, Table 1). Similarly, the number of potentially colonizing species increased linearly with pool size (Fig. 3d, Table 1). Consumer species richness showed no significant relations with pool size (Fig. 3e–g, Table 1), but the number of potential colonizers increased linearly with pool size (Fig. 3h, Table 1).

Under frequent external dispersal, local communities converged to similar species richness regardless of pool size, leaving little local community dissimilarity (Figs. 4, 5c, g). Basal species richness in both local and metacommunities increased linearly with pool size (Fig. 5a,b, Table 2). Consumer species richness at both scales increased curvilinearly (Fig. 5e,f, Table 2), but linear
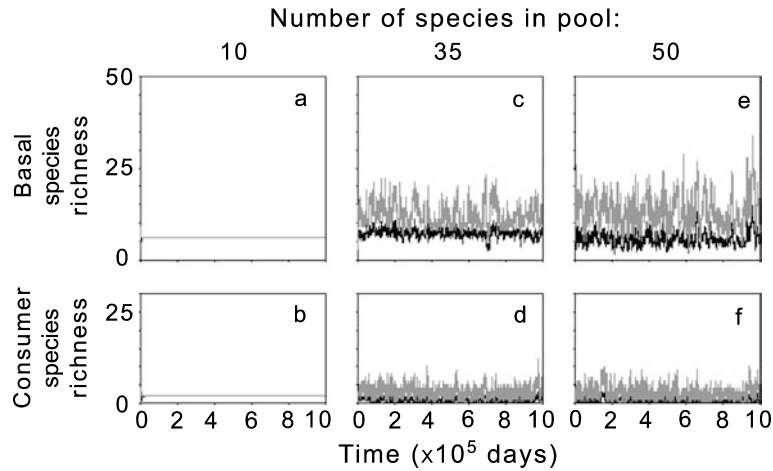
Number of species in pool:

Fig. 2a–f Representative examples of community dynamics under infrequent external dispersal. *Pale* and *dark lines* represent species richness in meta- and local communities, respectively. Because pale lines are drawn on top of dark lines, dark lines are hidden when the two overlap. Results in **a** and **b**, **c** and **d**, and **e** and **f** are each from the same simulation. Note that the number of species in the species pool (10, 35, and 50) is the number of basal (**a**, **c**, **e**) or consumer (**b**, **d**, **f**) species only; species pools also had an equal number of consumer or basal species

regressions explained the relationships almost as well as quadratic ones did (compare adjusted R^2 values in Table 2). Few potential colonizers existed (Fig. 5d,h).

These results are for one of the two internal dispersal rates used, i.e., once in 10 days, but the results qualitatively hold for the other rate, i.e., once in 100 days (data not shown).

Discussion

Implications for relating species diversity at multiple scales

The results for basal species richness under infrequent dispersal (Fig. 3a–d) show that local–regional richness relationships can be linear with no limit to local richness at the metacommunity scale (Fig. 3a), while being strongly curvilinear with a clear asymptote at the local community scale (Fig. 3b). How did this scale dependence emerge? The curvilinear pattern at the local community scale was expected because competition and predation was built into the model (see also Morton and Law 1997). These species interactions, coupled with the carrying capacity assumed in the model, presumably caused tighter species packing in local niche space as species pool size increased. Without species interactions, local richness would have been linearly related to regional richness. What is intriguing is that local communities did not assume a stable point with a fixed species composition; rather they experienced continued compositional changes (Fig. 2c–f). Therefore, local community dissimilarity was not a result of different local communities assuming alternative stable states

(Lewontin 1969; Sutherland 1974; Drake 1990; Law and Morton 1993; Chase 2003). Instead, the dissimilarity appears to represent what has been called mosaic cycles, which are sets of species compositions that replace one another over time in a cyclic or more complicated sequence, but, importantly, without recourse to abiotic perturbations (Remmert 1991; Lockwood et al. 1997; Steiner and Leibold 2004). Results for invasion resistance suggest that the number of states a local community could enter at a given time increased linearly with the size of the species pool (Fig. 3d, h). In other words, the larger the species pool, the harder it was to predict which species would invade which local community. Consequently, the linear local–regional relationship emerged at the metacommunity scale (Fig. 3a), despite the leveling off of richness increase at the local community scale owing to local interactions (Fig. 3b).

