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SPECIES DIVERSITY AND ASSEMBLY HISTORY IN ECOLOGICAL COMMUNITIES

Microcosm Experiments and Computer Simulations

A Dissertation Presented for the
Doctor of Philosophy Degree

The University of Tennessee, Knoxville

Tadashi Fukami
August 2003

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Dedicated to my parents, Noriko and Takushi Fukami

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ABSTRACT

Despite its academic and applied importance, it has proven difficult to understand patterns of species diversity. This is in large part because multiple processes operating at various scales interact to influence diversity patterns emerging at different scales. Here I examine how the history of community assembly may interact with other ecological variables to influence species diversity. I consider four variables: the level of productivity, the size of ecosystem, the rate of dispersal, and the size of species pool. These variables have received considerable attention as major determinants of species diversity. However, their joint effects with assembly history remain largely unexplored. In a laboratory experiment with bacteria, algae, protists, and rotifers, I show that assembly history can interact with productivity to create a remarkable variety of productivity-diversity patterns. In another experiment, I show that community assembly can interact with ecosystem size to affect diversity and that, through this interaction, assembly history can dictate when a significant size-diversity relationship is observed. Using computer simulations of community assembly, I also show that internal and external dispersal, though generally studied separately, reciprocally provide the context in which the other influences diversity at multiple spatial scales. I further show that assembly history and the size of the species pool can jointly affect diversity patterns and that their interaction has implications for determining the relative importance of local and regional processes governing diversity. One common theme that emerges from these studies is the presence of significant historical effects in the absence of alternative stable states. Overall, these studies suggest that it is promising, though rarely attempted, to incorporate the dynamics of community assembly into a conceptual framework for species diversity.

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Part 1

General background and overview

General background

Introduction

Up to thirty million species presently live on earth (May 1990). Though this number itself is impressive, perhaps the real fascination of species diversity comes from the highly uneven spatial distribution of species. Why does diversity vary so greatly from one place to another? Biologists have long asked this question, dating back at least to Darwin (1859). Recently, it has gained much importance beyond biology as well, as society becomes increasingly interested in decelerating the anthropogenic loss of biodiversity (Wilson 1992).

Despite its importance, however, species diversity has proven difficult to understand. This is in large part because multiple processes operating at various scales interact to influence diversity patterns emerging at different scales (Levin 1992, Huston 1999). On evolutionary scales, species diversity is a result of speciation and extinction. But evolutionary processes are variable across space, interactive over time, and consequently hard to identify. On ecological scales, diversity is a result of community assembly, how species join ecological communities over time (Drake 1991). But the same can be said about ecological processes as about evolutionary ones.

Purpose

In this dissertation, I attempt to provide a novel ecological perspective from which to view diversity patterns. Specifically, I argue that we can better understand diversity by explicitly considering how the history of community assembly interacts with other ecological variables to affect diversity. I will focus on four variables to make this point: the level of productivity, the size of ecosystem, the rate of dispersal, and the size of species pool. These variables have received much attention as major determinants of diversity. However, their joint effects with assembly history have been only sporadically discussed and remain largely unexplored. I will show that explicit consideration of the role of assembly history can significantly improve our ability to explain the relationship between species diversity and its ecological determinants.

Approach

For this purpose, I conducted laboratory experiments with aquatic microcosms and theoretical investigations with computer simulations. Microcosms and simulations admittedly lack the complexity of natural ecosystems, and uncritical extrapolations to real systems would be misguided (Carpenter 1996). Microcosms and simulations are nonetheless powerful heuristic tools to study historical effects of community assembly on species diversity (Lawler 1998, Morin 1998).

There are at least three advantages of using microcosms and simulations. First, most theoretical studies seeking conditions that regulate historical effects have considered interactions between only a few species or lumped groups of species (e.g., May 1977, Holt and Polis 1997). While valuable, results of these analytical studies cannot be directly applied to problems of species diversity involving many more species (but see Lockwood et al. 1997, Morton and Law 1997). Microcosms and simulations used here

directly deal with systems consisting of many species. Second, historical effects can easily be confounded with other environmental factors in field studies (see e.g., Connor and Simberloff 1979, Petersen 1984). Microcosms and simulations greatly minimize logistical problems in accurately detecting historical effects. Third, evaluation of historical effects requires one to monitor community dynamics over many generations of the species involved, but such long-term monitoring is not possible in most field studies. Microcosms and simulations allow for monitoring of community dynamics for a sufficiently long time to study community assembly (Lawler 1998).

Overview

Summary of results

The Parts to follow will each address one variable that I suspected would interact with assembly history. Part 2 reports an experiment that examined the effect of productivity, or the amount of energy available for ecosystem development in a given location. In natural ecosystems, the relationship between productivity and species diversity is known to take many forms, including hump-shaped, U-shaped, positive, negative, and flat patterns (Waide et al. 1999). My results show that community assembly can interact with productivity to create a remarkable variety of productivity-diversity patterns. It is therefore possible that the variety of productivity-biodiversity relationships seen in nature reflects differences in assembly as well as other factors.

Part 3 presents an experiment on the effect of ecosystem size. In natural systems, the relationship between ecosystem size and species diversity is so consistent that it has been called one of the few laws in ecology (Schoener 1976). Despite this established status of size-diversity patterns, its mechanistic explanations remain a central topic in ecology, because ecosystem size can be correlated with many other variables. My results show that community assembly can interact with ecosystem size to affect diversity and that, through this interaction, assembly history can dictate when a significant size-diversity relationship is observed. Thus, assembly history may be a key to explaining variation in size-diversity patterns in natural systems.

Part 4 uses simulations to examine the effect of the rate of two types of dispersal, specifically internal dispersal, which occurs among local communities within a metacommunity, and external dispersal, which supplies immigrants from outside of the metacommunity. The results show that the effect of internal dispersal on species richness depends on external dispersal, and vice versa. Moreover, internal and external dispersal interactively determine the extent to which assembly history generates variation in species composition among local communities. This interaction can lead to scale-dependent richness patterns. Therefore, the two dispersal types, though generally studied separately (e.g., compare Loreau and Mouquet 1999 and Mouquet and Loreau 2002), reciprocally provide the context in which each one influences diversity at multiple spatial scales.

Finally, Part 5 uses simulations to examine the effect of the size of species pool. The results show that community assembly can interact with the size of the species pool to affect local and regional diversity and the among-community variation in species

composition. Consequently, assembly history can produce scale-dependent relationships between local and regional species diversity (Srivastava 1999). Assembly history also affects how γ-diversity is partitioned into α- and β-diversity (Veech et al. 2002). Previously overlooked, these joint effects of pool size and assembly history have implications for determining the relative importance of local and regional processes in determining species diversity (cf. Ricklefs 1987, Huston 1999, Lawton 2000).

Common theme and overall conclusion

One common theme that emerges from these studies is the presence of significant historical effects in the absence of alternative stable states. Conventionally, assembly history is considered important when it is capable of leading local communities to alternative stable states even though the communities share the same species pool and environmental conditions (see Lewontin 1969, Sutherland 1974, Knowlton 1992). On the other hand, assembly history is deemed of minor importance when local communities converge to a single stable state regardless of assembly history. Consequently, much effort has been devoted to determining the conditions for historically induced alternative stable states (see e.g., Samuels and Drake 1997). They have also been called multiple stable points (e.g., Sutherland 1974), multiple domains of attraction (e.g., Gilpin and Case 1976), and alternative community states (e.g., Petraitis and Latham 1999).

In contrast, my results indicate that history has important implications for species diversity even without alternative stable states. The experiments show that transient dynamics can last for such long periods that the role of assembly history cannot be ignored even without multiple stable states. The simulations show that assembly history can maintain high among-community variation in species composition, without the communities reaching alternative stable states. The variation thus maintained 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, Morton and Law 1997). Broadly, these results are in accordance with the recent argument that long-term transient dynamics are prevalent and important in ecological systems (Hastings 2001). My results call for reevaluation of the conventional approach to assessing the importance of historical effects.

Overall, these studies suggest that it is promising, though rarely attempted, to incorporate the dynamics of community assembly into a general conceptual framework for species diversity. Besides mere intellectual merit, this dissertation and its future extension can ultimately contribute to biological conservation by providing insight into the ecological basics that we must learn before we can effectively preserve species diversity. This dissertation is, however, only a first step toward building an assembly-based framework. As identified in the following Parts, many more unanswered questions can be addressed with microcosms and simulations. These approaches will continue to serve as a useful first arena where the potential use of ecological ideas can be evaluated quickly. Of course, the ultimate goal is to understand species diversity in natural ecological communities. Microcosms and simulations will help reduce the number of hypotheses worthy of testing in future research with more natural, but much longer, larger-scale, and more expensive field experiments.

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Part 2

Productivity-biodiversity relationships depend on the history of community assembly

This Part is a lightly revised version of the following paper: Fukami, T., and P. J. Morin. 2003. Productivity-biodiversity relationships depend on the history of community assembly. Nature 424: 423-426. My co-author provided facilities and materials and helped with improving the main text of the manuscript. I did all other work from the inception to publication of this research.

Abstract

Identification of the causes of productivity-species diversity relationships remains a central topic of ecological research. Different relationships have been attributed to the influence of disturbance, consumers, niche specialization, and spatial scale. One unexplored cause is the history of community assembly, the partly stochastic sequential arrival of species from a regional pool of potential community members. The sequence of species arrival can greatly affect community structure. If assembly sequence interacts with productivity to influence diversity, different sequences may contribute to variation in productivity-diversity relationships. We tested this hypothesis by assembling aquatic microbial communities at five productivity levels using four assembly sequences. Approximately thirty generations after assembly, productivity-diversity relationships took various forms, including a positive, a hump-shaped, a U-shaped, and a non-significant pattern, depending on assembly sequence. This variation resulted from idiosyncratic joint effects of assembly sequence, productivity, and species identity on species abundances. We suggest that the history of community assembly should be added to the growing list of factors that influence productivity-biodiversity patterns.

Introduction

Productivity, the amount of energy available for ecosystem development in a given location, has a major impact on species diversity (Connell and Orias 1964, Leigh 1965, Pianka 1966, Morin 2000). Until recently, hump-shaped relationships, where diversity peaks at intermediate productivity levels, were the most widely observed pattern (Rosenzweig 1992, 1995, Tilman and Pacala 1993). We now know that the relationship takes many forms, including hump-shaped, U-shaped, positive, negative, and flat (non-significant) patterns, and that none of these patterns predominates (Waide et al. 1999). Possible causes of variation include the influence of disturbance (Huston 1994, Kondoh 2001), consumers (Worm et al. 2002, Leibold et al 1997), niche specialization (Kassen et al. 2000), and spatial scale (Currie 1991, Wright et al.1993, Abrams 1995, Gross et al. 2000, Scheiner et al. 2000, Mittelbach et al. 2001, Chase and Leibold 2002), which can create variation among taxonomic groups and habitat types (Waide et al. 1999, Mittelbach et al. 2001).

Here we show that differences in the sequence of community assembly can cause important variation in productivity-diversity relationships. A few studies suggest that productivity may control the probability that alternative community states are produced through assembly (Van de Koppel et al. 1996, Holt and Polis 1997, Chase and Leibold 2002). To our knowledge, however, no prior studies have rigorously tested for interactive effects of assembly and productivity on diversity.

We conducted a laboratory experiment using freshwater microbial communities as a model system to test for interactive effects of assembly and productivity on diversity. We manipulated productivity by changing the nutrient concentration of the medium. At each of the five productivity levels used, we first inoculated the medium with bacteria, microflagellates, and algae. After allowing them to become abundant, we assembled communities using four different introduction sequences of 18 protozoan and rotifer species, which consumed bacteria, microflagellates, and algae and thus potentially competed for these shared resources (Table 1). We used a total of 100 microcosms, i.e., 5 productivity levels x 4 assembly sequences x 5 replicates for each treatment.

Use of microcosms allowed rigorous control over assembly history, productivity, and other environmental conditions. It also enabled us to observe patterns resulting from long-term community dynamics. Use of an experimental duration spanning tens of generations limited the possibility that observed patterns were trivial over ecologically important time scales. It would have been impossible to ensure this level of experimental control in most other natural or laboratory settings. Because all of our microcosms ultimately received the same set of species, any differences in productivity-diversity relations could be attributed to different assembly sequences.

Materials and methods

Microcosms

Microcosms were covered sterile 118-ml polypropylene containers. These containers were filled with 30 ml of medium (made from Carolina Biological Supply protozoan pellet, Herpetivite powdered vitamin supplement, and soil in well water) and kept at 22 ^{o}C with 14:10 h light:dark cycles. The medium was autoclaved before use and inoculated with bacteria (*Bacillus subtilis*, *Bacillus cereus*, *Proteus vulgaris*, *Serratia marcescens* and other unidentified bacteria filtered from the stock cultures of all the protozoan and rotifer species used in the experiment), microflagellates, and algae (*Chlamydomonas* spp.). These inoculations were done before the medium was distributed to microcosms.

Manipulating productivity

We used five levels of productivity, evenly spaced on a log scale. The medium for the lowest productivity level consisted of 0.007 g of the protozoan pellet, 0.033 g of the soil, and 0.001g of the vitamins per liter of well water. The media for the other productivity levels consisted of 0.023 g, 0.073 g, 0.232 g, and 0.733 g of the pellet, 0.106 g, 0.334 g, 1.055 g, and 3.335 g of the soil, and 0.004 g, 0.013 g, 0.042 g, and 0.133 g of the vitamins per liter, respectively, from the second lowest to the highest levels. Removal and replacement of 3 ml (i.e., 10 %) of the medium of the corresponding nutrient concentration once a week renewed nutrients.

Manipulating assembly sequence

Protozoan and rotifer species were introduced to the microcosms sequentially according to predetermined schedules (Table 1). Stock cultures of 6 species were used

Table 1. Introduction sequences used to assemble communities

	Sequence			
	A	B	C	D
First introduction	Set 1	Set 1	Set 2	Set 2
Second introduction	Set 2	Set 3	Set 1	Set 3
Third introduction	Set 3	Set 2	Set 3	Set 1

Set 1	Set 2	Set 3
*Blepharisma americanum**‡	*Colpidium striatum**	*Aspidisca* sp.*
Chilomonas sp.*	*Colpoda cucullus**	*Holosticha* sp.*
*Colpoda inflata**	*Euplotes* sp.*†‡	*Lepadella* sp.* [r]
Loxocephalus sp.*	*Paramecium tetraurelia**†	*Rotaria* sp.* [r]
*Paramecium caudatum**†	*Tetrahymena vorax**‡	*Spirostomum* sp.*
*Tetrahymena thermophila**	*Uronema* sp.*	*Tillina magna**

Notes: Natural history of these rotifer (marked with [r]) and protozoan (all others) species indicates that they consume bacteria and/or microflagellates (*), algae (†), and/or small ciliates (‡). Regardless of their diets, all the species can sustain their populations solely on bacteria and/or microflagellates and thus potentially compete with one another.

for each introduction. First species were introduced 3 days after the algal inoculation. Subsequent introductions had 14-day intervals. Microcosms received a very small number of individuals, i.e., less than 0.7 % of carrying capacity, but at least 20 individuals per species to preclude trivial extinction by chance at initial stages. To standardize the number of individuals introduced across introduction occasions, population densities in stock cultures were estimated and, if necessary, diluted before introductions. The age of the stock cultures at the time of species introductions was also standardized to minimize variation in physiological conditions of species between different introduction occasions. Microcosms also contained 3 additional algal species, most likely from cultures of a particular species (*Euplotes* sp.). As such, they did not confound the effect of assembly sequence.

Our assembly protocol resembles assembly in some natural systems. For example, sets of species can colonize an island community simultaneously when they arrive on floating coarse woody debris or a chunk of floating soil. The use of our protocol also had a logistical rationale: for the purpose of our experiment, it was essential to minimize variation in physiological conditions of each species among introduction occasions. Using more introduction occasions than three would have been too time-consuming to ensure a reasonable level of minimization. Moreover, although our assembly protocol may not capture the essence of every single natural system possible, we believe that the conceptual novelty and broad implications of our results on the interactive effect of assembly and productivity outweigh the details of assembly manipulation.

Measuring population abundances

Population abundance of each species in each microcosm was measured once a week until 25 days after the last introduction. Twenty-five days corresponds to roughly 30 generations of the protozoa and rotifer species. Densities were estimated by counting protozoa and rotifers in samples of known volume, typically 0.3 ml, from the 3-ml medium removed for nutrient replacement. When species were too abundant to count reliably, the sample was diluted. When one or more species were absent in the 0.3-ml sample, the entire 3 ml of medium (and the entire microcosm on the last sampling occasion) was scanned and protozoa and rotifers counted.

Productivity-diversity relationships

Species diversity was expressed as the complement of Simpson's index (Simpson 1949), $1-\lambda = 1- \Sigma p_i(1-p_i)$ where p_i is the relative frequency of species i, using data obtained 18 and 25 days after the last introduction. We examined the relationship between productivity and species diversity by fitting data to the following models:

Model 1: $d = b_0 + b_1 p$,
Model 2: $d = b_0 + b_1 p + b_2 p^2$,
Model 3: $d = b_0 + b_1 \log_{10} p$,
Model 4: $d = b_0 + b_1 \log_{10} p + b_2 (\log_{10} p)^2$.

Here, d is species diversity ($1-\lambda$), p is productivity (g protozoan pellet/liter), and b_0, b_1, and b_2 are regression parameters. Models 1 and 3 linearly relate species diversity to

productivity and to log-transformed productivity, respectively. A quadratic term is added to models 1 and 3 to form models 2 and 4, respectively, to test for curvilinearity.

When $P>0.0125$ (=0.05/4, using a Bonferroni correction to retain Type I error rate of 0.05) for all models, we concluded that the relationship between productivity and diversity was not significant. When $P<0.0125$ for more than one model, we selected, as the best model, the one that had the highest value of adjusted R^2. Adjusted R^2 values are adjusted for the number of parameters in the models. When model 2 or 4 was selected, we determined whether the relationship was hump-shaped or U-shaped using a statistical test developed by Mitchell-Olds and Shaw (1987) (hereafter referred to as MOS test). We focused on the diversity of protozoan and rotifer species; our diversity index does not include bacteria, microflagellates, or algae.

The MOS test was originally developed to detect disruptive and stabilizing natural selection in evolutionary biology, but it has also been used to test for hump-shaped and U-shaped relationships between productivity and diversity (see, e.g., Chase and Leibold 2002). Below we explain this test in the context of productivity-diversity relationships by modifying the explanation offered by Simms and Rausher (1993), who used it for detecting disruptive and stabilizing selection.

The quadratic estimate of the productivity-diversity relationship is described by

$$d = \beta_0 + \beta_1 z + \beta_2 z^2 + \varepsilon, \quad (1)$$

with a maximum (in the case of hump-shaped relationships) or minimum (in the case of U-shaped relationships) at

$$z^* = - \beta_1 / 2\beta_2, \quad (2)$$

where d is species diversity and z is p for model 2 and $\log_{10} p$ for model 4. Thus, the partial regression coefficients for the productivity-diversity relationship constrained to have a stationary point at z_{Ho}^* are defined as $\beta_1^* = -2\, z_{Ho}^*\, \beta_2^*$. Letting, for each observation, $y_i = z_i^2 + 2\, z_{Ho}^*\, z_i$, then (1) can be rewritten as

$$d = \beta_0 + \beta_2 y + \beta_3 z + \varepsilon. \quad (3)$$

With the $\beta_3 z$ term, (3) equals (1), but without it, (3) equals the constrained model. Therefore, the null hypothesis of no hump-shaped or U-shaped relationship, which is equivalent to the null hypothesis that the maximum or minimum diversity occurs at an extreme productivity level, can be rejected only if β_3 in (3) is found to differ significantly from zero when z_{Ho}^* is set to be the maximum productivity value used in the experiment *and* when it is set to be the minimum value used in the experiment. We used a Type-I error rate of 0.05.

Additionally, we also looked at productivity-diversity relationships by using species richness (number of species per unit volume) rather than the complement of Simpson's index to express species diversity. The number of species per unit area or volume is one of several measures of species richness and is sometimes termed species density (Magurran 1988). The number of all species present in the community regardless

of their abundance can be higher than species density, because species density can miss rare species, as actually occurred in our study. In most field studies that assess productivity-diversity relationships in natural systems, it is not feasible to do a complete census of all individuals to obtain real species richness. For this reason, species density is more frequently used.

Local and regional diversity

Five sets of 20 microcosms each representing a unique assembly x productivity treatment were initiated on different days. That is, the first set started on a Monday, the second on the following Tuesday, the third on the following Wednesday, and so on. This temporal staggering of replicates ensured more accurate sampling than would have been possible if all replicates were started simultaneously on the same day. Hence, microcosms in a set experienced more similar conditions with one another than with microcosms from other sets (e.g., medium and species came from the same stock). We considered each set a "region" comprising 20 "local" communities. When we compared diversity at the local and regional scales (see Discussion), we obtained, at each productivity level and for each region, the mean Simpson diversity of the four local communities assembled with different assembly sequences as local diversity and the Simpson diversity based on regional population abundances summed over the four local communities as regional diversity.

Response of species

We conducted ANOVAs to test for effects of introduction sequence on species abundance at each productivity level. Abundance was transformed as $\log_{10}$ (individuals/ml +1) before analysis to minimize heteroscedasticity. For each species, we used a sequential Bonferroni correction for the five tests corresponding to the five productivity levels to preserve Type I error rate of 0.05. When ANOVAs found a significant effect of sequence, Tukey's Studentized range tests were used to identify which treatments differed.

Results

The specific assembly sequence used to create communities generated striking differences in productivity-diversity relationships. Statistical analysis revealed positive (F=11.23, P=0.0004, adjusted R^2=0.4601 for the best model [model 2], Fig. 1a), non-significant (flat) (F<1.45, P>0.2425, adjusted R^2<0.0181 for all the models, Fig. 1b), hump-shaped (F=6.31, P=0.0068, adjusted R^2=0.3066 for the best model [model 2] and P<0.05 for the MOS test, Fig. 1c), and U-shaped (F=19.96, P<0.0001, adjusted R^2=0.124 for the best model [model 2] and P<0.05 for the MOS test, Fig. 1d) patterns under sequences A, B, C, and D, respectively, 25 days after the last species introduction (Table 2). This endpoint corresponded to approximately 30 complete generations of the organisms involved in community dynamics.