My results demonstrate that community assembly alone can generate scale-dependent patterns without other factors that have been shown to confound interpretation of local–regional plots. For example, the problem of environmental heterogeneity (Cornell and Lawton 1992; Huston 1999; Loreau 2000) does not apply to this study, because environmental conditions were homogeneous across local communities and over time (i.e., the same set of constant b_i and a_{ij} values governed population dynamics in all communities in a metacommunity). Similarly, apparent saturation owing to a lognormal abundance distribution (Caley and Schluter 1997) or to physical limitation (Loreau 2000) is not a problem in this study for two reasons. First, I counted all species present regardless of abundance. Second, the basal species' carrying capacities were several orders of magnitude greater than the extinction threshold. Selection of comparable communities (Srivastava 1999; Ricklefs 2000), effects of differing region size (Srivastava 1999; Ricklefs 2000; Shurin et al. 2000), and pseudoreplication (Srivastava 1999; Fox et al. 2000) were not a problem in this study, either, because species pools were created independently and were comparable (i.e., each pool was created with new values of b_i and a_{ij}).
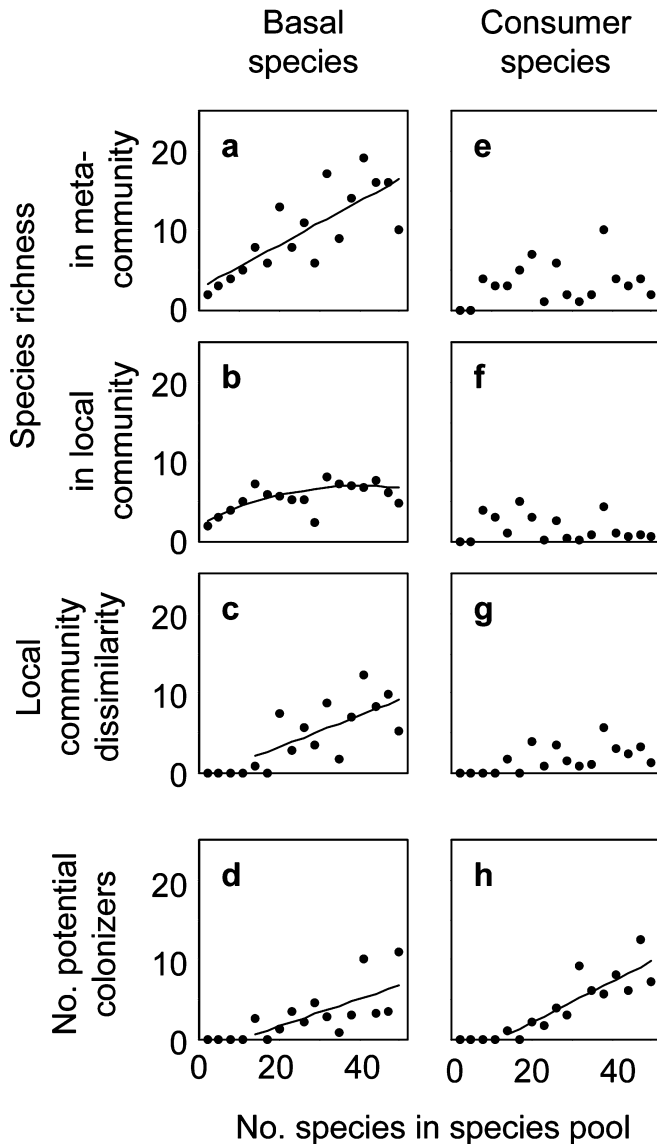
Fig. 3a–h Relationships between pool size and species richness (**a–c** and **e–g**) and invasion resistance (**d** and **h**) under infrequent external dispersal. Data are fitted to regression models where significant (Table 1). Note that pool size is the number of basal (**a–d**) or consumer (**e–h**) species only; species pools also had an equal number of consumer or basal species

The results thus highlight the importance of considering community assembly history for understanding species richness and species saturation (see also Mouquet et al. 2003). Assembly dynamics can make communities appear unsaturated (Fig. 3a) even when local species interactions strongly limit local species coexistence (Fig. 3b). If we want to test whether local richness is determined by species interactions, we need to look at the scale at which interactions potentially occur, i.e., the local-community scale in this study. Pooling richness across any higher scales starts to pull in assembly-derived community dissimilarity and automatically creates correlations with pool size even in the presence of strong local interactions (Fig. 3a, see also Hillebrand and

Blenckner 2002). Thus, community assembly presents a previously unrecognized, additional problem in interpreting local–regional richness relationships: they are sensitive to the local scale defined by the researcher relative to the scale at which community assembly occurs.

It is not certain why species saturation was not detected in basal species under frequent external dispersal (Fig. 5b). However, species interactions do not necessarily cause saturation pattern (Cornell and Lawton 1992). One possibility is that saturation would be observed over a greater range of species pool size than used in this study. Interestingly, dispersal rate may determine the range of regional richness required to detect species saturation (see also Mouquet and Loreau 2003).

Implications for partitioning species diversity at multiple scales

The results suggest that community assembly also has implications for understanding how regional species diversity (γ-diversity) is partitioned into within- (α-diversity) and between- (β-diversity) community components (Loreau 2000; Veech et al. 2002). There are no a priori criteria to determine the scales at which these diversity components should be measured. Appropriate scales depend on the scale at which the processes of interest are expected to operate. For example, if we are interested in the relative contribution of the diversity created and maintained by variation in assembly history in this study, the appropriate way to assign diversity components is as follows: species richness in local communities as α, richness in metacommunities as γ, and local community dissimilarity as β. It is convenient to draw the relationships between pool size and local community richness (e.g., Fig. 3a) and between pool size and metacommunity richness (e.g., Fig. 3b) on the same graph (e.g., Fig. 6a). Further, the partitioning of γ into α and β can be more directly visualized by the percentages of γ contributed by α and β (e.g., Fig. 6b).

The results show that pool size has a major effect on diversity partitioning (Fig. 6). The relative contribution of β increases considerably with pool size, especially when dispersal rate is low (Fig. 6a,b). The relative contribution changed from about 15% to about 60% (Fig. 6b). Because no environmental heterogeneity among local communities or over time existed in the simulation model, the only source of this increase in β-diversity is the variation in assembly history among local communities. Hence, the results demonstrate that community assembly and pool size can interact to greatly influence diversity partitioning.

Questions addressed by assembly studies have been largely limited to local community scale (reviewed in Samuels and Drake 1997; Law 1999) . Ecologists have only recently begun to view community assembly as a regulator of β-diversity (Lockwood et al. 1997; Chase 2003). It is environmental heterogeneity among local

Table 1 Regressions under infrequent external dispersal. Linear and quadratic regressions are $Y = a + bX$ and $Y = a + bX + cX^2$, respectively, where X is the number of species in the species pool and Y is the dependent variable. P values in parentheses are from a two-tailed and one-tailed test for a and for b and c, respectively. Selected models are in bold. The range of X used was from 2 to 50 for species richness in local and meta-communities and from 14 to 50 for local community dissimilarity and the number of potential colonizers. See Methods for model selection method

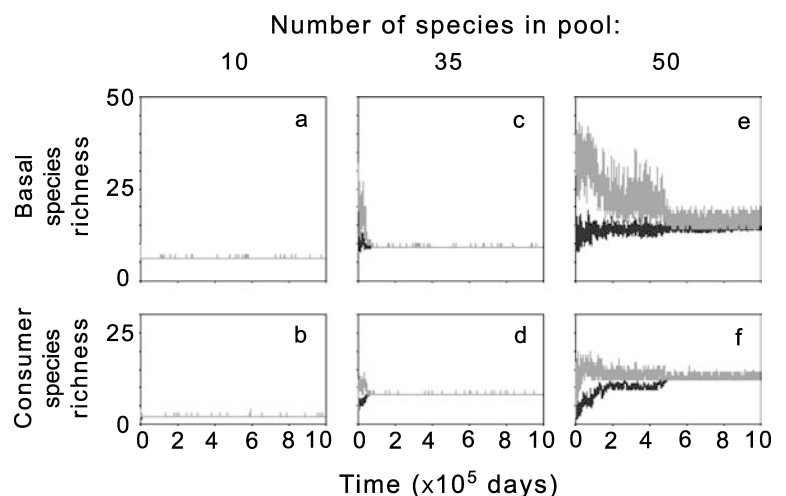| Dependent variable	Model	Regression parameter estimates with P values shown in parenthesis			Adjusted R^2
		a	b	c	
Basal species					
Species richness in local communities	Linear	3.782 (0.000)	0.066 (0.013)		0.251
	Quadratic	2.238 (0.066)	0.240 (0.015)	−0.003 (0.047)	0.349
Species richness in metacommunities	**Linear**	2.686 (0.122)	0.275 (0.000)		0.600
	Quadratic	0.260 (0.918)	0.549 (0.013)	−0.005 (0.110)	0.617
Local community dissimilarity	**Linear**	−0.680 (0.794)	0.198 (0.013)		0.334
Number of potential colonizers	**Linear**	−1.681 (0.472)	0.169 (0.014)		0.312
Consumer species					
Species richness in local communities	Linear	2.171 (0.020)	−0.021 (0.236)		0.000
	Quadratic	1.058 (0.420)	0.105 (0.184)	−0.002 (0.136)	0.000
Species richness in metacommunities	Linear	2.270 (0.097)	0.042 (0.174)		0.000
	Quadratic	0.219 (0.911)	0.273 (0.066)	−0.004 (0.092)	0.057
Local community dissimilarity	Linear	1.203 (0.380)	0.033 (0.209)		0.000
Number of potential colonizers	**Linear**	−3.056 (0.106)	0.258 (0.000)		0.670