These results also qualitatively hold for data collected 18 days after the last introduction (Fig. 1 e-h), confirming that the patterns were temporally consistent and long-lived over ecologically important time scales (Table 3). On both days, the

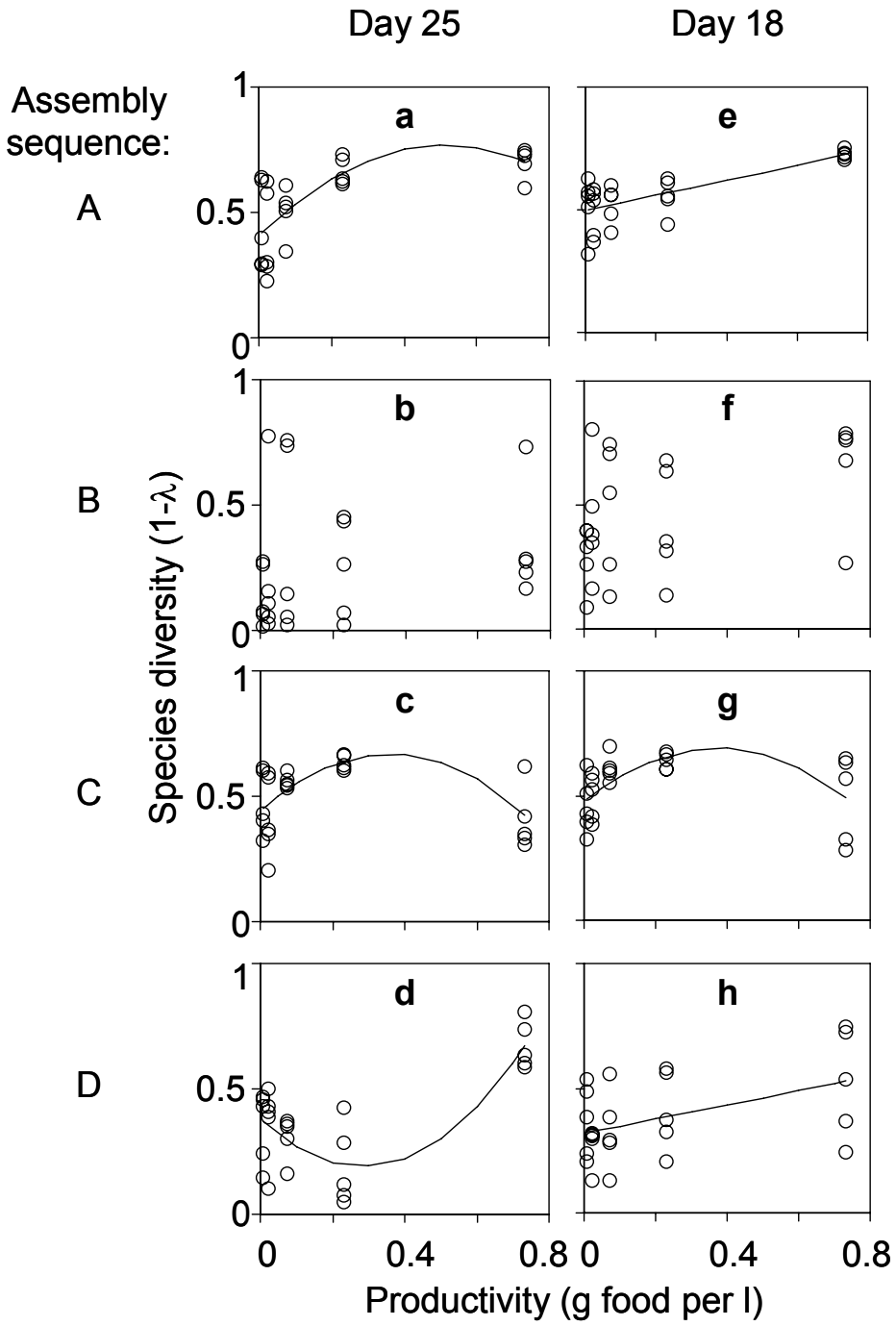


Figure 1. Response of species diversity to productivity. Data are fitted to the best regression models. Productivity refers to protozoan pellet concentration. Some data points are slightly moved vertically (no greater than ±0.005) from their original points so that they can be distinguished more clearly from one another.

Table 2. Summary of regression analysis for day 25 (corresponding to data for Fig. 1a-d)

Model	F	P	R^2	Adjusted R
Sequence A				
$d = b_0 + b_1 p$	13.97	0.0011	0.3779	0.3508
$d = b_0 + b_1 p + b_2 p^2$	11.23	0.0004	0.5051	0.4601*†
$d = b_0 + b_1 \log_{10} p$	17.87	0.0003	0.4373	0.4128
$d = b_0 + b_1 \log_{10} p + b_2 (\log_{10} p)^2$	9.65	0.0010	0.4672	0.4188
Sequence B				
$d = b_0 + b_1 p$	0.77	0.3884	0.0325	-0.0095
$d = b_0 + b_1 p + b_2 p^2$	0.41	0.6662	0.0362	-0.0514
$d = b_0 + b_1 \log_{10} p$	1.44	0.2424	0.0589	0.0180
$d = b_0 + b_1 \log_{10} p + b_2 (\log_{10} p)^2$	0.81	0.4556	0.0690	-0.0157
Sequence C				
$d = b_0 + b_1 p$	0.42	0.5213	0.0181	-0.0246
$d = b_0 + b_1 p + b_2 p^2$	6.31	0.0068	0.3644	0.3066*†
$d = b_0 + b_1 \log_{10} p$	0.41	0.5300	0.0174	-0.0254
$d = b_0 + b_1 \log_{10} p + b_2 (\log_{10} p)^2$	1.72	0.2014	0.1355	0.0570
Sequence D				
$d = b_0 + b_1 p$	14.50	0.0009	0.3867	0.3601
$d = b_0 + b_1 p + b_2 p^2$	19.96	<0.0001	0.6447	0.6124*‡
$d = b_0 + b_1 \log_{10} p$	2.91	0.1018	0.1121	0.0735
$d = b_0 + b_1 \log_{10} p + b_2 (\log_{10} p)^2$	6.97	0.0045	0.3878	0.3321

Notes: Regressions relate species diversity (d) to productivity (p) (see text for model description). For those sequences with one or more models with $P<0.0125$, the highest adjusted R^2 values are marked with an asterisk, indicating that that model best explains the data. †, ‡ The MOS test indicates that the relationship is hump-shaped (†) or U-shaped (‡). For sequence A, although the MOS test detected a hump-shaped pattern, adjusted R^2 values are roughly the same among the models, and the quadratic regressions depict an almost monotonic increase of diversity with productivity (see Fig. 1). We interpreted these results to indicate that the relationship was a positive pattern.

Table 3. Summary of regression analysis for day 18 (corresponding to data for Fig. 1e-h)

Model	F	P	R^2	Adjusted R^2
Sequence A				
$d = b_0 + b_1 p$	27.451	0.000	0.544	0.524*
$d = b_0 + b_1 p + b_2 p^2$	13.307	0.000	0.547	0.506
$d = b_0 + b_1 \log_{10} p$	13.115	0.001	0.363	0.335
$d = b_0 + b_1 \log_{10} p + b_2 (\log_{10} p)^2$	12.737	0.000	0.537	0.494
Sequence B				
$d = b_0 + b_1 p$	5.272	0.031	0.186	0.151
$d = b_0 + b_1 p + b_2 p^2$	2.527	0.103	0.187	0.113
$d = b_0 + b_1 \log_{10} p$	5.239	0.032	0.186	0.150
$d = b_0 + b_1 \log_{10} p + b_2 (\log_{10} p)^2$	2.530	0.103	0.187	0.113
Sequence C				
$d = b_0 + b_1 p$	0.047	0.830	0.002	0.000
$d = b_0 + b_1 p + b_2 p^2$	4.774	0.019	0.303	0.239(*), †
$d = b_0 + b_1 \log_{10} p$	1.605	0.218	0.065	0.025
$d = b_0 + b_1 \log_{10} p + b_2 (\log_{10} p)^2$	4.210	0.028	0.277	0.211
Sequence D				
$d = b_0 + b_1 p$	6.416	0.019	0.218	0.184(*)
$d = b_0 + b_1 p + b_2 p^2$	3.098	0.065	0.220	0.149
$d = b_0 + b_1 \log_{10} p$	3.854	0.062	0.144	0.106
$d = b_0 + b_1 \log_{10} p + b_2 (\log_{10} p)^2$	3.646	0.043	0.249	0.181

Notes: Regressions relate species diversity (d) to productivity (p) (see text for model description). For those sequences with one or more models with $P<0.0125$, the highest adjusted R^2 values are marked with an asterisk, indicating that that model best explains the data. For those sequence with all models with $P>0.0125$, the highest adjusted R^2 values of all that are marginally significant ($0.0125<P<0.02$), if any, are marked with an asterisk in a parenthesis. † The MOS test indicates that the relationship is hump-shaped.

relationship was positive, flat (non-significant), and hump-shaped under sequences A, B, and C, respectively. Under sequence D, the best model was positive linear for day 18 (Fig. 1h), whereas it was U-shaped for day 25 (Fig. 1d). However, model selection was relatively indecisive for this sequence on day 18, and a U-shaped model (adjusted R^2 = 0.181, model 4) explained data almost as well as the positive linear model selected did (adjusted R^2 = 0.184, model 1).

Productivity-biodiversity relationships depended on the history of community assembly when species richness (indexed as the number of species detected in the 0.3-ml sample), rather than the complement of Simpson's index, was used to express biodiversity, too. Statistical analysis revealed non-significant (flat) (F<1.95, P>0.1756, adjusted R^2<0.0382 for all the models), positive (F=6.93, P=0.0149 [i.e., marginally significant; note that α=0.0125, with a Bonferroni correction; see Methods], adjusted R^2=0.1981for the best model [model 3]), U-shaped (F=8.86, P=0.0015, adjusted R^2=0.3957 for the best model [model 4] and P<0.05 for the MOS test), and non-significant (flat) (F<2.63, P>0.1183, adjusted R^2<0.0635 for all the models) patterns under sequences A, B, C, and D, respectively, 25 days after the last species introduction.

We examined how each species responded to productivity and assembly sequence to search for processes that might have created different patterns. For many species, the effect of assembly sequence on abundance depended on productivity. For example, assembly sequence significantly influenced the abundance of *Uronema* sp. at three out of five productivity levels (Fig. 2). When significant, the impact of assembly sequence on abundance also depended on productivity. *Uronema* was more abundant in sequence C than in D at one productivity level (Fig. 2a), but the difference was reversed at another level (Fig. 2b) and became non-significant at the other levels (Fig. 2c-e). Thus, productivity determined whether a certain sequence either facilitated or inhibited population growth. Furthermore, the effect of sequence also depended on species identity (Table 4). Joint effects of assembly sequence, productivity, and species identity were highly idiosyncratic, with no discernable general trends across species (Table 4).

Discussion

Our results show that community assembly potentially interacts with productivity to create a remarkable variety of productivity-diversity patterns. We emphasize that different assembly sequences alone produced various productivity-diversity patterns, without experimental imposition of variation in disturbance (cf. Huston 1994, Kondoh 2001), consumers (cf. Worm et al. 2002, Leibold et al 1997), niche specialization (cf. Kassen et al. 2000), and spatial scale (cf. Currie 1991, Wright et al.1993, Abrams 1995, Gross et al. 2000, Scheiner et al. 2000, Mittelbach et al. 2001, Chase and Leibold 2002). We suspect that assembly sequence may have influenced the operation of these unmanipulated proximate mechanisms (Drake 1991). For example, some sequences may have caused consumers and niche specialization, realized by diet differences among species (Table 1), to exert a strong impact on productivity-diversity patterns, whereas other sequences may have minimized their influence. The next step in understanding this phenomenon would be to uncover general mechanisms that explain how assembly produces such diverse patterns. Our results caution against assuming that a single explanatory mechanism at the community level exists, because interactions among

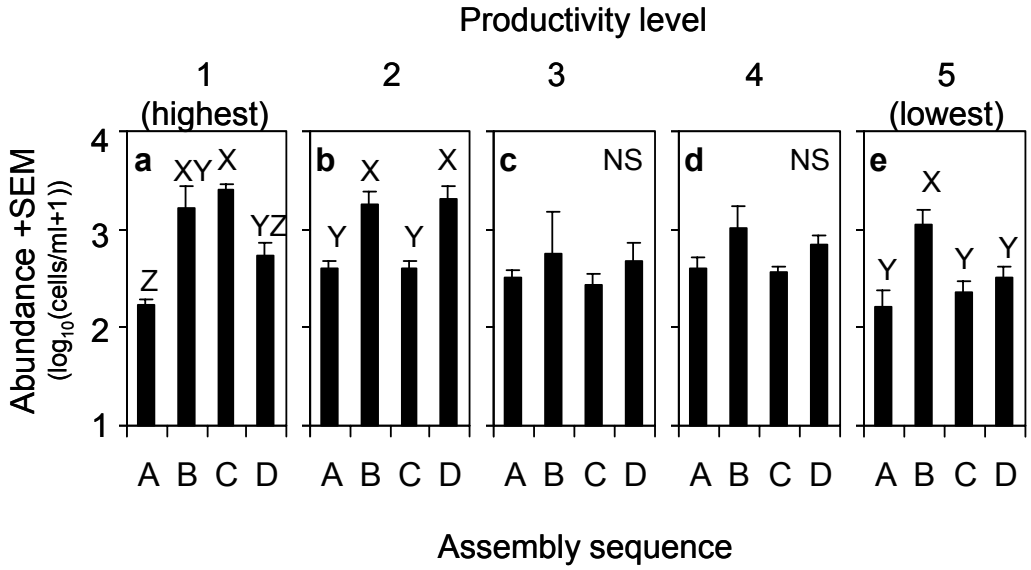


Figure 2. Response of the abundance of *Uronema* sp. to productivity and assembly sequence on day 25. Bars with the same letter above them did not differ in Tukey's Studentized range tests. We applied a sequential Bonferroni correction to preserve Type I error rate of 0.05. NS: not significant (see Table 2).

Table 4. Response of species to productivity and assembly sequence

Species	Productivity 1 (highest)	2	3	4	5 (lowest)
Aspidisca sp.	D C B A (2.89)	B D C A (1.98)	D B C A (1.82)	C B A D (0.88)	C A B D (9.22**)
Blepharisma americanum	A B D C (13.83***)	A C D B (1.69)	C D A B (0.67)	A D C B (3.30)	A D C B (6.65**)
Chilomonas sp.	D C A B (37.54***)	D A C B (1.00)	D A C B (1.00)	D A C B (1.00)	– –
Colpoda cucullus	A B C D (1.00)	A B C D (0.83)	A B C D (1.92)	A B D C (2.63)	A D C B (5.92*)
Euplotes sp.	A C B D (12.13***)	C A B D (6.78**)	C D B A (4.21*)	C A B D (19.50***)	C A B D (5.11*)
Holosticha sp.	C A D B (3.86)	C A D B (24.19***)	A B D C (4.07)	D B C A (1.09)	B D C A (0.28)
Lepadella sp.	A B C D (4.98)	B A D C (7.42**)	B D C A (2.20)	A B D C (0.86)	D C A B (1.79)
Paramecium tetraurelia	C D B A (7.75**)	B A D C (4.25)	A D C B (0.42)	A C D B (0.82)	A B D C (3.58)
Rotaria sp.	B A C D (160.78***)	B A D C (11.13***)	B A D C (13.21***)	B D A C (6.98**)	D B A C (2.96)
Spirostomum sp.	C A B D (1.03)	C A B D (1.57)	– –	– –	– –
Uronema sp.	C B D A (16.69***)	D B A C (12.90***)	B D A C (0.33)	B D A C (2.37)	B D C A (8.04**)

Notes: For each species and productivity level, assembly sequences (i.e., A, B, C, and D) are listed in order of decreasing abundance on day 25. Underlined groups cannot be distinguished statistically using Tukey's Studentized range tests. Numbers in parentheses indicate *F*-ratio (ANOVA). **P*<0.05, ***P*<0.005, ****P*<0.0005 (only those found to be significant after a sequential Bonferroni correction to preserve Type I error rate of 0.05 are marked with asterisk(s)). Dashes indicate that the species went extinct in all replicates at the corresponding productivity level. Species not listed here went extinct in all replicates at all productivity levels.

species apparently depend complexly on assembly sequence, productivity, and species identity (Table 4).

It would be trivial, for the purpose of our experiment, to show that communities of different assembly history had different structures, if either of the following did not apply to each species at the end of the experiment: (1) the species had had enough time to potentially attain their maximum abundance, or (2) the species' abundance was higher or the same in the communities to which the species was introduced at a late stage of assembly compared to those to which it was introduced at an earlier stage. To assess whether each species satisfied (1) at each productivity level, we first determined the number of days taken for the abundance of the species to reach a peak after it was introduced to the communities earliest (e.g., to the communities of sequences A and B, for *Blepharisma americanum*). If the number of days thus determined was less than the number of days elapsed between the time of the last introduction and that of the experimental termination (i.e., 25 days), we concluded that the species satisfied (1) at that productivity level. We also checked for (2) for each species at each productivity level. We found that 25 days was indeed long enough for all populations to satisfy at least one, and in most cases both, of the two conditions under all productivity conditions (Figs. 3-5). Therefore, our results are not trivial over ecologically important time scales.

It should be noted that, in some previous microcosm studies (e.g., Weatherby et al. 1998), communities were maintained for a much longer time (e.g., 100 days) than the present study to achieve a constant species composition. These studies were intended specifically to test the permanence theory of community assembly (Law and Morton 1993), whereas our study was not, although the two share conceptual backgrounds of community assembly. A central assumption of the permanence theory is that communities are free from disturbance for a sufficiently long time for them to reach equilibrium, which may take an unusually long time in natural system. This does not weaken the theory's important heuristic value. Given the relatively frequent disturbances that occur commonly in nature, however, the patterns as a result of dynamics involving ca. 30 generations (25 days) may rather be more generalizable to natural systems than the patterns after, e.g., 100 days.

Our interpretation of these data assumes that the spatial scale of productivity variation is smaller than that for assembly sequences. Some natural systems meet this assumption. Examples include situations where regular seasonal phenology of species arrival drives assembly or where species invade a region through biogeographic events and spread before the next species invade. Other systems contain local sites that vary in both productivity and assembly sequence. We note, however, that assembly has important implications even for these systems: it can make patterns sensitive to the scale of observation (Chase and Leibold 2002). We found that the productivity-diversity relationship was positive linear at a local scale (P=0.0017 and adjusted R^2=0.3255 for model 1, which was the best model), whereas it was non-significant at a regional scale (P>0.02 for all models; note that α=0.0125 with Bonferroni correction; see Materials and Methods for how we calculated local and regional diversity).

We studied only four of the many possible assembly sequences that could have been used with our species pool. This small sample of assembly sequences makes it impossible to say whether any one of the specific patterns that we observed might

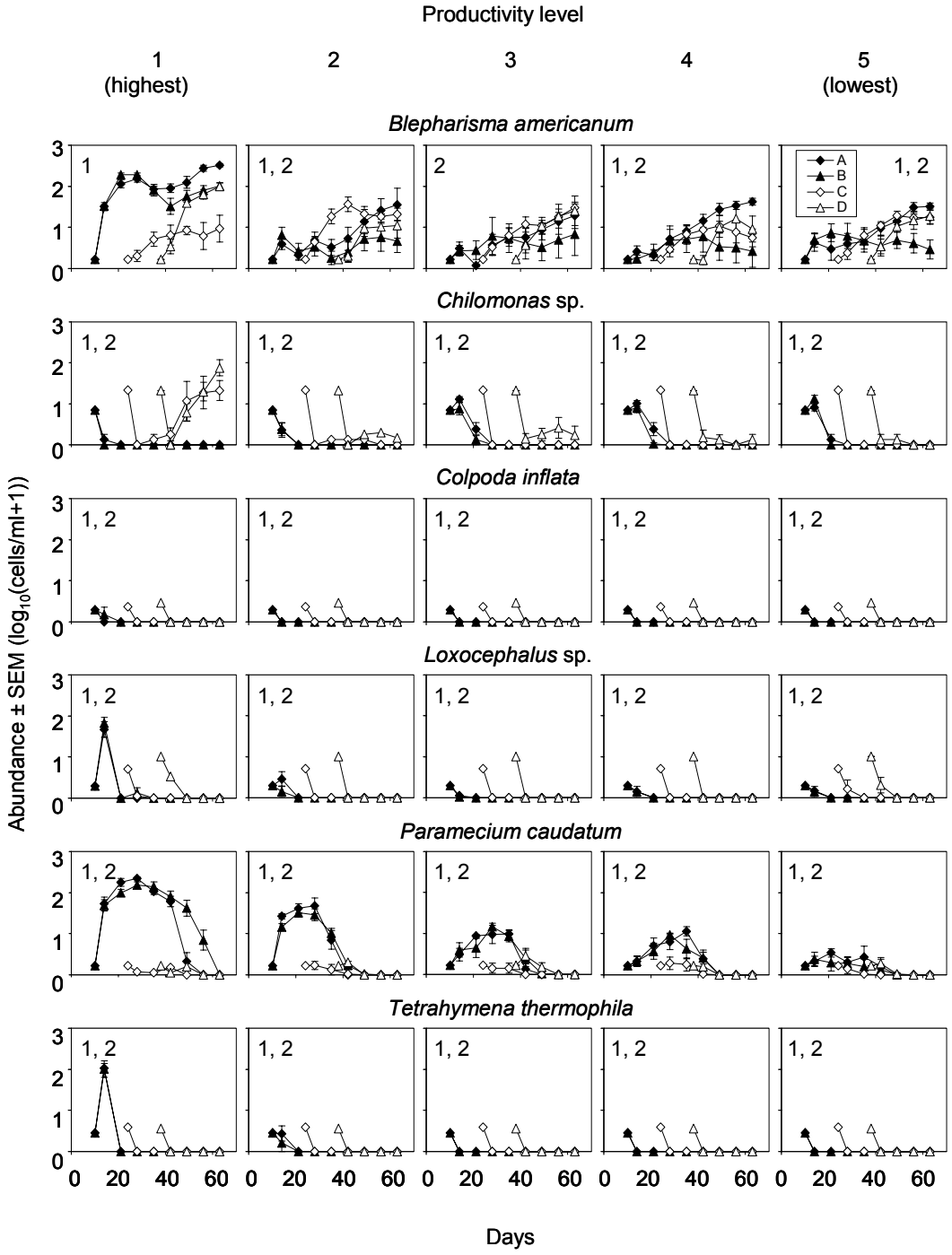


Figure 3. Population dynamics of the species in set 1. Each data point represents the mean abundance (± S. E. M.) over the five replicates. A, B, C, and D represent assembly sequences. Days represent the number of days passed since bacterial inoculation. The numbers (1 and 2) in each graph indicate that the species satisfies conditions (1) and (2) (see text) at that productivity level, respectively.

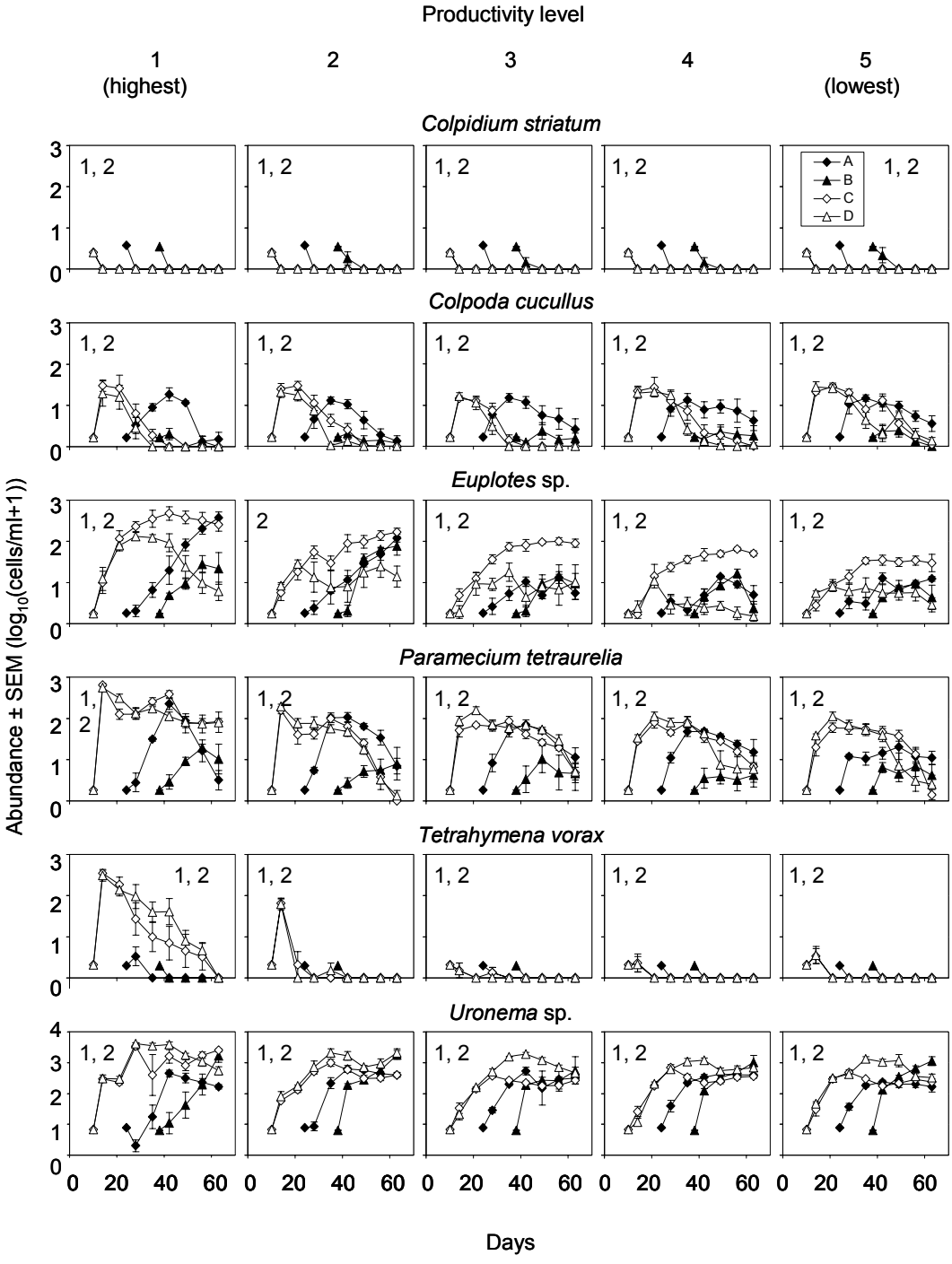


Figure 4. Population dynamics of the species in set 2. Symbols as in Fig. 3.