sites that has been treated as the main regulator of β-diversity (e.g., Whittaker 1972; Huston 1999; Loreau 2000). This is perhaps because Whittaker (1972), who coined the term β-diversity, defined it mainly to describe variation caused by environmental heterogeneity (Veech et al. 2002). It may also be because the effects of community assembly and environmental heterogeneity are hard to differentiate from each other, which has resulted in lively discussions (e.g., Connor and Simberloff 1979; Connell and Sousa 1983; Gilpin and Diamond 1984; Petersen 1984; Sutherland 1990; Grover and Lawton 1994). The results from this simulation study support the argument that future biodiversity research will benefit from considering the role that assembly history and its interaction with environmental heterogeneity may play in controlling the relative contribution of α- and β-diversity to γ-diversity (Wilson 1992; Chase 2003).

Dispersal rate and community assembly

Permanence theory predicts that, given a species pool, most assembly sequences will tend to a very limited number of invasion–resistant endpoints (Law and Morton 1996; Morton and Law 1997). This prediction seemingly contradicts my results, namely (1) the large divergence of local communities within a metacommunity and (2) the general absence of invasion resistance even after local and meta-communities have reached equilibrium. These two aspects of the results were essential for the scale-dependent diversity patterns to emerge in this study. Because I used a method of assigning b_i and a_{ij} values similar to Law and Morton's (1996), this difference warrants explanation.

A likely explanation concerns dispersal rate. Permanence theory assumes that local population dynamics

Fig. 4a–f Representative examples of community dynamics under frequent external dispersal. *Pale* and *dark lines* are as in Fig. 2. Results in **a** and **b**, **c** and **d**, and **e** and **f** are each from the same simulation. For each pair, the same pool was used as for the corresponding pair in Fig. 2
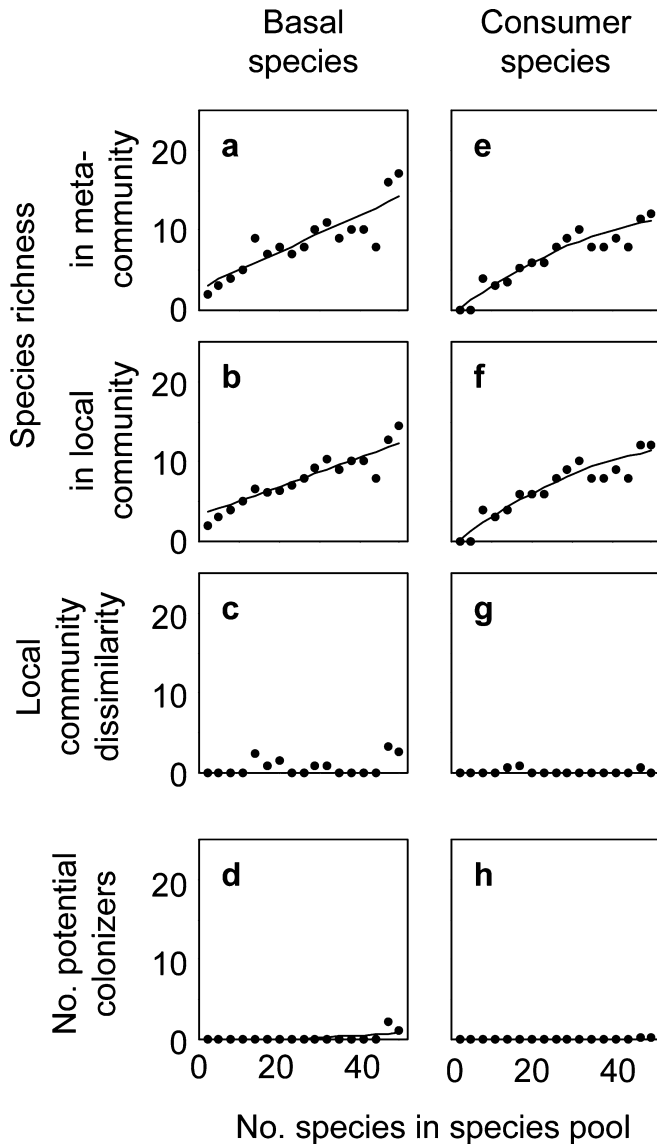
Fig. 5a–h Relationships between pool size and species richness (**a–c** and **e–g**) and invasion resistance (**d** and **h**) under frequent external dispersal. Data are fitted to regression models where significant (Table 2). As in Fig. 3, pool size is the number of basal (**a–d**) or consumer (**e–h**) species