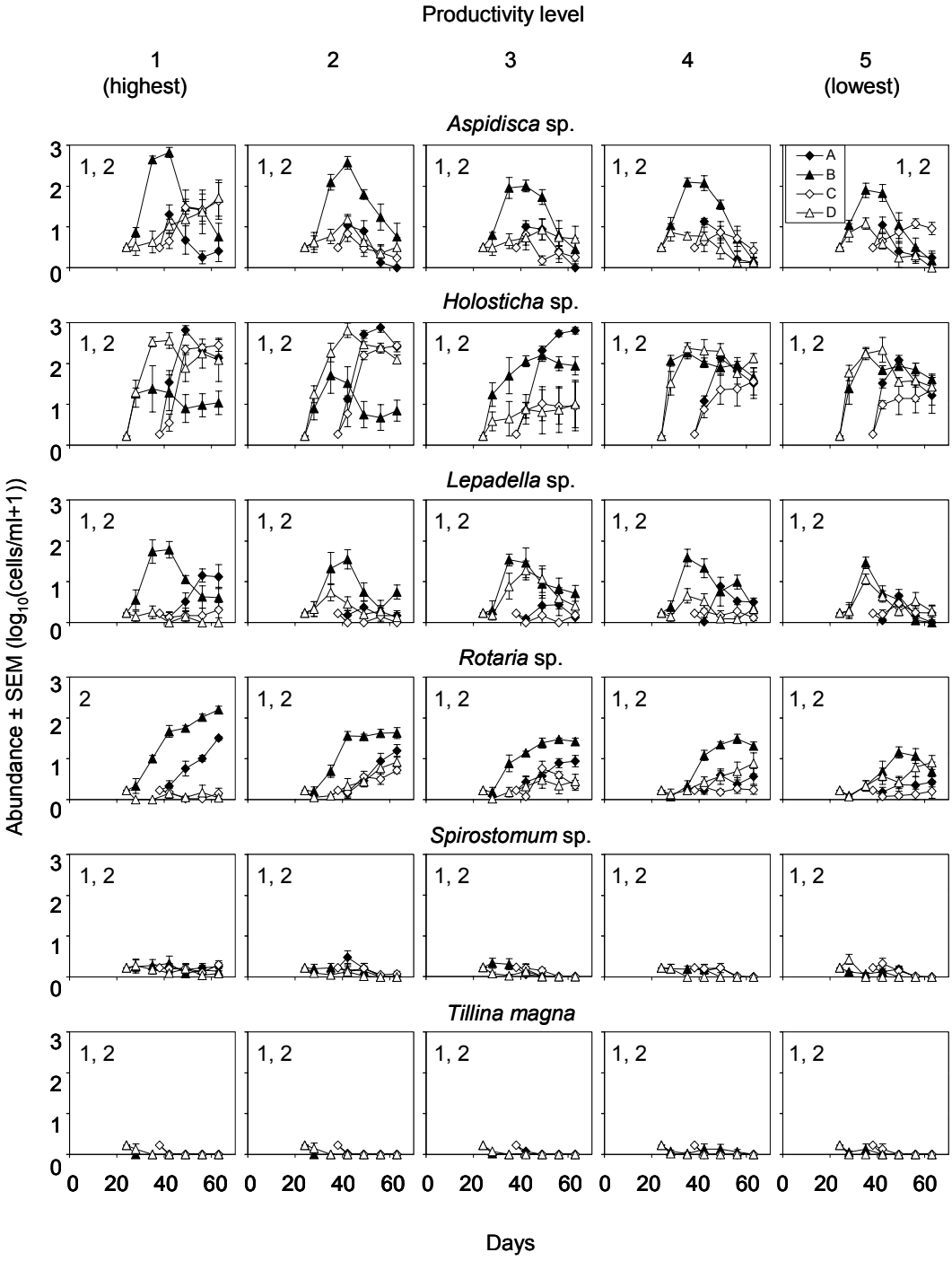


Figure 5. Population dynamics of the species in set 3. Symbols as in Fig. 3.

predominate in a larger sample. Nonetheless, it is possible that the variety of productivity-biodiversity relationships seen in nature reflects differences in assembly as well as other factors. We suggest that the history of community assembly should be added to the growing list of factors that influence productivity-biodiversity patterns. Assembly history does not preclude the importance of other factors. However, because the detailed assembly history of natural communities is seldom known, it may be difficult to deduce unambiguously the proximal causes of natural productivity-diversity patterns. For this reason, manipulative experiments remain an essential tool for exploring the possible causes of productivity-diversity relationships within the historical context of community assembly.

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Part 3

Interactive effects of ecosystem size and assembly history on species diversity: experimental evidence

Abstract

Although species diversity is often correlated with ecosystem size in a consistent manner, mechanistic explanations of whether and how diversity is related to size remain a central topic of ecological research. Rarely considered in understanding size-diversity relationships is the potential role of the history of community assembly. I conducted a laboratory microcosm experiment with freshwater protists and rotifers to test for interactive effects of assembly history and ecosystem size on diversity. The experiment used a two-way factorial design with four assembly sequences and four ecosystem sizes as treatments. Community dynamics were monitored for approximately one hundred generations. The results show that the assembly x size interaction can occur and that, through this interaction, assembly history can influence whether and when a significant relationship between ecosystem size and species diversity is observed. These results were most clearly demonstrated when diversity was measured as biomass-based Simpson diversity. The results also show that transient dynamics can last for such a long period compared to the generation times of the species involved that assembly history can play a significant role even in the absence of multiple stable states. The unequivocal experimental evidence provided here suggests that assembly x size interaction may shape size-diversity patterns in natural systems and that it may do so even in the absence of multiple stable states.

Introduction

Species diversity is often correlated with ecosystem size in a consistent manner. For example, the way species richness, a measure of species diversity, is related to area, a measure of ecosystem size, is so general that it has been called one of the few laws in ecology (Schoener 1976, Gotelli 1995). However, ecosystem size itself can be correlated with a number of other ecological factors, such as disturbance frequency, habitat diversity, extinction rate, speciation rate, and the ratio of edge to interior habitats (reviews in Rosenzweig 1995, Gotelli and Graves 1996). Moreover, patterns found between size and diversity can depend on geographical location, the scale of observation, and the range of ecosystem size considered, suggesting site- and scale-dependent mechanisms (MacArthur and Wilson 1967, Rosenzweig 1995, Crawley and Harral 2001). Consequently, mechanistic explanations of the relationship between ecosystem size and species diversity remain a central topic of ecological research.

Rarely considered in understanding size-diversity relationships is the potential role of the history of community assembly. Community assembly, the partly stochastic sequential immigration of species from a pool of potential community members, can greatly influence many aspects of local community structure, including species diversity (Post and Pimm 1983, Drake 1990, Law and Morton 1996, Belyea and Lancaster 1999). If assembly sequence interacts with ecosystem size to influence diversity, it can affect how diversity is related to ecosystem size. However, largely because assembly history is difficult to control experimentally or to reconstruct in specific detail, much remains unknown about whether and how history may regulate relationships between ecosystem size and species diversity. Although a limited number of experimental studies have manipulated ecosystem size, assembly history, or both (Dickerson and Robinson 1985, 1986, Drake 1991, Petraitis and Latham 1999, Dudgeon and Petraitis 2001), their primary

purposes were not to examine interactive effects of size and history. Most of them did not manipulate the two factors simultaneously, did not have a gradient of varying ecosystem size, or lacked sufficient control over habitat quality that was likely correlated with ecosystem size.

How might the importance of assembly history to diversity change with ecosystem size? I suggest that two contrasting expectations exist, depending on whether species interactions are strong enough to affect local species diversity (Fig. 1). If species interactions are weak, assembly history is expected to affect diversity longer and more strongly in larger systems (Fig. 1a). An increase in ecosystem size should result in a decrease in initial densities of immigrated species, requiring for each population a longer time after a disturbance event to reach a significant density to affect species diversity. This effect of history would always be highly transient and restricted to initial stages of community assembly. The shape of the inverse relation between ecosystem size and initial densities may vary among habitat types and taxonomic groups. In some cases, a concomitant increase in invasion rate with ecosystem size, as a result of increased passive sampling (Coleman et al. 1982) or a target effect (Lomolino 1990), may compensate for the decrease in initial densities. However, increases in ecosystem size should never weaken the effect of assembly history. I will call this hypothesis an autecological hypothesis.

In contrast, if species interactions are strong, assembly history can affect diversity more weakly and for a shorter time in larger systems (Fig. 1b). Decreases in initial densities owing to increases in ecosystem size would mean that species require more time to become abundant to modify local habitat conditions such as resource availability to affect the performance of species arriving later. With immigration rate held constant across a size gradient, species are less likely in larger systems to have enough time to exert priority effects (*sensu* Paine 1977; see Morin 1999 for examples of priority effects) on later arrivers. Moreover, invasion rate may increase with ecosystem size, as mentioned above, which may mean less time available for early immigrants to alter habitat conditions before later immigrants arrive. For these reasons, assembly history can be relatively unimportant in larger systems, while long-lasting priority effects may impact diversity in smaller systems. I will call this hypothesis a synecological hypothesis. The autecological hypothesis may be considered a more parsimonious null hypothesis (Gotelli and Graves 1996), and the synecological hypothesis an alternative hypothesis that invokes effects of species interactions.

One widely used approach to evaluating the importance of assembly history in community structuring has been to ask whether variation in history results in realization of multiple stable states (Lewontin 1969, Sutherland 1974, Knowlton 1992, Law and Morton 1996, Samuels and Drake 1997, Petraitis and Latham 1999). Local communities can, at least in theory, take alternative stable states that are irreversible unless destroyed by disturbance (MacArthur 1972: 247-250, Gilpin and Case 1976). Assembly history is deemed important when it is capable of leading local communities to alternate stable equilibria even though the communities share the same species pool and environmental conditions. On the other hand, assembly history is considered of minor importance when local communities converge to a common state regardless of assembly history. I argue, however, that even when historical effects do not persist, but gradually weaken to allow community convergence, that may not necessarily diminish the importance of history.

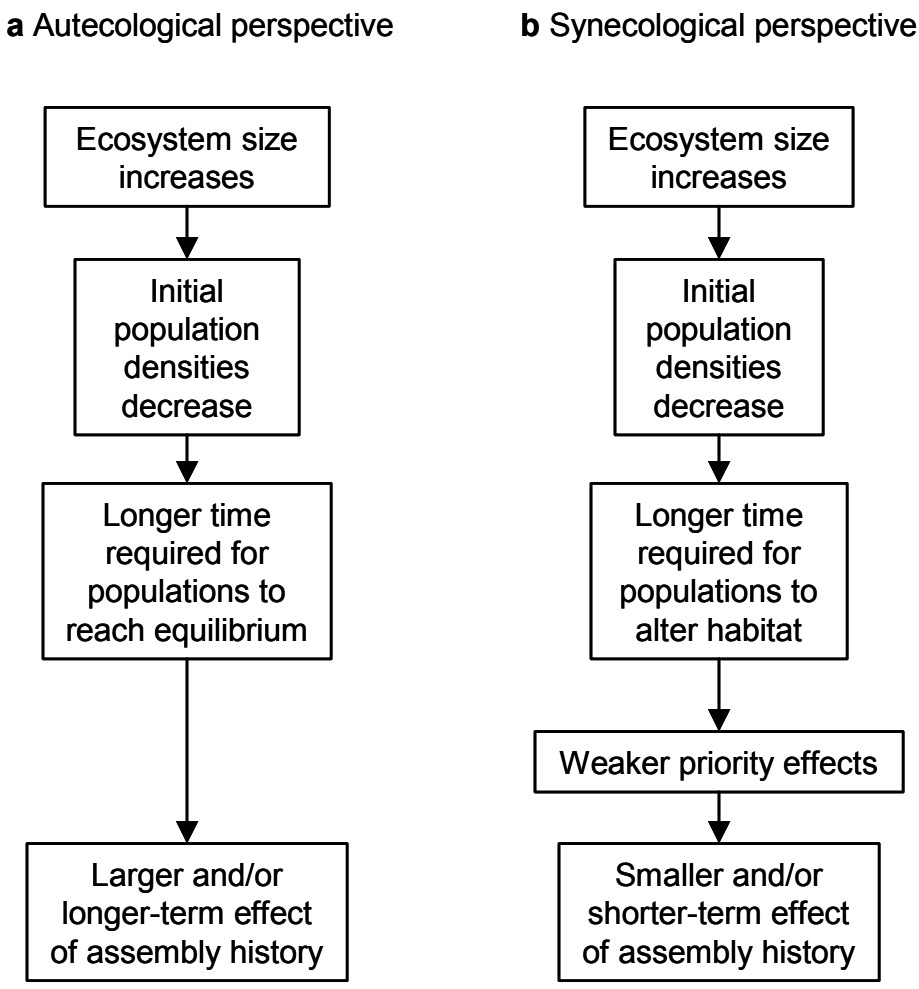


Figure 1. Two contrasting hypotheses on how ecosystem size may regulate the effect of assembly history on species diversity, in the absence (a) and presence (b) of strong species interactions. Immigration rate is assumed constant across an ecosystem size gradient. See text for details.

Recent theory suggests that transient dynamics before convergence can be so long as to be practically indistinguishable from persistent stable states (Hastings 2001). Long-term studies are therefore essential for assessing the effect of assembly history (Grover and Lawton 1994, Samuels and Drake 1997). This is especially true when the focus of interest is interactive effects of assembly history and ecosystem size; it is important to ensure that size-dependent effects of history, if any are observed, are not an artifact of not monitoring community dynamics until all systems of differing size have reached a relatively stable state.

In this study, I conducted a laboratory microcosm experiment with freshwater protists and rotifers to test the above hypotheses on interactive effects of assembly history and ecosystem size on species diversity. Specifically, I asked: Does the importance of assembly history vary with ecosystem size, over time, or both? I further explored implications of the history x size interaction for understanding size-diversity relationships by asking: Does the dependence of historical effects on ecosystem size and time, if any, lead to assembly-, time-, and/or scale-dependent relationships between ecosystem size and diversity? Laboratory microcosms were a powerful model system with which to ask these questions. They allowed rigorous control over assembly history, ecosystem size, and other potentially confounding factors. They also enabled me to monitor community dynamics for many more generations of the species involved than would otherwise have been possible. This study covered approximately one hundred generations. Of course, these advantages of laboratory microcosms come at the sacrifice of a realistic natural context (Carpenter 1996, Morin 1998). Yet, microcosms serve as a useful first arena where ecological ideas can be tested and refined to reduce the number of hypotheses worthy of testing in future research with more natural, but much longer, larger-scale, and more expensive field experiments (Lawler 1998, Morin 1998).

Materials and methods

Microcosms

Microcosms were initially sterile glass containers. Throughout the experiment, the containers were loosely covered with sterilized lids, which minimized contamination and evaporation, while allowing a certain level of air exchange. At the beginning of the experiment, the containers were filled with a medium made of 0.55 g of crushed protozoan pellet (Carolina Biological Supply) and 0.10 g of powdered vitamin supplement (Herpetivite) per 1.5 liter of commercially available spring water (Crystal Springs) and were kept in the laboratory at 20-23 ^{o}C. The medium was autoclaved before use and inoculated with bacteria (*Bacillus subtilis*, *Bacillus cereus*, *Proteus vulgaris*, and *Serratia marcescens*, purchased from the Carolina Biological Supply Company) and, two days after bacterial inoculation, with unidentified microflagellates (isolated from ponds in New Brunswick, New Jersey, USA). These inoculations were done before the medium was distributed to microcosms 6 days after the introduction of microflagellates. Bacteria and microflagellates served as food for the protozoa and rotifer species introduced afterwards (see *Manipulating assembly sequence* below). Microcosms were semi-continuous batch culture: throughout the experiment, I renewed nutrients once a week by gently mixing and homogenizing the medium and then removing and replacing 0.5, 1.5, 10, and 85 ml of the medium with fresh sterile medium of the same composition as

specified above for each of 5-, 15-, 100-, and 850-ml microcosms (see *Manipulating ecosystem size* below for size manipulation methods), respectively (i.e., 10% for all ecosystem size treatments). The timing of medium replacement was set in such a way that it occurred four days after each introduction occasion during the initial phase of the experiment.

Study organisms

Natural history and the knowledge gained through laboratory culturing of the protozoa and rotifer species used here indicate that all species can sustain their population by feeding on bacteria and microflagellates only, though some of them differ in their diet (Table 1). They are known to compete with one another for these shared resources under conditions similar to those used in this study (see, e.g., McGrady-Steed and Morin 2000, Fox 2002, Long and Karel 2002). The species were either isolated from ponds and other freshwater habitats in New Brunswick, New Jersey, USA, or purchased from the Carolina Biological Supply Company, and had each been separately cultured for many generations under conditions similar to those of the experiment.

Experimental design

I used a two-way factorial design with four assembly sequences and four ecosystem sizes as treatments. Each of the 16 treatments (4 sequences x 4 sizes) had 5 replicates. Thus, there were a total of 80 microcosms. Five sets of 16 microcosms each representing a unique treatment were initiated on different, but consecutive days, i.e., the first set started on a Monday, the second on the following Tuesday, the third on the following Wednesday, and so on. This temporal staggering of replicates ensured more accurate sampling than would have been possible if all replicates were started simultaneously. The 16 microcosms in a given set, therefore, experienced more similar experimental conditions (e.g., the medium distributed to them came from the same stock prepared in a 2000-ml flask; the species were introduced from the same stock cultures) than they did with microcosms from the other sets. Therefore, each of these sets could collectively be considered an independent ecological "region" consisting of four local communities that experienced similar environmental conditions, but were of different assembly history (though no dispersal was allowed between the local communities; see discussion).

Manipulating ecosystem size

I manipulated ecosystem size by using containers of four different sizes. At the start of the experiment, the smallest microcosms received 5 ml of the medium already inoculated with bacteria and microflagellates. The other microcosms received 15, 100, or 850 ml of the medium. Thus, the four sizes were approximately evenly spaced on a log scale. Containers were chosen so that the microcosms had the same shape (cylindrical with flat bottom), water depth (33 mm), and air-water surface area-volume ratio (0.30) across size treatments. This choice of containers standardized spatial heterogeneity and oxygen availability across size treatments and therefore prevented them from being confounded with the effect of ecosystem size *per se* on community structure (as in e.g., Dickerson and Robinson 1986, Holyoak and Lawler 1996, Spencer and Warren 1996, Warren 1996, Holyoak 2000).

Table 1. Introduction sequences used to assemble communities

		Sequence			
	Day	A	B	C	D
First introduction	9	Set 1	Set 1	Set 2	Set 2
Second introduction	16	Set 2	Set 3	Set 1	Set 3
Third introduction	23	Set 3	Set 2	Set 3	Set 1

Set 1	Set 2	Set 3
Colpoda cucullus *, mb	*Chilomonas* sp.*	*Coleps* sp.*
(5.77 x 10^{-8} g/cell)	(1.42 x 10^{-9} g/cell)	(2.02 x 10^{-8} g/cell)
Colpoda inflata *, mb	*Colpidium striatum* *, mb	*Euplotes* sp.*, †, hb
(1.14 x 10^{-8} g/cell)	(1.52 x 10^{-8} g/cell)	(8.05 x 10^{-8} g/cell)
Lepadella sp.*, r, mb	*Spirostomum* sp.*	*Holosticha* sp.*, hb
(9.68 x 10^{-8} g/cell)	(3.76 x 10^{-6} g/cell)	(2.21 x 10^{-8} g/cell)
Paramecium caudatum *	*Tetrahymena thermophila* *	*Rotaria* sp.*, r, mb
(2.27 x 10^{-7} g/cell)	(4.77 x 10^{-9} g/cell)	(1.34 x 10^{-7} g/cell)
Paramecium tetraurelia *	*Uronema* sp.* , mb	
(4.30 x 10^{-8} g/cell)	(2.95 x 10^{-10} g/cell)	

Notes: Natural history of these rotifer (marked with ^{r}) and protozoan (all others) species indicates that they consume bacteria and/or microflagellates (*) and/or small ciliates (†). Regardless of their diets, all the species can sustain their populations solely on bacteria and/or microflagellates and thus potentially compete with one another. Some species are moderately (marked with ^{mb}) or highly (marked with ^{hb}) benthic, while others mainly use the water column. Estimated cell mass of each species is provided in parentheses.

Manipulating assembly sequence

A total of 14 protozoan and rotifer species were introduced to the microcosms sequentially according to predetermined schedules (Table 1). A set of 4 or 5 species was used for each introduction. Species were assigned to sets haphazardly. First, second, and third sets of species were introduced 7, 14, and 21 days after the microflagellate inoculation, respectively. Introductions were done with a very small number of individuals compared to the maximum densities realized, but no less than 15 individuals per species to preclude trivial extinction by chance at initial stages. To standardize the number of individuals introduced across introduction occasions, population densities in stock cultures were estimated and, if necessary, diluted before introductions. The age of the stock cultures at the time of species introductions was also standardized: the stock cultures were12 days old for species in sets 1 and 2 and 19 days old for species in set 3, counting from the day of the transfer of species from older cultures to the stock cultures. This standardization of culture age minimized variation in physiological conditions of species between different introduction occasions. Initial population abundances, but not initial population densities, were standardized across the ecosystem size gradient.

Measuring population abundance and biomass

Population abundance of each of the protozoa and rotifer species in each microcosm was monitored once in one, two, or three weeks for 109 days past the last introduction (see Fig. 2-4 for the timing of sampling). One hundred nine days corresponds to roughly 100 generations of the protozoa and rotifer species. This duration has been shown to be sufficient for comparable microcosm communities to reach persistent species composition (Weatherby et al. 1998, Law et al. 2000). For each replicate, densities were estimated by gently mixing the medium removed for nutrient replacement to homogenize the content and counting individuals in a 0.2-ml sub-sample of the medium. When species were too abundant to count reliably, the sample was diluted. I did not monitor bacterial or microflagellate abundance.

Following McGrady-Steed and Morin (2000) and Petchey et al. (2002), I calculated species biomass by multiplying the abundance of a species by the average cell mass of ten individuals of that species (Table 1). Cell mass was estimated based on cell volume, which in turn was estimated using equations that approximate cell shapes (Wetzel and Likens 1991).

Measures of species diversity

I used population abundance and biomass estimated as above to obtain three measures of species diversity: species richness, abundance-based Simpson diversity, and biomass-based Simpson diversity. Species richness is defined here as the number of species observed per unit volume, i.e., in the 0.2-ml sample. This measure is sometimes called species density to distinguish it from real species richness, the number of all species present in a given community regardless of their abundance (Magurran 1988). Real species richness can be higher than species density, because species density can miss rare species. In most field studies that assess size-diversity relationships in natural systems, it is not feasible to do a complete census of all individuals present in a

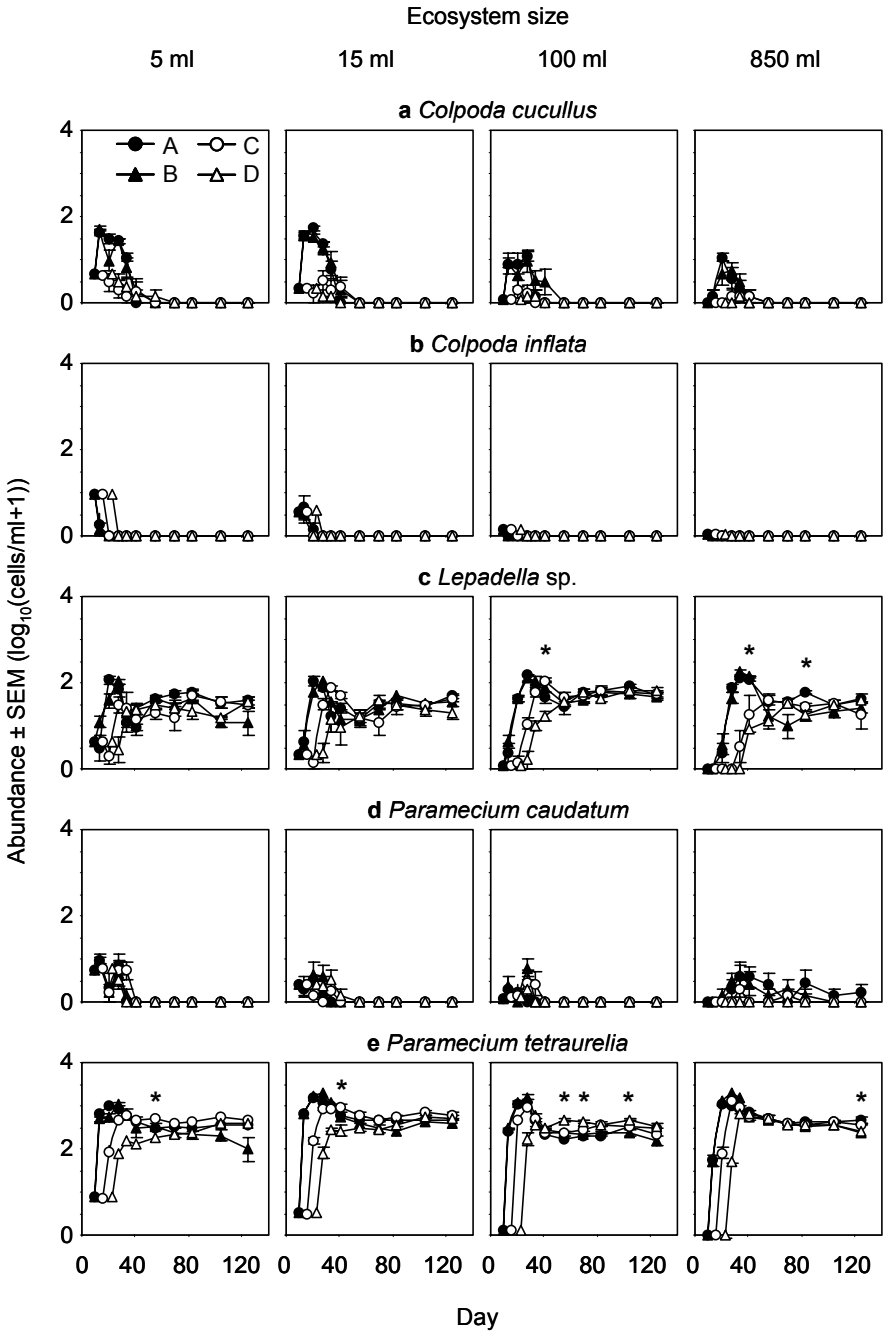


Figure 2. Population dynamics of the species in set 1. Each data point represents the mean of log-transformed abundance (± S.E.M.) over the five replicates. A, B, C, and D represent assembly sequences. Days represent the number of days passed since bacterial inoculation. Asterisks indicate that ANOVA detected a significant effect of assembly sequence on log-transformed abundance on the corresponding day ($P < 0.0083$ with Bonferroni correction, i.e., 0.05 / 6 sampling days; see text).

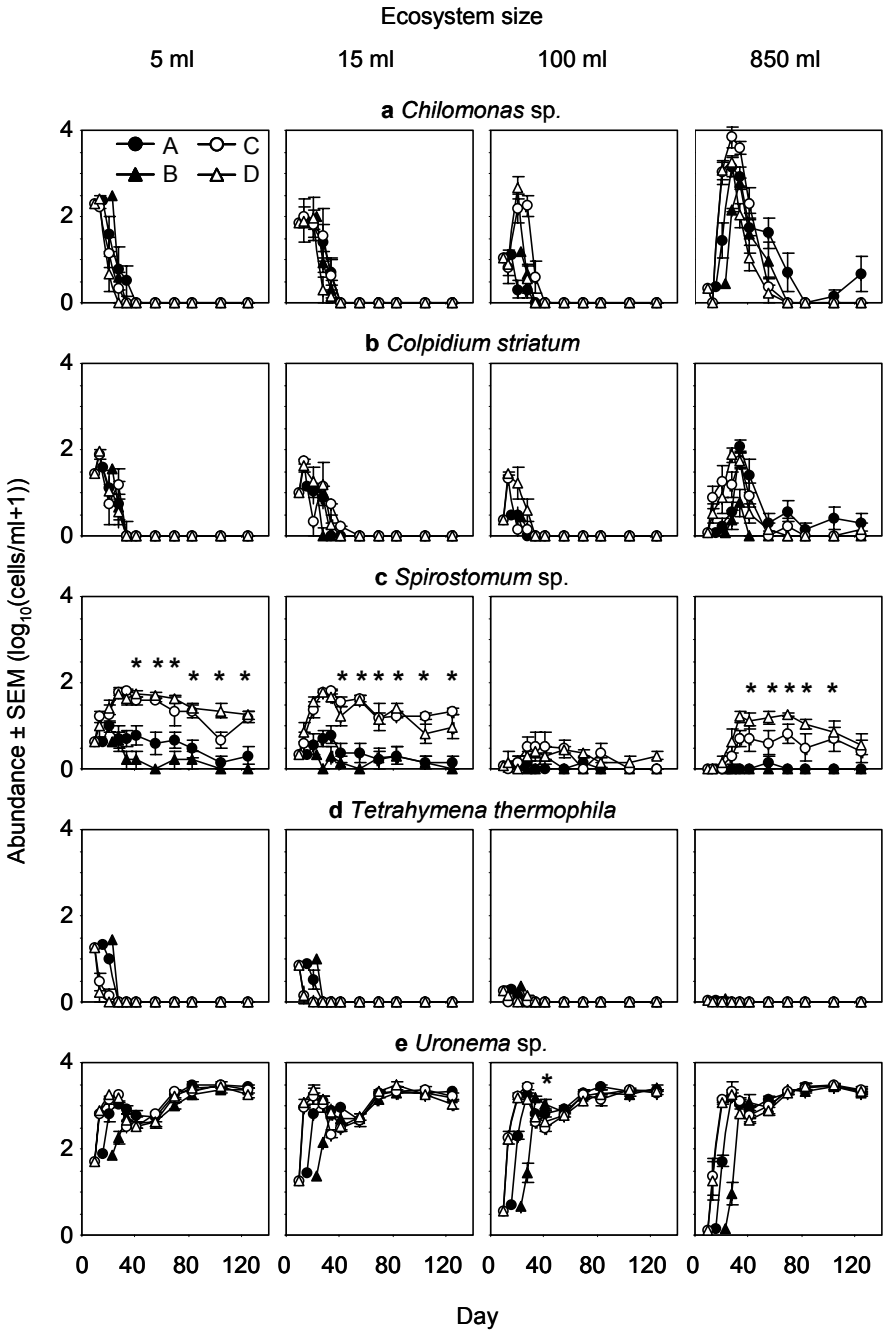


Figure 3. Population dynamics of the species in set 2. Symbols are as in Fig. 2.

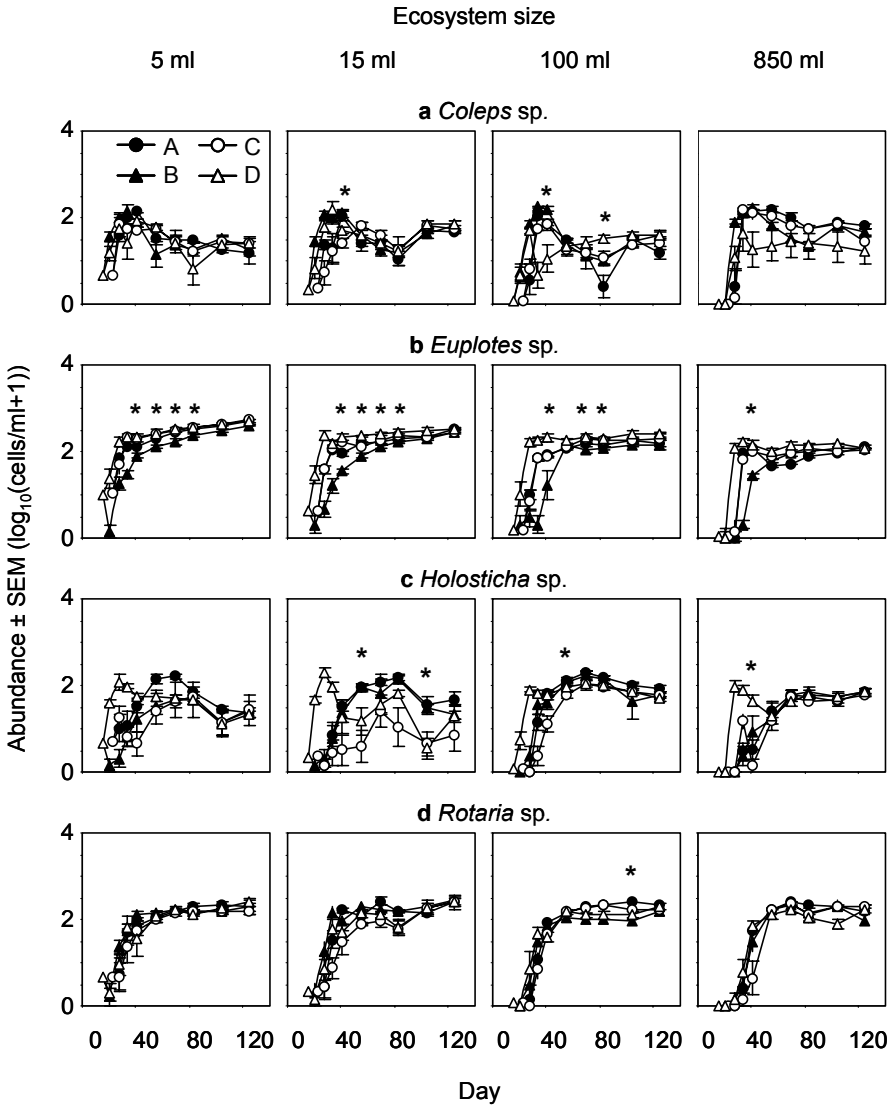


Figure 4. Population dynamics of the species in set 3. Symbols are as in Fig. 2.

community to obtain real species richness. For this reason, species density is more frequently used.

Abundance-based Simpson diversity is the complement of Simpson's index (Simpson 1949):

$$1 - \sum_i \{p_i(1 - p_i)\}. \quad (1)$$

Here, p_i is the relative frequency of species i in terms of the number of individuals in the community. Simpson diversity is less prone to sampling bias than Shannon diversity, a more frequently used diversity measure (Pielou 1969, Lande 1996).

Biomass-based Simpson diversity is the same as abundance-based Simpson diversity, except that the relative frequency is not based on the number of individuals but on the biomass of each population. Despite the similarity in their ecological role as grazers of bacteria and microflagellates, the species used in this study varied greatly in cell mass, over four orders of magnitude, with the largest being *Spirostomum* sp. (estimate: 3.76×10^{-6} g/cell) and the smallest *Uronema* sp. (estimate: 2.95×10^{-10} g/cell) (Table 1). Therefore, though abundance-based Simpson diversity is more frequently used in ecology, the biomass-based counterpart may more appropriately reflect the manner in which resource use is partitioned among the species used here. Also, the biomass-based measure may have more direct relevance to studies with plant communities, for which population sizes are frequently defined and measured with biomass rather than with the number of individuals.

In addition to calculating these diversity measures for each replicate microcosm, which I will call diversity at the "local" scale, I also calculated the diversity measures at the "regional" scale. I regarded sets of the four replicate microcosms that were of the same size, were initiated at the same time, but were each assembled with a different introduction sequence, as "regions" each consisting of four local communities (see *Experimental design* above). Species richness at the regional scale is the total number of species observed in the 0.2-ml sample of at least one of the four local communities. Simpson diversities at the regional scale are calculated as follows (Lande 1996):

$$1 - \sum_i \left\{ \left(\sum_j q_j p_{ij} \right)^2 \right\}. \quad (2)$$

Here, p_{ij} is the frequency of species i in local community j, and q_j is the proportional weight associated with local community j based on total abundance or biomass summed across all species in that community.

Statistical analyses

Effects of ecosystem size, assembly sequence, and time – I tested for effects of assembly sequence, ecosystem size, and their interaction on each of the three diversity measures, using analyses of variance (ANOVAs) separately for each sampling day (from

day 27 on, i.e., after all species had been introduced) in order to make explicit changes through time evident. For each diversity measure, a Bonferonni correction was used to account for conducting the same tests repeatedly for multiple sampling days (alpha = alpha / k = 0.05 / 6 = 0.0083, where k is the total number of sampling days). Additionally, ANOVAs were also conducted to examine effects of assembly sequence on diversity separately for each ecosystem size and for each sampling day. These ANOVAs (hereafter "additional ANOVAs") helped to compare the impact of assembly history among size treatments more directly.

I further used repeated-measures ANOVAs to determine whether the effect of assembly sequence on each of the three diversity measures varied among ecosystem size treatments, depended on time, or both. Diversity measures on each of the six sampling days from day 41 on were the repeated measures. Thus, the repeated-measures ANOVAs examined overall effects of assembly sequence, ecosystem size, time, and their interactions on diversity. The repeated-measures were used to confirm the robustness of the results from the ANOVAs performed separately for each sampling day. For the repeated-measures ANOVAs, I did not use data prior to day 41, because visual inspection of data on population dynamics indicated that populations were still at initial stages where they were yet to achieve their maximal size (Fig. 2-4). At least under the more parsimonious assumption of no strong species interactions (Fig. 1a), populations should have required the longest time to reach their carrying capacity in the largest systems (i.e., 850-ml microcosms) because the greatest amount of resource was available there, while initial population sizes were constant across the size gradient. Past day 41, most populations do seem to have reached their maximum size in the largest microcosms (Fig. 2-4), suggesting that diversity patterns after day 41 were not trivial over ecologically important time scales.

Linear regressions – I also used linear regressions to determine whether each of the three diversity measures was related to the logarithm of ecosystem size at a given time. Following the convention of using log-log regressions for the relationship between ecosystem size (which could be area or volume) and species richness, I log-transformed species richness for the regressions, but not the Simpson diversity measures. Separate regressions were performed for each assembly sequence and for each sampling day staring day 41, which enabled me to assess whether size-diversity relationships depended on assembly sequence, time, or both. A Bonferonni correction was used to account for conducting the same tests repeatedly for multiple sampling days (alpha = alpha / k = 0.05 / 6 sampling days = 0.0083). Regressions were also performed at the local and regional scales separately, testing whether size-diversity relationships depended on the scale of observation.

Population dynamics – I conducted ANOVAs to test for effects of assembly sequence on species abundance for each ecosystem size and for each sampling day starting day 41. Abundance was transformed as $\log_{10}$(individuals/ml +1) before analysis to minimize heteroscedasticity. For each species, assembly sequence, and ecosystem size, I used the same Bonferroni correction as above.

All statistical analyses were conducted using the software SYSTAT version 10 (SPSS 2000).

Results

Species richness

Effects of ecosystem size, assembly sequence, and time – Soon after all species were introduced, species richness seems to have quickly reached equilibrium, by approximately day 55 (Fig. 5). Once equilibrium had been achieved, relatively little variation existed in local species richness with respect to ecosystem size or assembly sequence, with most mean values ranging between 7 and 8. Despite this low variation, however, the logarithm of ecosystem size (hereafter referred to as ecosystem size for simplicity) significantly affected species richness on all sampling days except on day 125 (Table 2 and 3). Assembly sequence also affected it significantly on four sampling days (Table 3). There was, however, no significant interactive effect of ecosystem size and assembly sequence (Table 2 and 3). When the effect of assembly sequence was compared among ecosystem sizes over time using the additional ANOVAs, no clear differences existed among size treatments (Fig. 6a). But when assembly sequence did affect species richness significantly, it was always in the smaller (5-ml and 15-ml) microcosms.

Linear regressions – No significant relations were observed between the logarithm of ecosystem size and the logarithm of local species richness under any assembly sequences on any sampling days (highest $F_{1, 18} = 7.287$, highest $R^2 = 0.288$, lowest $P = 0.015$, note that alpha = 0.0083). At the regional scale, however, more variation existed in species richness (Fig. 7), and there was a significant positive relationship between the two variables on days 41 ($F_{1, 18} = 11.227$, $R^2 = 0.384$, $P = 0.004$) and 55 ($F_{1, 18} = 10.352$, $R^2 = 0.365$, $P = 0.005$).

Abundance-based Simpson diversity

Effects of ecosystem size, assembly sequence, and time – Abundance-based Simpson diversity continued to change for a longer time than did species richness, with some signs of reaching a relatively static state by day 83 (Fig. 8). After initial stages of assembly (i.e., after day 34), ecosystem size significantly affected abundance-based Simpson diversity on days 55, 104, and 125; assembly sequence affected it on day 41 only; and no significant interactive effects of size and sequence were detected on any sampling days (Tables 2 and 3). After initial stages of assembly (after day 41), the additional ANOVAs detected no clear trend when the effect of assembly sequence was compared among ecosystem size over time (Fig. 6b).

Linear regressions – Occasionally, a significant negative linear relationship was found between ecosystem size and abundance-based Simpson diversity, depending on assembly sequence and sampling day (Table 4). On which sampling days it was significant differed among assembly sequence treatments (Table 4). At both local and regional scales, a significant negative linear relationship existed between ecosystem size and abundance-based Simpson diversity on one of the six sampling days examined, on day 55 (Table 5), though overall variation in diversity on this day was relatively small among size treatments at both scales (Fig. 9).

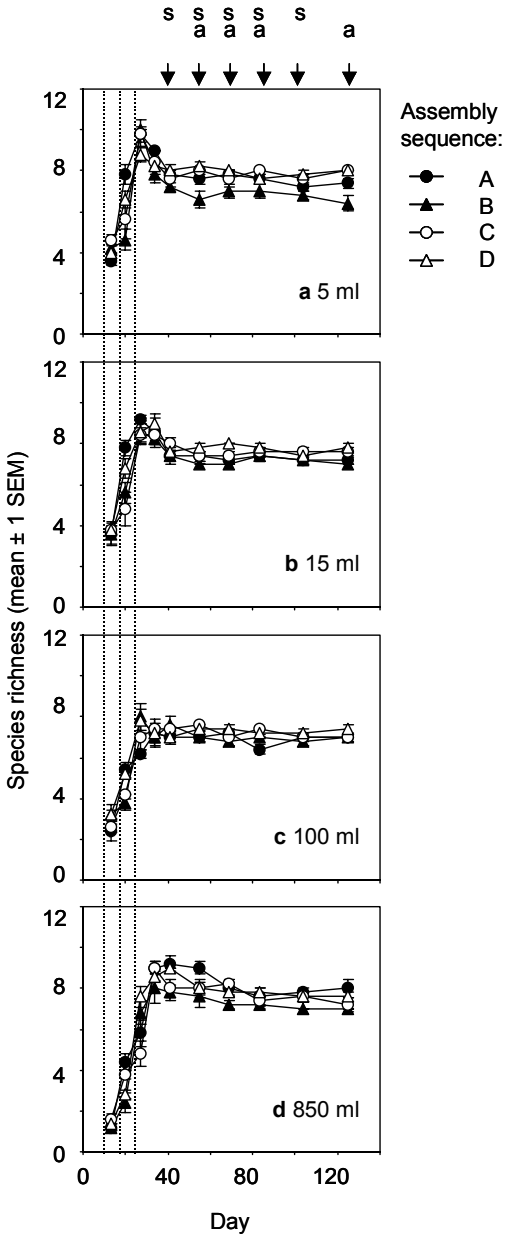


Figure 5. Temporal changes in species richness in communities assembled with different introduction sequences (sequences A, B, C, and D) in microcosms of different sizes (5, 15, 100, and 850 ml of medium). Microcosms were inoculated with bacteria on day 0, with microflagellates on day 2, and with protozoa and rotifer species on days 9, 16, and 23. Dashed lines indicate the timing of these three occasions of protist and rotifer introductions. The letters shown above the graphs indicate that, on the corresponding day (starting from day 41), the logarithm of ecosystem size (s), assembly sequence (a), and/or their interaction (s x a) significantly affected species richness in the ANOVAs (see Table 3). $n = 5$ for all treatment groups.

Table 2. Summary of repeated-measures analyses of variance on effects of assembly sequence, ecosystem size, and time on species diversity

		Response variable								
		Log(species richness)			Abundance-based Simpson diversity			Biomass-based Simpson diversity		
Source of variation	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Between subjects										
Assembly sequence	3	0.032	15.620	**0.000**	0.036	3.334	**0.025**	0.192	16.856	**0.000**
Ecosystem size	3	0.031	15.100	**0.000**	0.152	13.971	**0.000**	0.229	20.089	**0.000**
Sequence x Size	9	0.006	3.078	**0.004**	0.021	1.897	0.068	0.063	5.541	**0.000**
Error	64	0.002			0.011			0.011		
Within subjects										
Day	5	0.007	8.180	**0.000**	0.907	140.820	**0.000**	0.091	19.621	**0.000**
Day x Sequence	15	0.001	1.190	0.277	0.016	2.463	**0.002**	0.032	6.907	**0.000**
Day x Ecosystem size	15	0.002	2.378	**0.003**	0.029	4.467	**0.000**	0.023	5.048	**0.000**
Day x Sequence x Size	45	0.001	1.313	0.096	0.009	1.330	0.086	0.013	2.791	**0.000**
Error	320	0.001			0.006			0.005		

Notes: *P* values in bold indicate statistical significance ($P < 0.05$). Ecosystem size was log-transformed for the analyses.