Leibold 2004) may play a more prominent role in community assembly than alternative stable states do. Traditionally, alternative stable states have been used to evaluate the importance of assembly history (reviewed in Samuels and Drake 1997; Chase 2003). For example, although Chase's (2003) suggestion that β-diversity would increase with species pool size seems consistent with my results (Fig. 3c), the hypothesized mechanisms are fundamentally different: Chase (2003) suggested that assembly history would create more alternative stable states in local species compositions under larger species pools, whereas my results suggest that it may not be the number of alternative stable states, but the number of species involved in cyclic compositional changes that increases with species pool size. Cyclic changes, which can be single stable states as opposed to alternative stable states, may be more important for understanding the role of assembly history than generally thought.

Future directions

An important direction is to test the predicted scale-dependent patterns empirically. The data would need to have a high enough resolution to divide local areas into multiple patches. Such data are not readily available but may be obtained with species assemblages in small, discrete, and numerous habitats such as fallen wood branches (Fager 1968), pitcher plants (Harvey and Miller 1996), and tree holes (D.S. Srivastava, personal communication). An alternative approach that is less direct but still useful is to compare slopes of local–regional plots from different studies (Shurin and Srivastava 2004) . Laboratory microcosm experiments would also be valuable because they uniquely allow for rigorous control over assembly history, though in less natural settings (e.g., Fox et al. 2000; Fukami and Morin 2003).

Theoretically, the way dispersal was simulated here is one of many that could have been used. For example, dispersal occurred in a spatially implicit fashion. But nearest neighbor distances and the species composition and abundance in neighboring communities may affect local community structure (Selmi and Boulinier 2001). Likewise, I assumed equal dispersal ability among species. But dispersal ability may correlate with body size and other traits and vary more greatly among species than assumed in this study (Hillebrand and Blenckner 2002). Future studies will need to assess the robustness of the results to these variations.

It will also be interesting to assemble model communities with a wider range of dispersal rates than used here, both external and internal, to explore more fully how dispersal regulates interactive effects of community assembly history and species pool size on species diversity. For this purpose, using a gradient of dispersal rates (as in, e.g., Mouquet and Loreau 2003) will be more illuminating than using only a few rates. Although internal and external dispersal did not interact to influence local–regional richness relationships in this study,

always reach equilibrium between adjacent dispersal events, whereas this study allowed external dispersal to occur once in every 10 or 100 days. Additional simulation trials indicate that populations can frequently take a longer time, even more than 1,000 days, to reach equilibrium (T. Fukami, unpublished data). Lockwood et al. (1997) suggest that communities do not become resistant to invasions if assembled with high dispersal rate. The dynamics observed in this study appear to represent this situation.

The low dispersal rate implicit in permanence theory may not be encountered in many natural systems. Many systems may receive immigrants while still experiencing transient dynamics. If so, cyclic compositional changes such as those found in this study (see also Steiner and

Table 2 Regressions under frequent external dispersal. All notes for Table 1 apply

Dependent variable	Model	Regression parameter estimates with P values in parenthesis			Adjusted R^2
		a	b	c	
Basal species					
Species richness in local communities	**Linear**	2.472 (0.001)	0.203 (0.000)		
	Quadratic	2.160 (0.037)	0.238 (0.007)	−0.001 (0.340)	0.860
Species richness in metacommunities	**Linear**	2.544 (0.022)	0.228 (0.000)		0.740
	Quadratic	2.801 (0.100)	0.199 (0.091)	0.001 (0.418)	0.722
Local community dissimilarity	Linear	0.587 (0.568)	0.011 (0.358)		0.000
Number of potential colonizers	**Linear**	−0.805 (0.120)	0.033 (0.019)		0.277
Consumer species					
Species richness in local communities	Linear	0.845 (0.223)	0.219 (0.000)		0.857
	Quadratic	−0.640 (0.501)	0.386 (0.000)	−0.003 (0.027)	0.883
Species richness in metacommunities	Linear	0.975 (0.176)	0.218 (0.000)		0.847
	Quadratic	−0.521 (0.598)	0.387 (0.000)	−0.003 (0.031)	0.874
Local community dissimilarity	Linear	0.423 (0.111)	−0.008 (0.134)		0.030
Number of potential colonizers	**Linear**	−0.098 (0.082)	0.004 (0.011)		0.338

additional simulation trials show that the effect of internal dispersal on diversity depends on external dispersal rate when a greater range of external dispersal rate than assumed in this study is considered (T. Fukami, unpublished data). Much remains to be investigated regarding interactive effects of external and internal dispersal.

Conclusion

This study has demonstrated that community assembly history can interact with species pool size to affect species diversity at multiple spatial scales. Specifically, the results show that community dissimilarity caused by assembly history can increase linearly with pool size, though local interactions sets a limit to local diversity. I have discussed two implications of these results for understanding multi-scale diversity patterns. First, assembly history provides a possible explanation for the scale-dependent relationships between local and regional diversity: assembly causes the relationship to be curvilinear at one scale (local community) and linear at another (metacommunity). Second, assembly history influences how γ-diversity is partitioned into α- and β-diversity: assembly causes the relative contribution of β-diversity to increase with increasing pool size.
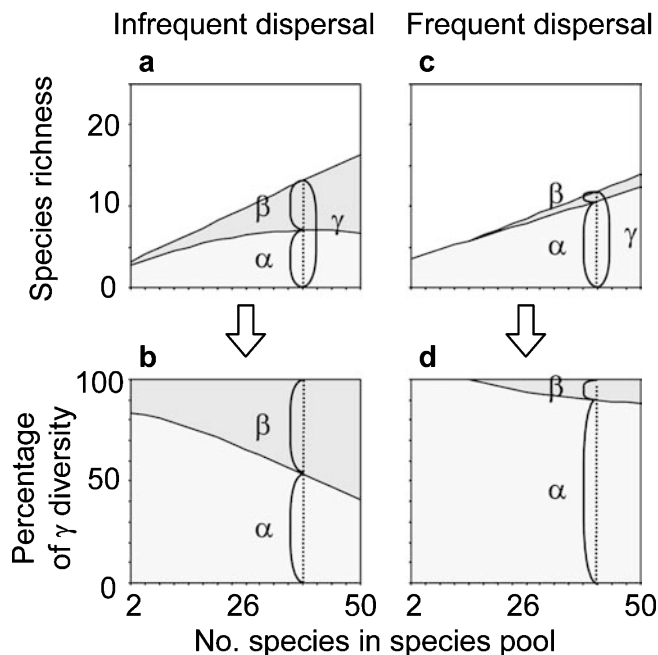
Fig. 6a–d Relationships between α-, β-, and γ-diversities in basal species as a function of pool size. Here, α is mean richness in a local community, β is local community dissimilarity, and γ is richness in a metacommunity. In **a** and **c**, regression lines for meta- (Figs. 3a, 5a) and local communities (Figs. 3b, 5b) are drawn together to show the absolute values of α, β, and γ. In **b** and **d**, richness in local communities is divided by richness in metacommunities to show the relative contributions of α and β to γ

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