Table 3. Summary of analyses of variance performed separately for each sampling day on effects of assembly sequence and ecosystem size on species diversity

			Response variable								
			Log(species richness)			Abundance-based Simpson diversity			Biomass-based Simpson diversity		
Day	Source of variation	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
27	Log(ecosystem size)	3	0.158	30.188	**0.000**	0.053	7.615	**0.000**	0.037	3.022	0.036
	Assembly sequence	3	0.017	3.162	0.030	0.193	27.653	**0.000**	0.082	6.686	**0.001**
	Log(size) x sequence	9	0.014	2.713	0.010	0.023	3.349	**0.002**	0.154	12.617	**0.000**
	Error	64	0.005			0.007			0.012		
34	Log(ecosystem size)	3	0.027	10.405	**0.000**	0.008	2.060	0.114	0.088	9.363	**0.000**
	Assembly sequence	3	0.006	2.135	0.104	0.038	9.844	**0.000**	0.107	11.372	**0.000**
	Log(size) x sequence	9	0.001	0.437	0.910	0.015	3.848	**0.001**	0.059	6.305	**0.000**
	Error	64				0.004			0.009		
41	Log(ecosystem size)	3	0.016	10.961	**0.000**	0.005	0.693	0.560	0.119	10.675	**0.000**
	Assembly sequence	3	0.002	1.249	0.299	0.050	6.538	**0.001**	0.150	13.436	**0.000**
	Log(size) x sequence	9	0.003	2.139	0.039	0.011	1.454	0.185	0.029	2.617	0.012
	Error	64	0.001			0.008			0.011		
55	Log(ecosystem size)	3	0.009	6.865	**0.000**	0.043	9.643	**0.000**	0.129	19.298	**0.000**
	Assembly sequence	3	0.010	7.515	**0.000**	0.006	1.416	0.246	0.123	18.517	**0.000**
	Log(size) x sequence	9	0.003	2.152	0.037	0.005	1.166	0.332	0.038	5.718	**0.000**
	Error	64	0.001			0.004			0.007		
69	Log(ecosystem size)	3	0.006	7.026	**0.000**	0.019	2.926	0.040	0.059	10.302	**0.000**
	Assembly sequence	3	0.008	9.507	**0.000**	0.002	0.249	0.862	0.041	7.234	**0.000**
	Log(size) x sequence	9	0.001	1.100	0.376	0.017	2.555	0.014	0.037	6.392	**0.000**
	Error	64	0.001			0.007			0.006		
83	Log(ecosystem size)	3	0.005	5.339	**0.002**	0.029	2.863	0.044	0.019	3.332	0.025
	Assembly sequence	3	0.004	4.129	0.010	0.022	2.149	0.103	0.034	6.030	**0.001**
	Log(size) x sequence	9	0.002	1.575	0.142	0.016	1.546	0.151	0.015	2.719	0.009
	Error	64	0.001			0.010			0.006		
104	Log(ecosystem size)	3	0.003	4.583	**0.006**	0.067	10.928	**0.000**	0.013	4.904	**0.004**
	Assembly sequence	3	0.004	6.466	**0.001**	0.002	0.251	0.860	0.002	0.882	0.455
	Log(size) x sequence	9	0.001	1.110	0.369	0.005	0.895	0.535	0.006	2.228	0.031
	Error	64	0.001			0.006			0.003		
125	Log(ecosystem size)	3	0.002	1.770	0.162	0.133	16.235	**0.000**	0.007	2.613	0.059
	Assembly sequence	3	0.009	9.812	**0.000**	0.034	4.180	0.009	0.001	0.472	0.703
	Log(size) x sequence	9	0.003	2.778	0.008	0.009	1.135	0.352	0.003	1.026	0.429
	Error	64	0.001			0.008			0.003		

Note: *P* values in bold are significant after Bonferroni correction (alpha = 0.05 / 8 days = 0.00625; see text). Ecosystem size was log-transformed for the analyses.

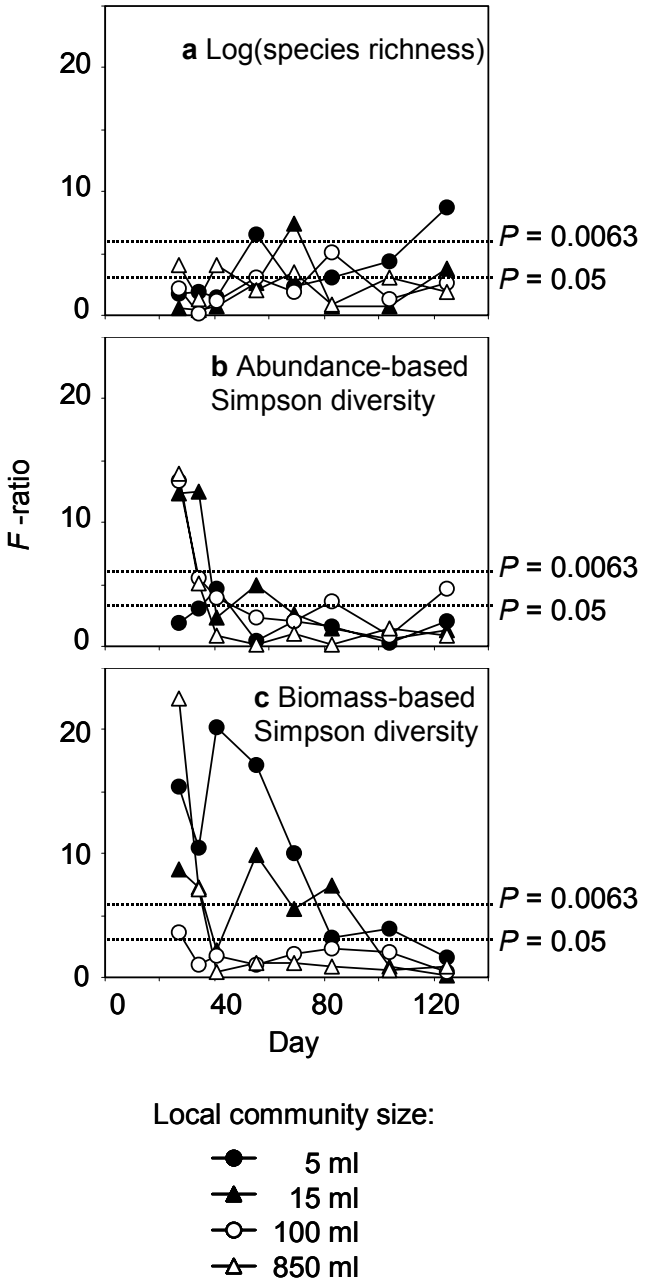


Figure 6. Temporal change in the *F*-ratio from the ANOVAs on effects of assembly sequence, performed separately for each sampling and for each size treatment. Dashed lines indicate *F*-ratio values that correspond to $P = 0.05$ and $P = 0.00625$ (critical value after Bonferonni correction = 0.05 / 8 sampling days; see text).

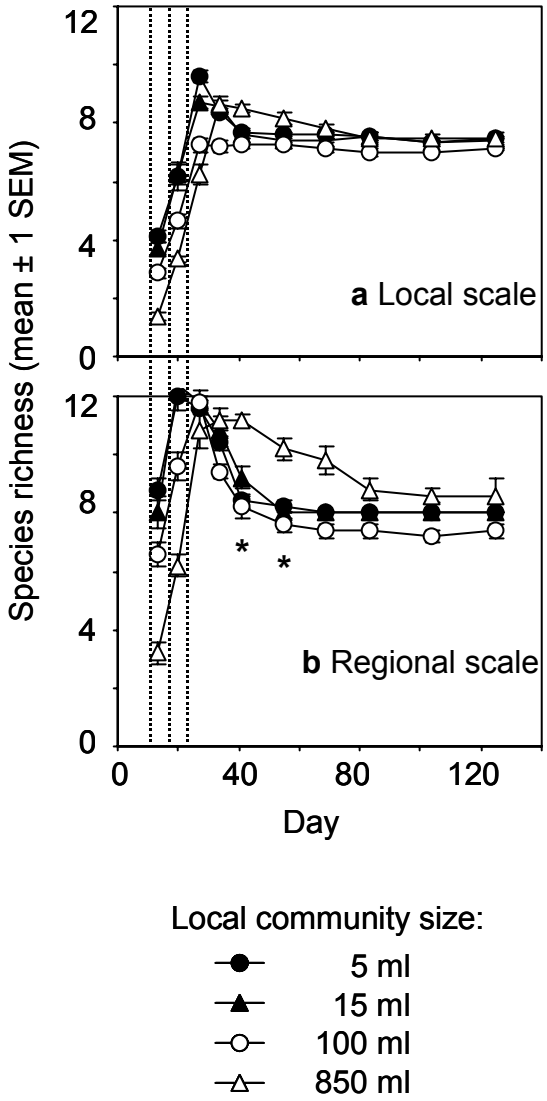


Figure 7. Temporal changes in species richness in microcosms of different sizes at local and regional scales (see text for definition of local and regional scales). Asterisks indicate that linear regression analysis found a significant relationship between the logarithm of ecosystem size and that of species richness at the corresponding scale on the corresponding day (see text). Other symbols are as in Fig. 5.

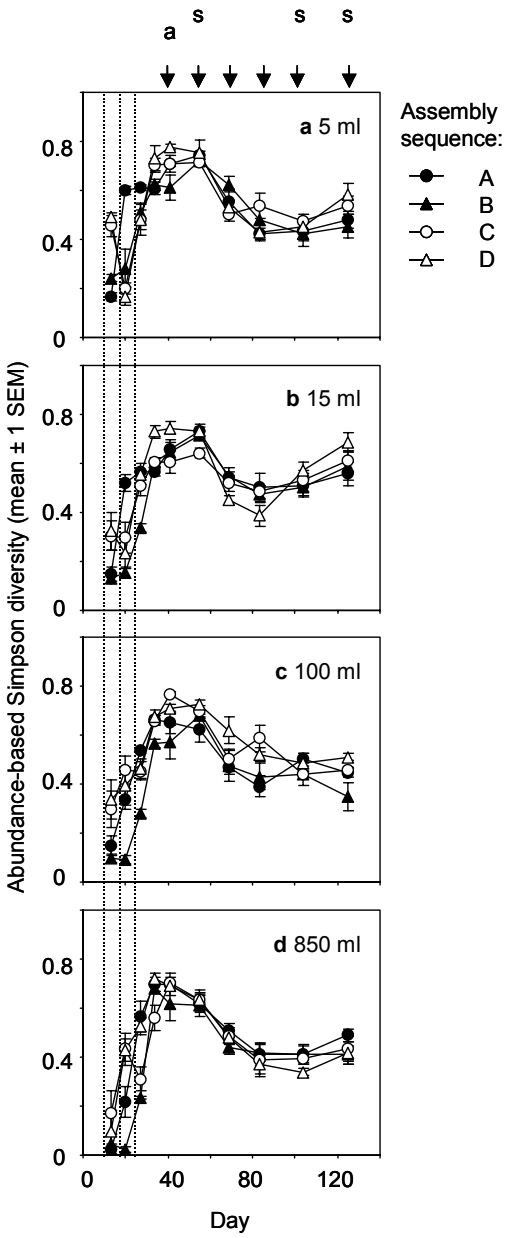


Figure 8. Temporal changes in abundance-based Simpson diversity in communities assembled with different introduction sequences. The letters shown above the graphs indicate that, on the corresponding day, the logarithm of ecosystem size (s), assembly sequence (a), and/or their interaction (s x a) significantly affected abundance-based Simpson diversity in the ANOVAs (see Table 3). Other symbols are as in Fig. 5.

Table 4. Linear regression statistics for the relations between the logarithm of ecosystem size as the independent variable and abundance-based Simpson diversity as the dependent variable for different assembly sequences

		ANOVA		Regression		
					Estimates (±SE)	
Sequence	Day	$F_{1, 18}$	P	R^2	Intercept	Slope
A	41	0.004	0.947	0.000	0.681 ± 0.045	-0.002 ± 0.024
	55	11.684	**0.003**	0.394	0.786 ± 0.035	-0.064 ± 0.019
	69	1.420	0.249	0.073	0.562 ± 0.040	-0.025 ± 0.021
	83	0.817	0.378	0.043	0.472 ± 0.049	-0.023 ± 0.026
	104	0.451	0.510	0.024	0.491 ± 0.046	-0.016 ± 0.024
	125	0.413	0.529	0.022	0.517 ± 0.041	-0.014 ± 0.021
B	41	0.064	0.802	0.004	0.625 ± 0.063	-0.008 ± 0.033
	55	10.018	**0.005**	0.358	0.766 ± 0.030	-0.049 ± 0.016
	69	11.880	**0.003**	0.398	0.659 ± 0.045	-0.081 ± 0.024
	83	1.485	0.239	0.076	0.504 ± 0.049	-0.031 ± 0.026
	104	0.501	0.488	0.027	0.474 ± 0.046	-0.017 ± 0.024
	125	2.390	0.139	0.117	0.543 ± 0.068	-0.055 ± 0.036
C	41	1.167	0.294	0.061	0.656 ± 0.040	0.023 ± 0.021
	55	2.142	0.161	0.106	0.709 ± 0.028	-0.022 ± 0.015
	69	0.317	0.580	0.017	0.520 ± 0.035	-0.011 ± 0.019
	83	1.991	0.175	0.100	0.581 ± 0.065	-0.048 ± 0.034
	104	6.548	0.020	0.267	0.540 ± 0.035	-0.047 ± 0.018
	125	7.617	0.013	0.297	0.623 ± 0.045	-0.066 ± 0.024
D	41	12.673	**0.002**	0.413	0.795 ± 0.020	-0.038 ± 0.011
	55	6.570	0.020	0.267	0.801 ± 0.039	-0.053 ± 0.020
	69	0.000	0.998	0.000	0.521 ± 0.049	0.000 ± 0.026
	83	0.081	0.779	0.004	0.439 ± 0.049	-0.007 ± 0.026
	104	7.544	0.013	0.295	0.574 ± 0.046	-0.066 ± 0.024
	125	14.655	**0.001**	0.449	0.715 ± 0.048	-0.097 ± 0.025

Notes: *P* values in bold are significant after Bonferroni correction (alpha = 0.05 / 6 days = 0.0083; see text). For intercepts, *P* values were all less than 0.001; for slopes, they were virtually identical to those for the corresponding analysis of variance.

Table 5. Linear regression statistics for the relations between the logarithm of ecosystem size as the independent variable and abundance-based Simpson diversity as the dependent variable at local and regional scales

				Regression		
		ANOVA			Estimates (±SE)	
Scale	Day	$F_{1, 18}$	P	R^2	Intercept	Slope
Local	41	0.247	0.625	0.014	0.678 ± 0.036	-0.009 ± 0.019
	55	17.078	**0.001**	0.487	0.758 ± 0.020	-0.044 ± 0.011
	69	4.109	0.058	0.186	0.550 ± 0.024	-0.026 ± 0.013
	83	2.100	0.165	0.104	0.488 ± 0.037	-0.028 ± 0.019
	104	5.613	0.029	0.238	0.516 ± 0.030	-0.037 ± 0.016
	125	6.734	0.018	0.272	0.585 ± 0.039	-0.054 ± 0.021
Regional	41	0.671	0.423	0.036	0.726 ± 0.030	-0.013 ± 0.016
	55	19.189	**0.000**	0.516	0.784 ± 0.021	-0.049 ± 0.011
	69	4.091	0.058	0.185	0.560 ± 0.025	-0.027 ± 0.013
	83	1.897	0.185	0.095	0.495 ± 0.038	-0.028 ± 0.020
	104	5.569	0.030	0.236	0.522 ± 0.031	-0.038 ± 0.016
	125	7.473	0.014	0.293	0.599 ± 0.040	-0.057 ± 0.021

Note: *P* values are as in Table 4.

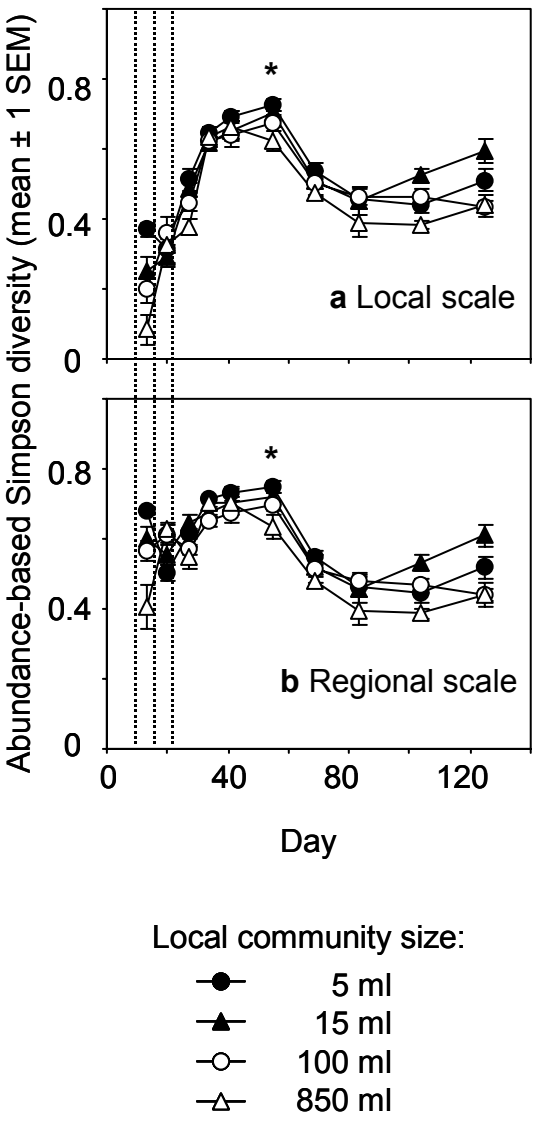


Figure 9. Temporal changes in abundance-based Simpson diversity at local and regional scales. Asterisks indicate that linear regression analysis found a significant relationship between the logarithm of ecosystem size and abundance-based Simpson diversity at the corresponding scale on the corresponding day (see Table 5). Other symbols are as in Fig. 5.

Biomass-based Simpson diversity

Effects of ecosystem size, assembly sequence, and time – In 100-ml and 850-ml microcosms, biomass-based Simpson diversity seems to have reached a stable state by around days 41 and 55 (Fig. 10), roughly as quickly as did local species richness (Fig. 5). In 5-ml and 15-ml microcosms, however, it took about 80 days since last species introduction, more than twice as long as it did in the larger microcosms, for biomass-based diversity to cease to increase and reach a possible stable state under sequences C and D (Fig. 10). Compared among size treatments, biomass-based diversity had similar trajectories under sequences A and B. Consequently, assembly sequence had large and long-lasting effects on biomass-based Simpson diversity in 15-ml and especially 5-ml microcosms, but not in 100- or 850-ml microcosms. After initial stages of assembly (i.e., after day 34), a significant effect on biomass-based diversity of ecosystem size was detected on four sampling days, of assembly sequence on four days, and of their interaction on two sampling days (Table 2 and 3). The additional ANOVAs confirmed that the effect of assembly history was larger and lasted longer in 5-ml and 15-ml microcosms than in 100-ml and 850-ml microcosms (Fig. 6c).

Linear regressions – Regression results on biomass-based diversity were similar to those on abundance-based diversity in that significant relationships were detected occasionally depending on assembly sequence and sampling day (Table 6), though on which sampling day and under which sequence the relation was significant differed between biomass- and abundance-based measures. Moreover, unlike abundance-based diversity, the significant relationships were positive in all cases but one (Table 6). At both local and regional scales, a significant positive linear relationship existed between ecosystem size and biomass-based Simpson diversity on two sampling days, on day 41 and 55 (Table 7, Fig. 11).

Population dynamics

Most populations appear to have either reached their peak abundance or gone extinct by day 41 or 55, after which population dynamics were relatively stable (Fig. 2-4). Exceptions include *Chilomonas* sp. (Fig. 3a) in 850-ml microcosms and *Uronema* sp. (Fig. 3e) in all size treatments, which did not go extinct or stabilize populations, respectively, until approximately day 83. Another possible exception was *Spirostomum* sp. (Fig. 3c), which tended to decrease slowly in number throughout the entire course of the experiment.

Some of the species that normally suffered local extinction occasionally maintained a small population throughout the experiment. This occurred only in the largest, 850-ml microcosms. These species include *Chilomonas* sp. (Fig. 3a), *Colpidium striatum* (Fig. 3b) and *Paramecium caudatum* (Fig. 2d).

Assembly sequence had strong and long-lasting effects on the abundance of one species, *Spirostomum* sp., in 5-, 15-, and 850-ml microcosms (Fig. 3c). This species also happened to be the exceptionally large species used in this experiment (see biomass data in Table 1). Assembly sequence sometimes affected several other species, too, especially *Euplotes* sp. (Fig. 4b), *Holosticha* sp. (Fig. 4c), and *P. tetraurelia* (Fig. 2e), but the

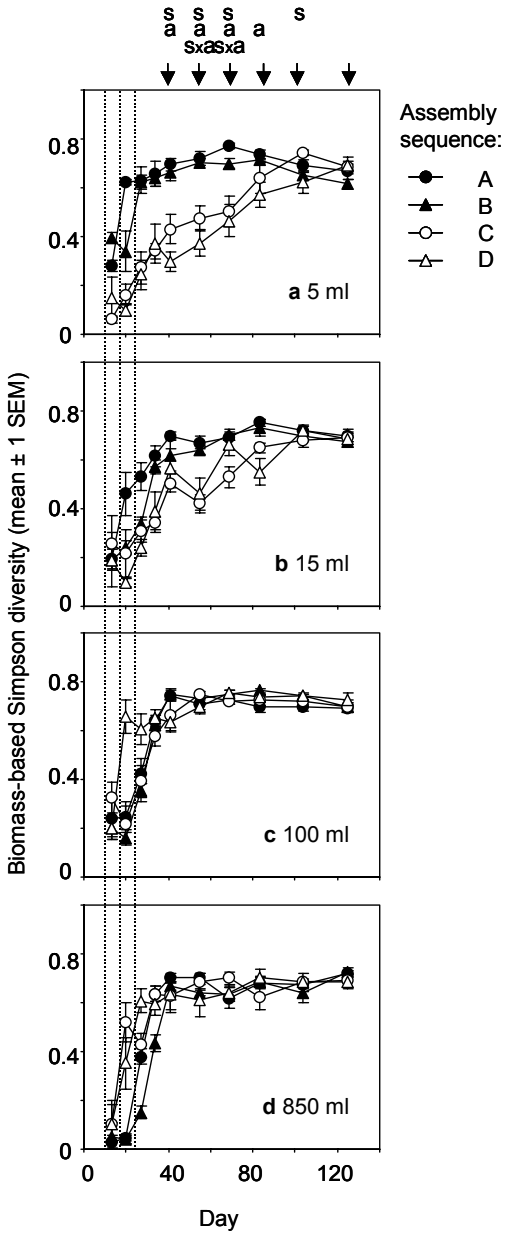


Figure 10. Temporal changes in biomass-based Simpson diversity in communities assembled with different introduction sequences. The letters shown above the graphs indicate that, on the corresponding day, the logarithm of ecosystem size (s), assembly sequence (a), and/or their interaction (s x a) significantly affected biomass-based Simpson diversity in the ANOVAs (see Table 3). Other symbols are as in Fig. 5.

Table 6. Linear regression statistics for the relations between the logarithm of ecosystem size as the independent variable and biomass-based Simpson diversity as the dependent variable for different assembly sequences

		ANOVA		Regression		
					Estimates (±SE)	
Sequence	Day	$F_{1, 18}$	P	R^2	Intercept	Slope
A	41	0.336	0.569	0.018	0.697 ± 0.024	0.007 ± 0.013
	55	0.000	0.986	0.000	0.701 ± 0.027	0.000 ± 0.014
	69	11.819	**0.003**	0.396	0.795 ± 0.030	-0.055 ± 0.016
	83	6.983	0.017	0.280	0.768 ± 0.022	-0.031 ± 0.012
	104	0.896	0.356	0.047	0.713 ± 0.021	-0.011 ± 0.011
	125	2.688	0.118	0.130	0.661 ± 0.023	0.020 ± 0.012
B	41	0.033	0.620	0.441	0.642 ± 0.046	0.019 ± 0.024
	55	0.832	0.374	0.044	0.700 ± 0.026	-0.012 ± 0.014
	69	2.016	0.173	0.101	0.736 ± 0.030	-0.022 ± 0.016
	83	0.535	0.474	0.029	0.740 ± 0.027	-0.010 ± 0.014
	104	0.038	0.848	0.002	0.688 ± 0.032	-0.003 ± 0.017
	125	14.671	**0.001**	0.449	0.603 ± 0.022	0.045 ± 0.012
C	41	7.712	0.012	0.300	0.395 ± 0.066	0.096 ± 0.034
	55	17.123	**0.001**	0.488	0.365 ± 0.059	0.128 ± 0.031
	69	14.999	**0.001**	0.455	0.441 ± 0.050	0.101 ± 0.026
	83	0.000	0.983	0.000	0.659 ± 0.051	0.001 ± 0.027
	104	1.757	0.202	0.089	0.734 ± 0.021	-0.015 ± 0.011
	125	0.021	0.886	0.001	0.689 ± 0.022	0.002 ± 0.012
D	41	9.722	**0.006**	0.351	0.311 ± 0.079	0.130 ± 0.042
	55	9.760	**0.006**	0.352	0.334 ± 0.072	0.118 ± 0.038
	69	3.983	0.061	0.181	0.516 ± 0.065	0.068 ± 0.034
	83	8.614	0.009	0.324	0.509 ± 0.050	0.077 ± 0.026
	104	1.029	0.324	0.054	0.655 ± 0.040	0.021 ± 0.021
	125	0.294	0.595	0.017	0.684 ± 0.034	0.010 ± 0.018

Note: *P* values are as in Table 4.

Table 7. Linear regression statistics for the relations between the logarithm of ecosystem size as the independent variable and biomass-based Simpson diversity as the dependent variable at local and regional scales

		ANOVA		Regression		
					Estimates (±SE)	
Scale	Day	$F_{1, 18}$	P	R^2	Intercept	Slope
Local	41	11.104	**0.004**	0.382	0.418 ± 0.052	0.092 ± 0.027
	55	11.353	**0.003**	0.387	0.421 ± 0.052	0.092 ± 0.027
	69	4.821	0.041	0.211	0.551 ± 0.043	0.050 ± 0.023
	83	1.303	0.269	0.068	0.631 ± 0.033	0.020 ± 0.017
	104	0.034	0.857	0.002	0.686 ± 0.019	0.002 ± 0.010
	125	7.299	0.015	0.289	0.661 ± 0.012	0.017 ± 0.006
Regional	41	10.397	**0.005**	0.366	0.518 ± 0.052	0.088 ± 0.027
	55	12.277	**0.003**	0.405	0.531 ± 0.040	0.074 ± 0.021
	69	6.588	0.019	0.268	0.642 ± 0.031	0.043 ± 0.017
	83	7.271	0.015	0.288	0.690 ± 0.019	0.026 ± 0.010
	104	0.005	0.947	0.000	0.749 ± 0.008	0.000 ± 0.004
	125	0.206	0.655	0.011	0.735 ± 0.014	0.003 ± 0.007

Note: *P* values are as in Table 4.

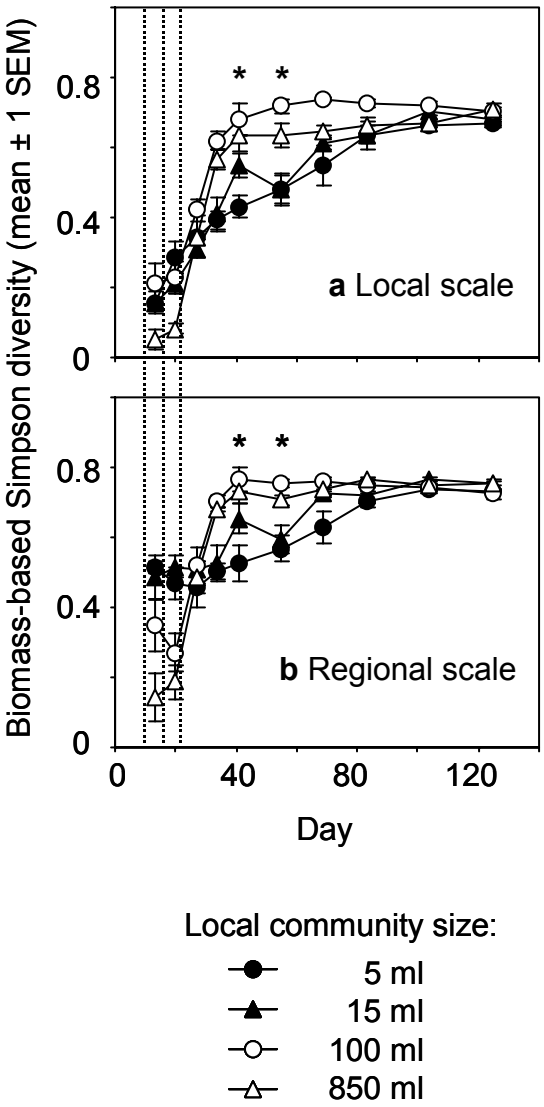


Figure 11. Temporal changes in biomass-based Simpson diversity at local and regional scales. Asterisks indicate that linear regression analysis found a significant relationship between the logarithm of ecosystem size and biomass-based Simpson diversity at the corresponding scale on the corresponding day (see Table 7). Other symbols are as in Fig. 5.

magnitude of sequence effect on these species tended to be considerably smaller and less consistent than on *Spirostomum* sp.

Discussion

This study clearly indicates that assembly history and ecosystem size can interact to affect species diversity, depending on the measure of diversity. Through this interaction, assembly history can influence whether and when a significant relationship between ecosystem size and species diversity is observed. In this experiment, these predictions were most strongly supported when diversity was measured as biomass-based Simpson diversity. Furthermore, the experimental support of the synecological hypothesis demonstrates that transient dynamics can last for such a long period compared to the generation times of the species involved that assembly history can play a significant role even in the absence of multiple stable states. It is at present uncertain to what extent the results obtained here can be generalized to natural systems of larger scale and complexity. While this caveat should be remembered, the unequivocal empirical evidence provided here for the assembly x size interaction and the significant historical effects without multiple stable states suggests that these novel results may be of general importance and worthy of consideration in other systems as well.

Below I will first examine the autecological and synecological hypotheses (Fig. 1) in the light of the experimental results and discuss their implications for size-diversity relationships. Next, I will search mechanisms responsible for interactive effects of assembly and size on biomass-based diversity. Finally, I will suggest future directions and comment on the potential generality of the experimental results.

Hypothesis testing and implications

The experiment yielded little support for either the autecological or synecological hypothesis with respect to species richness (Fig. 6a) and abundance-based Simpson diversity (Fig. 6b). Interactive effects of assembly history and ecosystem size were weak on species richness. They were detected by the repeated-measures ANOVA (Table 2), but by none of the ANOVAs performed separately for different days (Table 3). Similarly, none of the ANOVAs detected interactive effects of size x assembly on abundance-based Simpson diversity (Table 2 and 3), except at an initial stage of assembly, on days 27 and 34 (Table 3 and Fig. 6b). These interactive effects at an early assembly stage are consistent with the autecological hypothesis. But no clear evidence existed, and the effect, if any, was short-lived.

Consequently, the results showed no indication of a role of assembly history in determining the relationship between ecosystem size and species richness or abundance-based Simpson diversity. Because interactive effects were weak and because little variation in species richness existed in the first place for assembly history or ecosystem size to act upon, no statistically significant relationships between ecosystem size and species richness were found at the local scale. Although there were two sampling days when a significant size-richness relationship was found at the regional scale (Fig. 7b), interactive effects of assembly and size were not detected on these days (Table 3), indicating no role of assembly history. Similarly, although relationships between size

and abundance-based Simpson diversity were sometimes significant depending on assembly sequence and time (Table 4), assembly did not seem to play a role in creating them; size x assembly interactions were not significant when significant size-diversity relationships were observed (Table 2 and 3). Instead, the combination of day x sequence and day x size interactions (Table 2) was responsible for the history- and time-dependent relationships. And no scale-dependent patterns were observed with abundance-based diversity (Table 5).

Contrary to these results for species richness and abundance-based Simpson diversity, the results for biomass-based Simpson diversity provided strong support for the synecological hypothesis, but not for the autecological one. Two aspects of the results, taken together, provide evidence for the synecological hypothesis. First, the ANOVAs detected strong interactive effects of size and assembly even past initial stages, i.e., even after most populations had grown to their maximum size by day 41 (Table 2 and 3). Second, there was a clear indication that assembly affected diversity in smaller systems (5-ml and 15-ml microcosms) to a greater extent and for a longer time than in larger systems (100-ml and 850-ml microcosms) (Fig. 6c). Communities of different assembly history, however, eventually converged to an indistinguishable level of biomass-based Simpson diversity in all size treatments approximately 100 generations after the last species introduction (Fig. 10). It is not certain whether they would have continued to assume this common state or have diverged again if they were monitored further (cf. Samuels and Drake 1997). Yet, it seems more probable from the results that there was a single stable state common to all assembly x size treatments. Despite this likely absence of alternative stable states, however, transient dynamics toward community convergence were sufficiently long that size and assembly had ample time to exert a large interactive effect before convergence.

In fact, this interactive effect was so strong that it ultimately influenced size-diversity relationships. Whether and when a significant relationship was observed depended on assembly history and the time of observation (Table 6). This should have been caused by the interactive effect of assembly history and ecosystem size (Table 2 and 3), at least on days 55 and 69, because the ANOVA detected significant interactive effects on these sampling days (Table 3).

Mechanisms of assembly x size interaction

The patterns in biomass-based Simpson diversity appeared to be driven mostly by the population dynamics of a single species, *Spirostomum* sp. To confirm this hypothesis quantitatively, I performed simple linear regressions separately for each species, using log-transformed abundance as the independent variable and biomass-based diversity (all values from day 41 on) as the response variable. I also performed similar linear regressions with a quadratic term added as another independent variable. *Spirostomum* sp. with and without the quadratic term explained 30 and 77 % of variation in diversity, respectively, whereas other species explained no more than, and usually much less than, 9 % (Fig. 12).

It is indeed clear from the results that a large priority effect operated on *Spirostomum* sp. (Fig. 3c). In 5-ml, 15-ml, and, to a lesser extent, 850-ml microcosms,

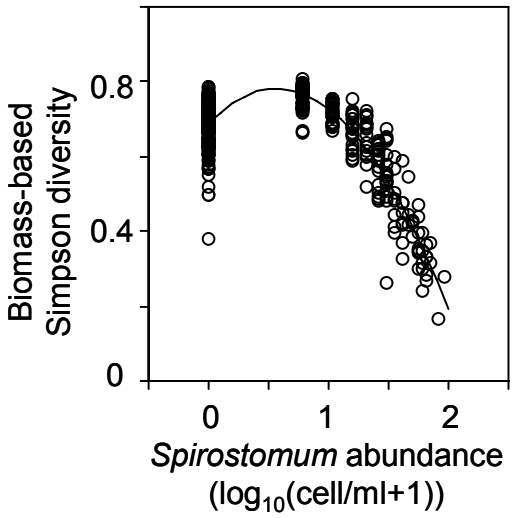


Figure 12. Much of the variation in Biomass-based Simpson diversity (d) could be explained by the abundance of *Spirostomum* (s) ($F_{2, 477} = 785.561$, $P < 0.0005$, adjusted $R^2 = 0.766$, model: $d = 0.689 + 0.327\ s - 0.288\ s^2$). Data points represent data from all replicates since day 41.

Spirostomum populations were able to grow only when they were among the species that were first introduced (i.e., only under sequences C and D, and not under A or B). Once they had achieved high abundance in these microcosms, they were capable of keeping it for a long term relative to their generation time, hence the long-lasting priority effect. Priority effects were also observed on several other species, but were not nearly as large in magnitude. Because of this focused priority effect on a single species, combined with the fact that *Spirostomum* sp. happened to have far greater biomass than other species (Table 1), its population dynamics dictated patterns in biomass-based diversity. Furthermore, the magnitude of this priority effect depended on ecosystem size in such a way that it had the greatest and longest effect in 5-ml and 15-ml microcosms, a smaller and shorter effect in 850-ml microcosms, and virtually none in 100-ml microcosms (Fig. 3c). It is not clear why the effect was greater in 850-ml systems than in 100-ml systems. Nonetheless, the overall tendency for the greater priority effect on smaller systems resulted in the interactive effect of assembly sequence and ecosystem size. The focused priority effect on the exceptionally large species was also responsible for the absence of scale-independent patterns (Table 7, Fig. 7); it overrode the size x assembly interactive effect observed at the local scale and precluded it from influencing patterns at the regional scale.

It should be noted that identifying the mechanisms of the priority effect itself was beyond the scope of this study. The experimental design did ensure that all environmental conditions were constant, on average, across size x assembly treatments. The only difference imposed among assembly treatments was the order of species introduction. Therefore, the difference in the abundance of *Spirostomum* sp. among assembly treatments is attributable to the influence of other species. But the process of species interactions was not clearly reflected in their population dynamics (Fig. 2-4). Thus, the priority effect may have operated through other changes induced indirectly by other species of protists and rotifers, such as changes in the composition of bacteria and microflagellates, chemical properties of the medium, or any other factors (Petersen 1984, Sutherland 1990) not monitored in this experiment.

Future directions and generality

Since it would be considerably costly and time-consuming, if not impossible, to manipulate assembly history experimentally in natural communities along an ecosystem size gradient, there seems to remain much room for more laboratory microcosm experiments to contribute to a further understanding of the size x assembly interaction. Factors that can potentially influence the interaction, but not manipulated in this study, include resource diversity, species pool size, immigration rate, the range of ecosystem size examined, and the number of invasion attempts allowed per species. Resource diversity has been suggested to regulate the importance of history (Long and Karel 2002), a larger species pool than used here may allow greater variation in species richness for assembly history and ecosystem size to act upon (cf. McGrady-Steed and Morin 2000, Fox et al. 2002), lower immigration rates may increase the importance of assembly history (cf. Robinson and Dickerson 1987, Spencer and Warren 1996), and wider size ranges and multiple introductions may also alter the importance of history (cf. Robinson and Dickerson 1987). These factors could be readily manipulated in microcosm experiments with sufficient control, although the large number of replicates required could potentially be a problem.

To my knowledge, no field data currently exist that can unequivocally test the hypotheses examined in this study (but see Dudgeon and Petraitis 2001, Bertness et al. 2002). As such, the role of the interaction between ecosystem size and assembly history in size-diversity patterns in natural systems remains uncertain. However, natural communities can vary greatly in the history of assembly owing to the highly stochastic nature of species immigration (e.g., Simberloff 1978). Moreover, strong species interactions are certainly not uncommon in natural communities (Connell 1983, Schoener 1983, Sih et al. 1985, Gurevitch et al. 1992). Neither are priority effects (see Morin 1999 for examples). And undoubtedly, ecosystem size varies widely in nature. Therefore, it would not seem surprising if assembly history were found to influence size-diversity relationships in many natural systems.

Acknowledgments

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Part 4

Incorporating internal and external dispersal in the assembly of local communities and metacommunities: effects on species diversity

Abstract

I incorporate internal dispersal, which occurs among local communities within a metacommunity, and external dispersal, which supplies immigrants from outside of the metacommunity, to simulate the assembly of local communities and metacommunities structured by competition and predation. By manipulating dispersal rate in a factorial fashion, I show that the effects of internal dispersal on species richness depend on external dispersal, and vice versa. At one trophic level, for example, internal dispersal does not affect species richness under frequent external dispersal, whereas it enhances richness in local communities and decreases it in metacommunities under infrequent external dispersal. Conversely, external dispersal influences species richness in local communities more greatly in the absence of internal dispersal than in its presence, though it does not affect richness in metacommunities regardless of internal dispersal. The scale dependence of richness patterns arises because internal and external dispersal interactively determine the extent to which dispersal history generates variation in species composition among local communities. These richness patterns are explained by species' relative abundances. Overall, these results suggest that the two dispersal types reciprocally provide the context in which each influences species diversity and that the effects of each cannot be fully understood in isolation of the effects of the other.

Introduction

Dispersal of individuals across ecological communities can significantly affect species diversity at multiple spatial scales. Ecology has a long tradition in examining the role of dispersal in species coexistence (Skellam 1951, Hutchinson 1951), but it is during the last decade that dispersal research exploded in quantity (Nathan 2003). Recent studies have involved both theoretical and empirical studies and various organisms ranging from viruses to butterflies and marine mammals (Bullock et al. 2002). Although dispersal occurs over a wide range of scales, its ecological implications for species diversity have generally been studied at either of two types of spatial scale relative to the communities in question. Here I will refer to them as internal and external dispersal.

Studies on internal dispersal are conceptually based on models in which a set of local communities, which may collectively be called a metacommunity (e.g., Wilson 1992, Holt 1993), are connected to one another by dispersal, but in which no dispersal occurs from outside of the metacommunity (Fig. 1a). Numerous theoretical studies (e.g., Levins and Culver 1971, Levin 1974, Chesson 1985, Iwasa and Roughgarden 1986, Wilson 1992, Caswell and Cohen 1993, Holt 1993, 1997, Hastings and Gavrilets 1999, Amarasekare and Nisbet 2001, Hubbell 2001, Shurin and Allen 2001, Mouquet and Loreau 2002, Kondoh 2003) as well as a somewhat more limited number of experimental studies (e.g., Huffaker 1958, Holyoak and Lawler 1996, Spencer and Warren 1996, Warren 1996, Burkey 1997, Holyoak 2000, Forbes and Chase 2002, Kerr et al. 2002) have shown that, depending on the rate and distance of dispersal, internal dispersal can either facilitate or destabilize species coexistence in local communities and metacommunities. Moreover, because internal dispersal can be both beneficial and detrimental to a given species or community, it has fueled much debate in conservation biology, specifically over the use of habitat corridors that may promote internal dispersal (Simberloff et al. 1992, Beier and Noss 1998, Earn et al. 2000).

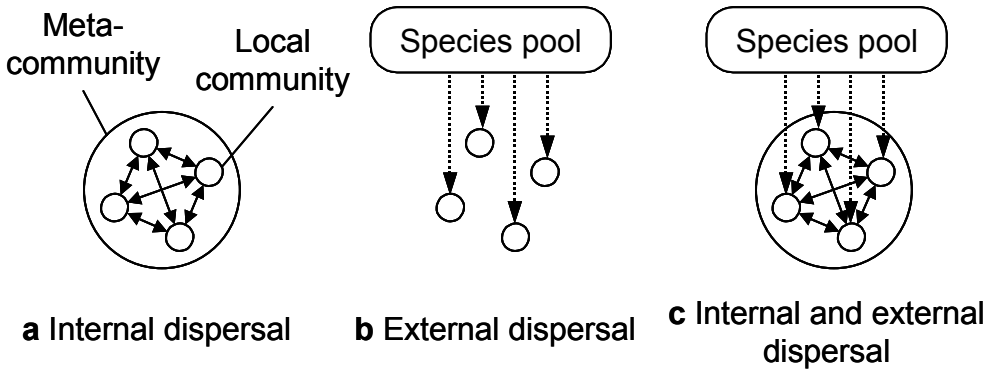


Figure 1. Models that incorporate internal dispersal (a), external dispersal (b), and both internal and external dispersal (c). Solid and dashed arrows represent the direction of internal and external dispersal, respectively.

On the other hand, studies on external dispersal are concerned with dispersal from outside of the set of local communities under consideration (Fig. 1b). Unlike internal dispersal, the rate of external dispersal is independent of the dynamics of local communities or metacommunities. These models are sometimes called mainland-island metapopulations, in which dispersal is unidirectional from a species pool where species never go extinct to local communities where species may frequently go extinct (Hanski and Simberloff 1997). An earliest and most influential model of this kind is MacArthur and Wilson's (1967) island biogeography theory, which predicts that species diversity is partly a function of the rate of external dispersal. More recent theoretical studies on external dispersal explicitly incorporated species interactions that MacArthur and Wilson's (1967) theory did not (e.g., Post and Pimm 1983, Drake 1990, Law and Morton 1996, Morton and Law 1997, Lockwood et al. 1997, Loreau and Mouquet 1999, Moore et al. 2001, Holt and Barfield 2003). In doing so, they found that not only the rate of dispersal, but also the sequence and timing in which different species disperse from the species pool to the local community could greatly influence local species diversity. These predictions have received some empirical support from experimental studies (e.g., Sutherland 1974, Robinson and Dickerson 1987, Houle and Phillips 1989, Drake 1991, Lawler 1993, Tilman 1997, Levine 2000, Fukami and Morin 2003). External dispersal has implications for conservation biology as well, specifically for restoration ecology, whose goal is to construct self-functioning ecosystems by introducing species artificially from external sources (Lockwood 1997, Young et al. 2000), and for invasion biology, in which the rate of external dispersal, sometimes referred to as propagule pressure, can be a key to predicting which exotic species becomes successful invaders in which native communities (Levine 2000, Mack et al. 2000).

Despite these advances in understanding the role of internal and external dispersal, however, there have been surprisingly few attempts to consider the two simultaneously. One notable exception is Gotelli (1991, Gotelli and Kelley 1993, Gotelli 1995: 89-109), who combined the rescue effect (Brown and Kodric-Brown 1977), an effect of internal dispersal, and the propagule rain (Harper 1977), an effect of external dispersal, in a single metapopulation model (see also MacArthur and Wilson 1967 on stepping stones and Holt 1992). These studies found that internal and external dispersal interact to influence metapopopulation dynamics and that the unified model answers some criticisms of earlier metapopulation models, for example, on the prediction of core-satellite distributions (Hanski 1982). Nonetheless, these metapopulation studies focused on populations of single species rather than communities of multiple interacting species. Much remains unknown about how internal and external dispersal may interact to influence community dynamics and consequently species diversity when local interactions among species are taken into consideration. Moreover, consideration of multiple interacting species raises the new question of to what extent variation in dispersal sequence and timing may contribute to interactive effects of internal and external dispersal. No complete study of species diversity can afford to ignore these questions, because species diversity in most natural communities is probably affected by both kinds of dispersal simultaneously (Harrison and Taylor 1997).

In this paper, I incorporate internal and external dispersal (Fig. 1c) in a simulation model of communities and metacommunities that are structured by two types of local species interactions, competition and predation. The model used here is built after the general Lotka-Volterra systems that have been extensively used for studying

community assembly, thereby rendering the results here comparable to those of earlier assembly models. The simulation assembles local communities and metacommunities through random sequential dispersal of species, both internal and external. Spatial and temporal heterogeneity of abiotic variables across local communities is deliberately omitted from the model, not because heterogeneity is absent in natural systems, but because removing it allows one to focus on the effects of dispersal. By manipulating dispersal rate in a factorial fashion, I ask (1) whether internal and external dispersal interact to influence species diversity, (2) whether the magnitude and direction of the interactive effects, if any, vary with the scale of observation, namely between the scales of local communities and of metacommunities, and (3) whether the magnitude and direction also depend on the trophic level at which species diversity is measured.

Methods

I simulated the assembly of local communities and metacommunities with seven replicates of species pools. In each simulation, each local community was assembled by dispersal of species from a common species pool (external dispersal) and, in some cases, by dispersal of species among local communities within the metacommunity (internal dispersal). In total, I assembled 1,120 local communities, i.e., 7 independently created species pools x 2 rates of external dispersal x 2 rates of internal dispersal x 10 metacommunity replicates per species pool x 4 local communities within each metacommunity. Below I will first describe how I constructed the species pools with which to assemble local communities and metacommunities. Next, I will explain how I simulated external and internal dispersal and local community dynamics. I will then describe how I manipulated dispersal rates and follow with an explanation of the statistical analyses performed.

Construction of species pools

I assumed that the dynamics of populations within each local community are governed by general Lotka-Volterra equations defining population growths and intra- and inter-specific interactions (see details in *Local community dynamics* below):

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

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 they disperse to local communities.

Each species pool was created independently using a method similar to that of Law and Morton (1996: 775) and Morton and Law (1997: 323-325). Their method remains one of the most biologically sound for modeling community assembly. Most other assembly models have been based on an assumption that is not empirically realistic, though argued to be a starting point to investigate general properties of Lotka-Volterra and other systems in the absence of reliable empirical data at the time. Specifically, they

assumed that the values of b_i's and a_{ij}'s are distributed uniform-randomly among species (Post and Pimm 1983, Case 1990, Drake 1990, Lockwood et al. 1997, Lundberg et al. 2000, Wilmers et al. 2002). Values assigned this way are not consistent with the recent finding that, in natural communities, most interactions are weak and only a small fraction of them are strong (Paine 1992, Berlow et al. 1999, McCann 2000, but see Abrams 2001, Sala and Graham 2002). This does not weaken the heuristic importance of these prior assembly studies. Nonetheless, the b_i and a_{ij} values used in them are in sharp contrast with those created by Morton and Law's (1997) empirically derived method, which gives values more consistent with the likely presence of many weak and a few strong interactions in natural communities (see also Huisman et al. 2001). Below I explain the method used in this study by modifying Morton and Law's description of their method.

Number of species – The set of m species that constitute a species pool is divided into m_1 basal species and m_2 consumer species. I used species pools consisting of m_1 = 20 basal species and m_2 = 20 consumer species. A basal species is able to grow in the absence of any other species from the species pool and does not eat other species from the pool. A consumer species eats some of the other species from the pool and cannot sustain its population in a local community without them.

Assigning body sizes – The method begins with assigning a body size, s_i, to each species i in the species pool. The logarithm of body size of species i, $\log_{10}(s_i)$, is drawn at random from a uniform distribution over the range [-2, -1] for basal species and [-1, 1] for consumer species. It is assumed that, if $s_i < s_j$, then species i may be eaten by species j, but not vice versa.

Assigning a_{ij} *between consumers and victims* – The strength of the interaction between a consumer and a victim is determined based on the empirically derived assumption that there is 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 consumer j and victim i on the per capita rate of increase of the victim is given as:

$$\begin{aligned} \overline{a_{ij}} &= -0.1 * \exp\left\{-\left(\log_{10}\left(10 * s_i / s_j\right) * c_1\right)^2\right\} && s_i < s_j \\ a_{ij} &= 0 && s_i \geq s_j . \end{aligned} \qquad (2)$$

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, 10. 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 is given as:

$$\begin{aligned} \overline{a_{ji}} &= -\overline{a_{ij}} * c_2 * s_i / s_j && s_i < s_j \\ a_{ij} &= 0 && s_i \geq s_j . \end{aligned} \qquad (3)$$

The parameter c_2 measures conversion efficiency. I used c_2 = 0.05, which lies within the biologically feasible range (Humphreys 1979). Note that, with this method of defining

consumer-victim interactions, consumer species, i.e., those from m_2 species, can also be victims of other consumer species, depending on their body sizes.

Assigning a_{ij} *between basal species* – The method assumes an upper limit to total biomass, or the carrying capacity K_i, of basal species within a local community. Assuming that the limit, K_i, is 100 biomass units for each basal species i, a self-limitation term for basal species i is:

$$\overline{a_{ii}} = -b_i * s_i / 100 . \quad (4)$$

(In Morton and Law [1997: 324], the corresponding equation, their equation 5, does not have the negative sign, most likely owing to a typographical error.) When different basal species occur together, they compete for limited resources such that the mean effect of basal species j and basal species i is:

$$\overline{a_{ij}} = -c_3 * b_i * s_j / 100 . \quad (5)$$

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 used $c_3 = 0.9$, as in Morton and Law (1997). Consumers are limited only by victim density, and their self-limitation term is zero.

Assigning b_i – Based on an empirical relationship between body size and the per capita intrinsic rate of increase, b_i, of basal species (Fenchel 1974, Blueweiss et al. 1978), it is assumed that:

$$\log_{10} \overline{b_i} = -1 - 0.25 * \log_{10} s_i . \quad (6)$$

Here, units are d^{-1} for b_i and g for s_i. It is less clear how b_i of consumers should be scaled with body size. Following Morton and Law (1997), I assume it is constant, with units of d^{-1}:

$$\overline{b_i} = -0.1 . \quad (7)$$

Allowing random variation around means – The above ecological parameters, a_{ij} and b_i, are unlikely to be solely determined by body size. Morton and Law (1997) assume there are random variables with mean values set by equations 2 to 7, and I follow this assumption. Thus, letting $\overline{p}$ be the mean value of a given parameter from equations 2 to 7, the parameter p itself is taken as a random variable from a normal distribution $N\left(\overline{p}, 0.1 * \overline{p}\right)$, truncating the distributions to ensure that p has the same sign as $\overline{p}$.

Assembly of local communities and metacommunities

External dispersal – 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 (i.e., external dispersal). If the first species

chosen for a given local community were a basal species, the population would start to grow according to the Lotka-Volterra equations (equations 1). If the first species were a consumer species, its population would start to decline according, again, to the Lotka-Volterra equations. When a predetermined period of time had passed since the first species introduction (see *Manipulation of dispersal rates* below), a second species was chosen randomly from the species pool for each local community and introduced to the corresponding community. This process of dispersal from the species pool was repeated for the entire course of the simulation (see below for when the simulations were terminated). Invading species were introduced with a low abundance ($x_{ik} = 1.0 \times 10^{-3}$). This initial abundance is significantly low relative to the mean carrying capacity of a basal species in a local community, which could range between 9.09×10^3 (i.e., 100 biomass units divided by the maximum body size possible = 100/(0.1x1.1)) and 1.11×10^4 (i.e., 100 biomass units divided by the minimum body size possible = 100/(0.01x0.9)). In keeping with the methods in pervious assembly modeling (e.g., Law and Morton 1996, Morton and Law 1997), a species already present at a given time in a given local community was not allowed to be chosen as the newly invading species for that community at that time.

Internal dispersal – Where appropriate (see *Manipulation of dispersal rates* below), species in local communities were also allowed to disperse among the local communities within a metacommunity (i.e., internal dispersal). Once in 10 days, total abundance summed across the four local communities in the metacommunity was measured for each species present in the metacommunity. For each species and for each local community, whether the species disperses to the community was determined probabilistically as a linear function of its total abundance in the metacommunity. For basal species, the dispersal probability was set out so that a species that had the maximum total abundance possible would have a dispersal probability of 0.25. The maximum total abundance possible was calculated as follows: the number of local communities in a metacommunity (4) x the maximum biomass units possible in a local community (100) / the minimum body size possible (0.01×0.9) = 4.44×10^4. For consumer species, the dispersal probability was set out so that a species that had 5 % of the maximum total abundance possible for basal species would have a dispersal probability of 0.25. Placing the five percent (same as the value of conversion efficiency, c_2) here was done on the assumption that consumers should tend to have a better ability to disperse between local communities than basal species do, so that consumers can efficiently forage basal species within a metacommunity. Species dispersing among local communities were introduced to the target communities with the same abundance as for those dispersing from the species pool ($x_{ik} = 1.0 \times 10^{-3}$). Species were allowed to disperse to a local community regardless of whether they were already present or absent in that community.

Local community dynamics – Throughout the simulation, the abundance of each species in each local community was calculated by numerically integrating the Lotka-Volterra equations (equations 1) using the commercially available algorithm, "d02ejc" (Numerical Algorithm Group 2002), which implements Backward Differentiation Formulae (see Hall and Watt 1976). This method more accurately tracks population dynamics than do other methods used in most earlier assembly studies, including those based on 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 Morton et al.

1996 for discussion on relevant technical issues). A species was removed from the local community if its abundance fell below an extinction threshold, $x_{ik} = 1.0 \times 10^{-3}$, which is the same as the initial density of dispersing species (see above).

Invasion resistance – For each metacommunity replicate, the following measures of invasion resistance were recorded 1.0×10^4 and 5.0×10^4 days after the first external dispersal and every 1.0×10^5 days afterwards to determine when to terminate the simulation (see below): (1) resistance to invasion averaged over the four local communities in a metacommunity, $\overline{R}$, and (2) proportion of local communities, in a metacommunity, for which R is one, P. Invasion resistance, R, of a local community is defined as the proportion of species absent from the community, but present in the species pool, which would go extinct after a certain time (1.0×10^3 days) had passed if it were introduced to the community. Therefore, when R is one, the community is resistant to invasion by any species present in the species pool, but absent from the community, at the time R is measured. This measure of invasion resistance is similar to that used by Morton and Law (1997), but different in that my measure assesses the invader's abundance after certain time units (=1.0×10^3 days), whereas Morton and Law's permanence criterion effectively checks for the presence or absence of the invader in the community after an infinitely long time has passed since its introduction. Also, because my simulations track population dynamics explicitly and there can be population fluctuations such as may be observed in predator-prey cycles, the value of P can both increase and decrease over time; whereas Morton and Law's permanence algorithm monitors species composition only and P can therefore only decrease over time in their simulations.

Termination of simulations – For each metacommunity replicate, the simulation was terminated when either of the following was satisfied: (1) the value of P had been zero for four consecutive samplings or (2) the assembly had been simulated for 2×10^6 days, which allowed a total of 2×10^5 and 2×10^3 species introductions, or 5×10^3 and 50 introductions per species on average, from the species pool in the frequent and infrequent external dispersal manipulations (see *Manipulation of dispersal rates* below), respectively. These two criteria maximized the possibility that the dynamics of community assembly had reached an equilibrium state, be it a stable point or a more complex attractor, by the time the simulations were terminated. Therefore, the measures of communities obtained at the end of the simulations (see below) reflect a consequence of long-term dynamics over an ecologically important time scale rather than initial stages of community development toward persistent states.

Manipulation of dispersal rates

I used two rates of external dispersal: once in 10 days and once in 1,000 days. I also used two rates of internal dispersal: potential dispersal of species once in 10 days subject to the dispersal probability specified above and no internal dispersal. I did not allow dispersal among metacommunities. The absence of among-metacommunity dispersal ensured that metacommunities could be treated as statistically independent replicates of community assembly for a given species pool.

Measures of community structure

For each metacommunity replicate, the following measures of species diversity and relative abundance were obtained at the end of each simulation. Although these measures were examined only at this single time point, they represent a result of long-term community dynamics as discussed above. Equally importantly, the robustness, both in statistical and ecological senses, of the results from this single point was ensured by a high level of replication, with a total of 70 replicated metacommunities for each dispersal treatment, i.e., 7 independently created species pools, each of which was used to assemble 10 metacommunity replicates.

Species richness – The measures of species richness included (1) mean number of basal species in a local community, averaged over the four local communities in the metacommunity, $\overline{n_{BL}}$, (2) number of basal species in the metacommunity, n_{BM}, (3) basal species richness found among the local communities, $n_{BM} - \overline{n_{BL}}$, (4) mean number of consumer species in a local community, averaged over the four local communities in the metacommunity, $\overline{n_{CL}}$, (5) number of consumer species in the metacommunity, n_{CM}, and (6) consumer species richness found among the local communities, $n_{CM} - \overline{n_{CL}}$. Obtaining species richness separately for basal and consumer species allowed clearer ecological interpretation of patterns in species diversity.

Relative abundance – I also examined the distribution of relative abundance among species in order to discern processes responsible for species richness. For each species in each local community and metacommunity, I calculated the relative abundance (i.e., the abundance of the focal species divided by the total abundance summed over all species present in the local community or metacommunity) separately for basal and consumer species at the end of the simulation, classified the species into 10 equally spaced abundance categories (i.e., species with a relative abundance between 0 and 0.1, between 0.1 and 0.2, between 0.2 and 0.3, and so on), and counted the number of species that belong to each abundance category. I visualized general trends in the distribution of relative abundance by finding the mean of the number of species belonging to each category averaged over all metacommunity replicates and then plotting them as a function of abundance categories. These distribution graphs, however, are only a convenient means to summarize general patterns across replicates. I also looked at distribution patterns for each local community and metacommunity separately; I will describe them in the results section where appropriate. Raw data for each replicate will not be provided in this paper, because space is limited. However, they are available from the author upon request.

Statistical analyses

I performed analyses of variance (ANOVAs) to test for the effects of species pool, the rate of external dispersal, the rate of internal dispersal, and all interaction terms among them on the six measures of species richness described above. Additionally, I did another set of ANOVAs to test for the effect of the four dispersal-rate manipulations on richness measures. When the ANOVA detected significant effects, I performed post-hoc tests using Tukey-Kramer HSD pairwise comparisons to determine which treatment

groups differed significantly. All statistical analyses were conducted using the software SYSTAT version 10 (SPSS 2000).

Results

Population and community dynamics

Visual inspection of population and community dynamics in several replicates of metacommunities indicated that the communities had reached equilibrium when the simulations were terminated (Figs. 2 and 3). Under frequent external dispersal, most local communities converged to a similar state no later than, and usually much earlier than, 2×10^5 days after the first species introduction (Fig. 2). Under the infrequent external dispersal, indications of equilibrium were more ambiguous; local communities and metacommunities continued to fluctuate widely in species richness and composition throughout the course of the simulation, but with no overall trends of increase or decrease in species richness (Fig. 3). In local communities, basal species richness, if averaged over time, was higher in the presence of internal dispersal (Fig. 3b, blue line) than in its absence (Fig. 3a, blue line); by contrast, in metacommunities, basal species richness was higher in the latter (Fig. 3a, red line) than in the former (Fig. 3b, red line) (see next section for statistical analyses).

Richness of basal species

For basal species, all of the main and interactive effects of external dispersal, internal dispersal, and species pool were significant on all measures of species richness, except the main effect of external dispersal on species richness in metacommunities (Table 1).

Species richness in local communities, $\overline{n_{BL}}$, was highest and nearly identical to that in metacommunities, n_{BM}, under the frequent external dispersal regardless of the presence or absence of internal dispersal; it was intermediate under the lower external dispersal rate and with internal dispersal; and it was lowest under the lower external dispersal rate and without internal dispersal (Fig. 4a, b).

On the other hand, species richness in metacommunities, n_{BM}, was relatively unaffected by dispersal manipulations (Fig. 4a, b), except that it was marginally (P=0.065, Tukey-Kramer HSD pairwise comparisons) higher in the absence of internal dispersal (A in Fig. 4a) than in its presence (B in Fig. 4b) when external dispersal was infrequent.

This dependence of species richness patterns on the scale of observation (i.e., local community scale vs. metacommunity scale) resulted partly from changes in species richness found among local communities, $n_{BM} - \overline{n_{BL}}$, with dispersal rate (X and Y in Fig. 4c, d).

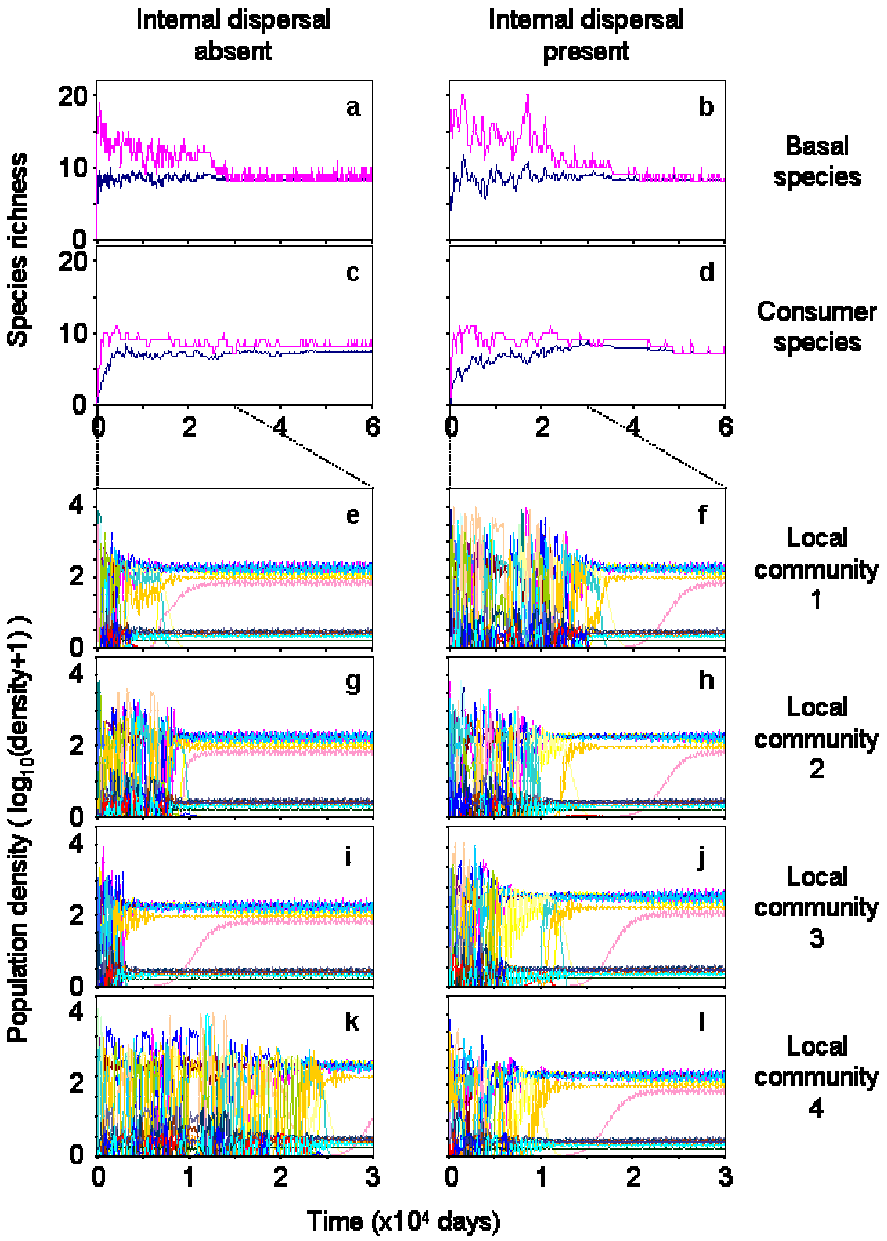


Figure 2. Representative examples of population and community dynamics when external dispersal occurs every 10 days. In a-d, blue lines are mean species richness in local communities, and red lines are species richness in metacommunities. In e-l, lines of different colors represent the population densities of different species, including both basal and consumer species. Results in a and c are for the metacommunity that consisted of the local communities shown in e, g, i, and k. Similarly, results in b and d are for the metacommunity that consisted of the local communities shown in f, h, j, and l. Note the different time scales for a-d and for e-l. Simulations were run for up to two million days, though only an initial part of it is shown here. The same species pool was used for both simulations.

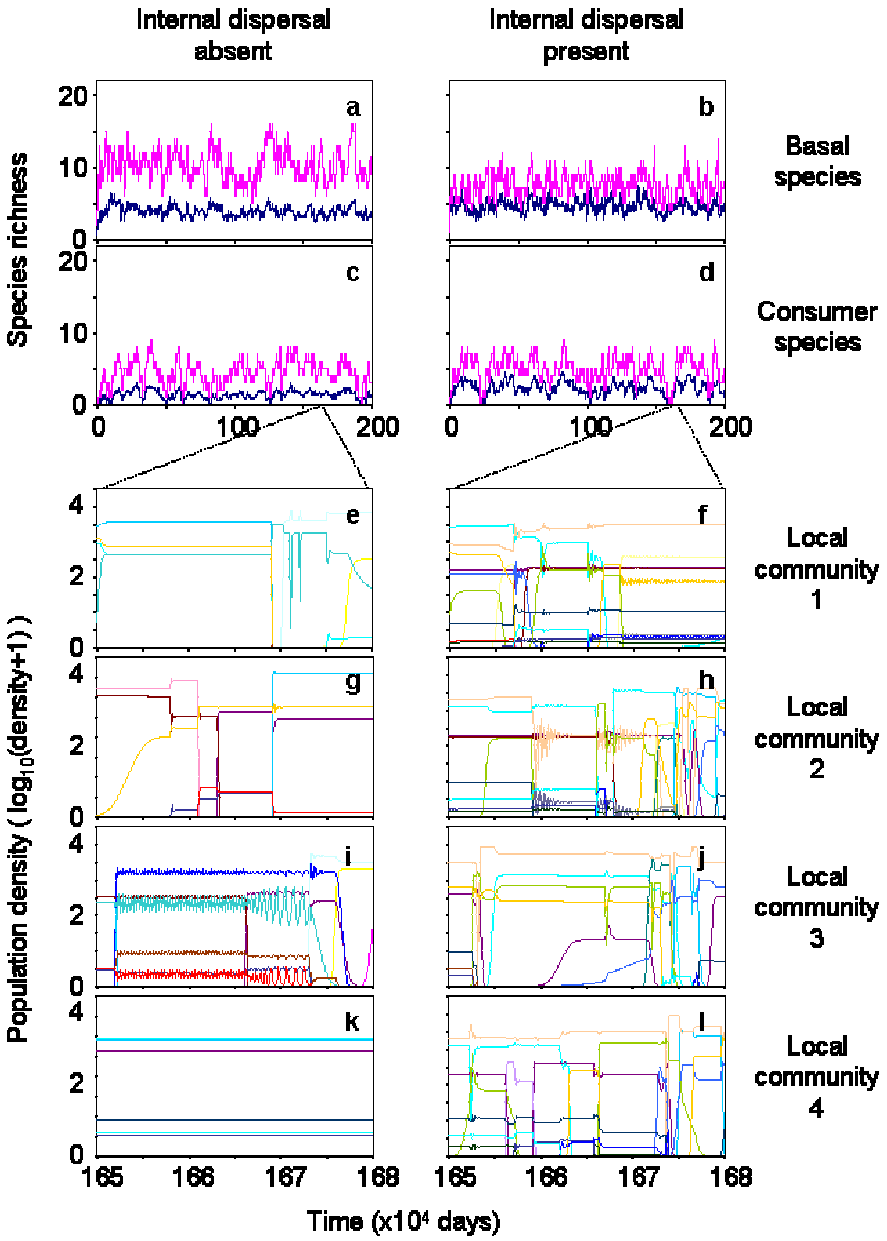


Figure 3. Representative examples of population and community dynamics when external dispersal occurs every 1000 days. Line colors are as in Fig. 2. Simulations were run for two million days, all of which is shown in a-d. Only a fraction of them is shown in e-l to make population dynamics more legible and more directly comparable with Fig. 2e-l, which shows dynamics for the same amount of time. The same species pool as for Fig. 2 was used for both simulations.

Table 1. Summary of ANOVA on basal species richness.

Source of variation	df	MS	*F*	*P*
Mean species richness in local communities ($\overline{n_{BL}}$)				
Species pool (P)	6	31.102	95.408	<**0.0005**
External dispersal (E)	1	436.251	1338.226	<**0.0005**
Internal dispersal (I)	1	9.289	28.495	<**0.0005**
P x E	6	22.020	67.548	<**0.0005**
P x I	6	0.916	2.809	**0.012**
E x I	1	7.394	22.681	<**0.0005**
P x E x I	6	0.962	2.951	**0.008**
Error	252	0.326		
Species richness in metacommunities (n_{BM})				
Species pool (P)	6	68.249	47.030	<**0.0005**
External dispersal (E)	1	1.289	0.888	0.347
Internal dispersal (I)	1	13.289	9.158	**0.003**
P x E	6	64.439	44.404	<**0.0005**
P x I	6	17.289	11.914	<**0.0005**
E x I	1	17.004	11.717	**0.001**
P x E x I	6	17.404	11.993	<**0.0005**
Error	252	1.451		
Species richness found among local communities ($n_{BM} - \overline{n_{BL}}$)				
Species pool (P)	6	52.529	71.264	<**0.0005**
External dispersal (E)	1	484.972	657.944	<**0.0005**
Internal dispersal (I)	1	44.800	60.778	<**0.0005**
P x E	6	56.879	77.166	<**0.0005**
P x I	6	15.264	20.708	<**0.0005**
E x I	1	46.822	63.522	<**0.0005**
P x E x I	6	15.253	20.693	<**0.0005**
Error	252	0.737		

Notes: *P* values in bold are significant with α=0.05.

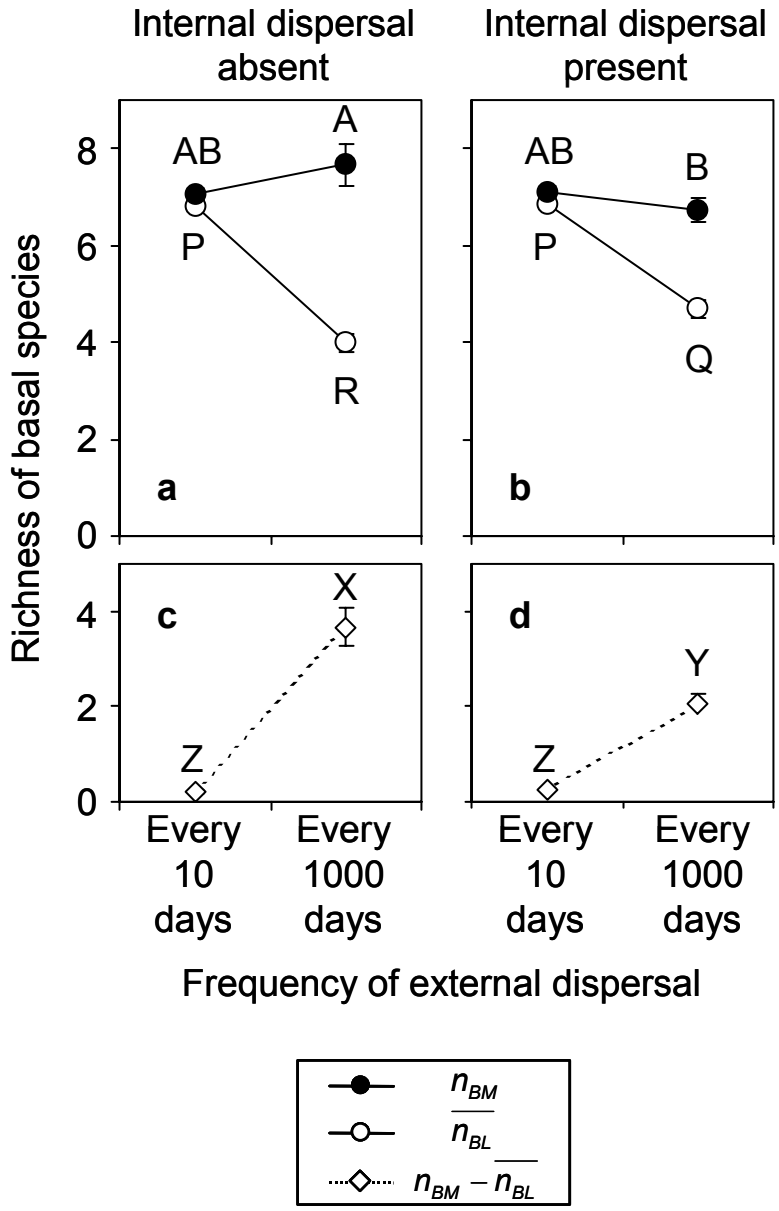


Figure 4. Richness of basal species found in local communities ($\overline{n_{BL}}$), in metacommunities (n_{BM}), and among local communities ($n_{BM} - \overline{n_{BL}}$) at the end of the simulations. Data points are the mean of 70 replicates (7 species pools x 10 metacommunity replicates for each species pool). Bars depict standard errors of the mean. Values labeled with different uppercase letters differ significantly (Tukey-Kramer HSD pairwise comparisons with α=0.05 except between A and B, for which *P*=0.065); note that comparisons were made separately for $\overline{n_{BL}}$, n_{BM} , and $n_{BM} - \overline{n_{BL}}$.

Relative abundance of basal species

Under frequent external dispersal, the distribution of relative abundance among basal species took essentially the same form regardless of the presence or absence of internal dispersal or the scale of observation (Fig. 5a, c, e, g). In all these cases, higher relative abundance categories contained fewer species, with the most dominant species occupying no more than 60% of total community abundance.

In contrast, under infrequent external dispersal, the relative abundance distribution depended on the scale of observation (Fig. 5b vs. f, and d vs. h) and the absence or presence of internal dispersal (Fig. 5b vs. d, and f vs. h):

At the metacommunity scale (Fig. 5b, d), the majority of species were relatively rare and belonged to the least abundant category, but more species tended to be in this category when internal dispersal was absent (Fig. 5b) than when it was present (Fig. 5d). This resulted in higher species richness observed in the former case (A in Fig. 4a) than in the latter (B in Fig. 4b). Comparison of Fig. 5a and b and of Fig. 5c and d also reveals that relative abundance was distributed differently between replicates of frequent and infrequent external dispersal, even though species richness did not differ significantly between them (AB vs. A in Fig. 4a, and AB vs. B in Fig. 4b).

At the local community scale (Fig. 5f, h), dominant species tended to occupy a larger proportion of total abundance and allowed fewer rare species to coexist with them when external dispersal was infrequent (Fig. 5f, h) than when it was frequent (Fig. 5e, g). However, a slightly greater number of less abundant species survived in local communities in the presence of internal dispersal (Fig. 5h) than in its absence (Fig. 5f). Although this difference was not large, it was large enough to cause local species richness to differ significantly between the two treatments (R in Fig. 4a vs. Q in Fig. 4b).

Richness of consumer species

Different trends were found in consumer species richness than in basal species richness. As in basal species, the majority of the main and interactive effects of dispersal and species pool on species richness were significant (Table 2). However, the main effect of internal dispersal and the interaction of external and internal dispersal were weak and, in most cases, insignificant (Table 2). Thus, species richness both in local communities, $\overline{n_{CL}}$, and in metacommunities, n_{CM}, was affected strongly by external dispersal, but not by internal dispersal (Fig. 6).

Some species richness was found among local communities under the infrequent external dispersal, whereas virtually none of it was found under the frequent external dispersal (Fig. 6c, d). This resulted in a larger difference in species richness between the frequent and infrequent external-dispersal treatments in local communities (P vs. Q in Fig. 6a, b) than in metacommunities (A vs. B in Fig. 6a, b). Unlike for basal species (Fig. 4a, b), however, the direction of changes in richness did not depend on the scale of observation; only the magnitude did.

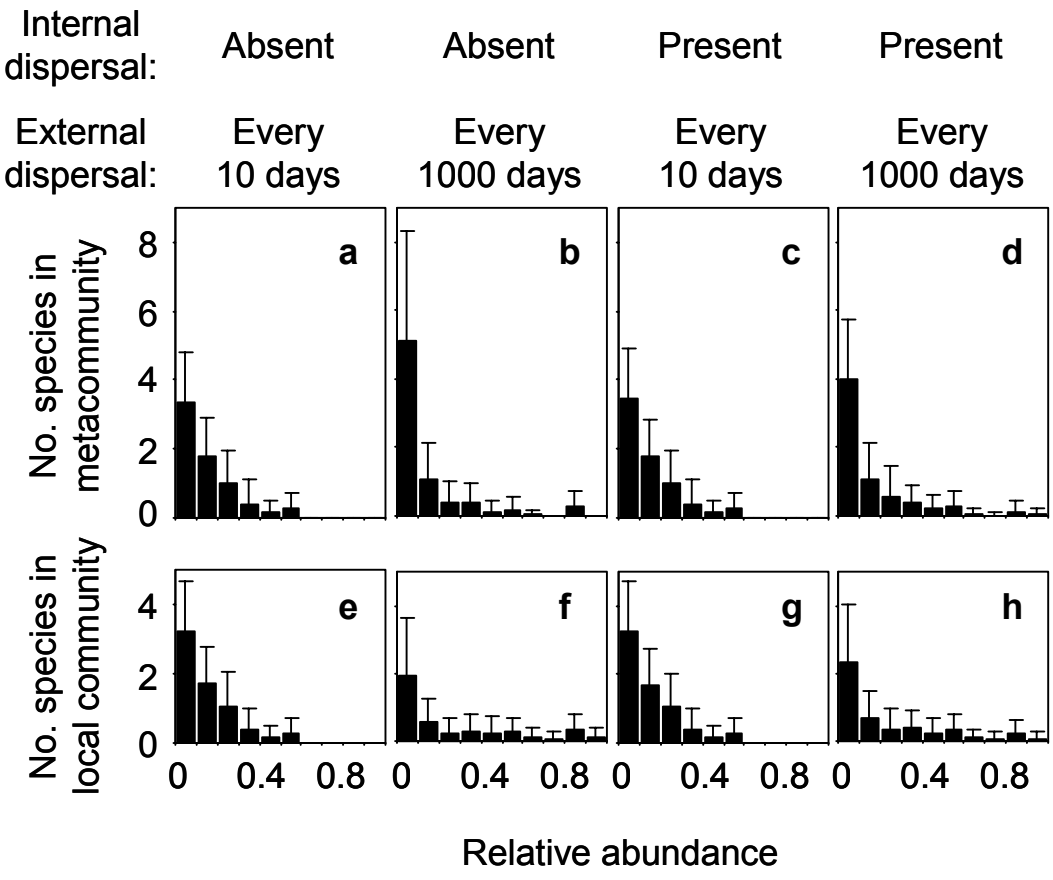


Figure 5. Distribution of relative abundance among basal species in local communities and metacommunities at the end of the simulations. Each bar represents the mean of 70 replicates (7 species pools x 10 metacommunity replicates for each species pool) with standard deviation.

Table 2. Summary of ANOVA on consumer species richness.

Source of variation	df	MS	*F*	*P*
Mean species richness in local communities ($\overline{n_{CL}}$)				
Species pool (P)	6	13.337	52.619	<**0.0005**
External dispersal (E)	1	1120.000	4418.630	<**0.0005**
Internal dispersal (I)	1	1.032	4.072	**0.045**
P x E	6	40.501	159.783	<**0.0005**
P x I	6	0.688	2.714	**0.014**
E x I	1	0.751	2.962	0.086
P x E x I	6	0.769	3.034	**0.007**
Error	252	0.253		
Species richness in metacommunities (n_{CM})				
Species pool (P)	6	37.683	35.236	<**0.0005**
External dispersal (E)	1	491.575	459.655	<**0.0005**
Internal dispersal (I)	1	0.175	0.164	0.686
P x E	6	38.933	36.405	<**0.0005**
P x I	6	4.383	4.099	**0.001**
E x I	1	0.004	0.003	0.954
P x E x I	6	5.229	4.889	<**0.0005**
Error	252	1.069		
Species richness found among local communities ($n_{CM} - \overline{n_{CL}}$)				
Species pool (P)	6	12.315	24.595	<**0.0005**
External dispersal (E)	1	127.575	254.796	<**0.0005**
Internal dispersal (I)	1	0.357	0.713	0.399
P x E	6	13.369	26.701	<**0.0005**
P x I	6	1.736	3.467	**0.003**
E x I	1	0.858	1.714	0.192
P x E x I	6	2.158	4.309	<**0.0005**
Error	252	0.501		

Notes: *P* values in bold are significant with α=0.05.

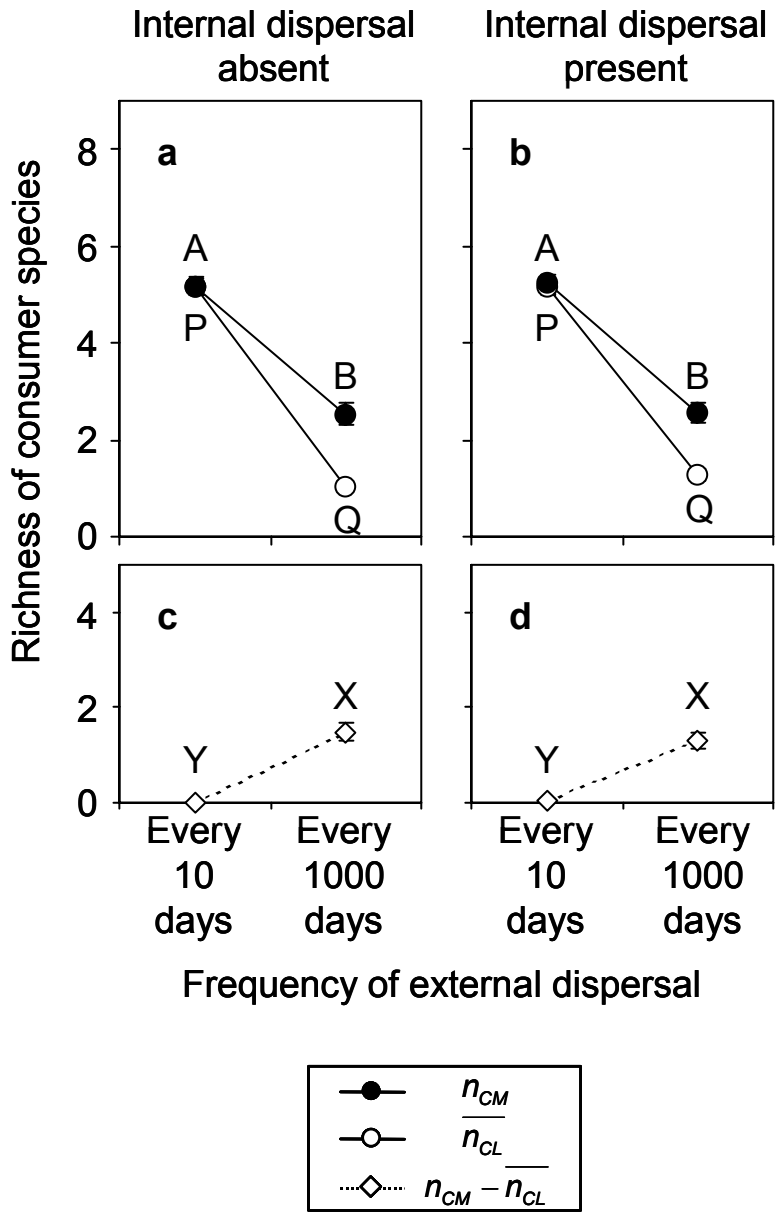


Figure 6. Richness of consumer species found in local communities ($\overline{n_{CL}}$), in metacommunities (n_{CM}), and among local communities ($n_{CM} - \overline{n_{CL}}$) at the end of the simulations. Data points and bars are as in Fig. 4. Values labeled with different capital letters differ significantly (Tukey-Kramer HSD pairwise comparisons with α=0.05); note that comparisons were made separately for $\overline{n_{BL}}$, n_{BM} , and $n_{BM} - \overline{n_{BL}}$.

Relative abundance of consumer species

Under the frequent external dispersal, the distribution of relative abundance among consumer species did not differ regardless of the presence or absence of internal dispersal or the scale of observation (Fig. 7a, c, e, g). In all these cases, a mode was found at the 10-20% relative abundance category. In one of the seven species pools used, consumer communities were dominated by a single species, and this species contributed to the 90-100% category in the relative abundance distribution (Fig. 7a, c, e, g).

Under the infrequent external dispersal, the abundance distribution showed different patterns depending on the scale of observation (Fig. 7b vs. f, and d vs. h), but only slightly on the presence or absence of internal dispersal (Fig. 7b vs. d, and f vs. h):

At the local community scale, 49% of consumer communities were dominated by a single species, and 34% of them contained no species. As a result, the relative abundance distribution showed, on average, a nearly complete dominance by a single species (Fig. 7f, h), leading to the low species richness at this scale (Q in Fig. 6a, b).

At the metacommunity scale (Fig. 7b, d), only a small proportion of replicates (10%) consisted of a single species, and even fewer replicates (3%) had no species, resulting in the presence of more subordinate species at this scale. The contrast between the two scales of observation arose because different dominant species tended to occupy different local communities within a given metacommunity, as reflected in $n_{CM} - \overline{n_{CL}}$ (X in Fig. 6c, d). Consequently, more species were found in lower relative abundance categories at the metacommunity scale (Fig. 7b, d) than at the local community scale (Fig. 7f, h).

Discussion

The simulation results show that the effect of external dispersal on species diversity can depend on the presence or absence of internal dispersal. Although effects of external dispersal on the dynamics of community assembly have been recognized (Lockwood et al. 1997), this study is, to my knowledge, the first to demonstrate that it can interact with internal dispersal to affect species diversity in the presence of local species interactions. For example, the magnitude of the change in basal species richness in local communities, $\overline{n_{BL}}$, between frequent and infrequent external dispersal was greater when internal dispersal was absent (P vs. R in Fig. 4a) than in its presence (P vs. Q in Fig. 4b). Moreover, patterns in basal species richness in metacommunities, n_{BM}, show that even the direction of the effect of external dispersal can depend on internal dispersal (AB and A Fig. 4a vs. AB and B in Fig. 4b). These effects may reflect either a qualitative or quantitative difference between the two types of dispersal. It may have been only quantitative on $\overline{n_{BL}}$. That is, to local communities, both types of dispersal supplied species from outside of the system, so their effects may have been additive. However, the difference must have been qualitative on n_{BM}. External dispersal, which supplied species from outside of metacommunities, is qualitatively different from internal dispersal, which caused mixing of individuals inside the metacommunity.

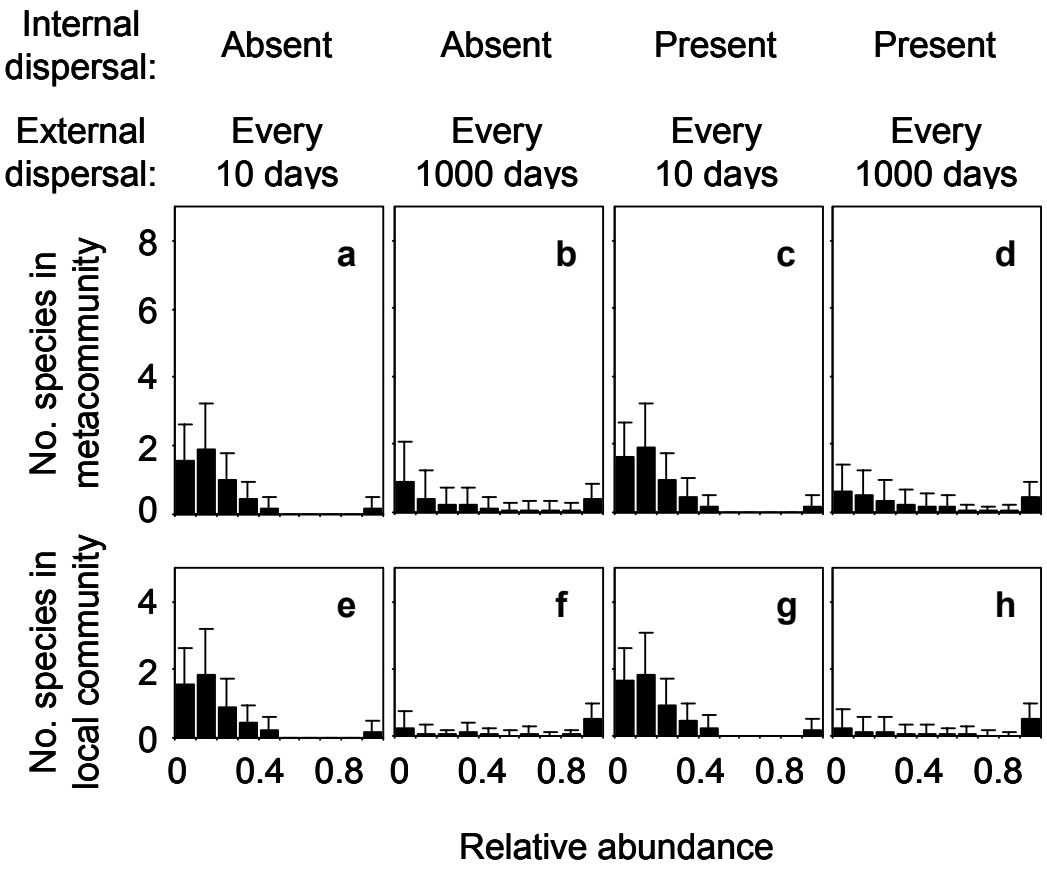


Figure 7. Distribution of relative abundance among consumer species in local communities and metacommunities at the end of the simulations. Bars are as in Fig. 5.

The results also show that the effect of internal and external dispersal depends on the scale of observation. For example, as discussed above, the magnitude and direction of the effect of external dispersal on basal species richness depended on whether richness was measured at the local community or metacommunity scale (Fig. 4a, b). Intriguingly, external and internal dispersal interacted with each other to affect not just $\overline{n_{BL}}$ and n_{BM} (Fig. 4a, b), but also between-local community species diversity, $n_{BM} - \overline{n_{BL}}$ (Fig. 4c, d). Thus, the results demonstrate that external and internal dispersal can jointly regulate the level of historical contingency (Levin 1974, Hastings 1980,Wilson 1992, Lockwood et al. 1997) in determining species diversity. Because no environmental heterogeneity was assumed in this study, random variation in dispersal sequence was the only source of variation in local community structure within a metacommunity.

The results further indicate that whether external dispersal interacts with internal dispersal may depend on the trophic level at which species diversity is observed. Internal dispersal mattered for basal species richness (Fig. 4), but not for consumer species richness (Fig. 6). Similarly, the scale of observation mattered more for basal species richness (both the magnitude and directions were affected by the scale of observation) than for consumer species richness (only the magnitude was affected). However, it should be noted that the observed difference between the trophic levels may not reflect anything about trophic level itself, but merely the difference in internal dispersal rate between the trophic levels. The abundance of consumer species was considerably lower than that of basal species throughout the simulations (Figs. 2 and 3), which may have been responsible for the difference in diversity patterns between the two.

Conversely, interactive effects of external and internal dispersal also mean that the effect of internal dispersal depends on the rate of external dispersal. For example, internal dispersal affected basal species richness only when external dispersal was infrequent (Fig. 4). Further, only when external dispersal was infrequent did the direction of the effect of internal dispersal differ between the local-community and metacommunity scales. This contrast was caused by the joint regulation of the importance of historical contingency by external and internal dispersal.

Morton and Law (1997) and this study differ in the number of the end states to which local communities tended given a species pool. In Morton and Law (1997), local communities converged to a single end state regardless of variation in dispersal sequence. In this study, local communities did not converge to a single state under infrequent external dispersal, though they did under frequent external dispersal (Figs. 4c, d and 6c, d). Because I used a method of assigning b_i and a_{ij} values similar to Morton and Law's, this difference warrants explanation. Two of the more likely reasons concern the size of species pool and the rate of external dispersal.

Species pools were larger in this study (m = 40) than in Morton and Law (1997) (m = 5, 10, 15, or 20). Law and Morton (1993) predicted that alternative end states of local communities become more probable as the number of interactions among species increases. With everything else held constant, the total number of species interactions in a community and the average number of species interactions per species are positively correlated with the size of species pool. Therefore, the difference in pool size may be a reason for the difference in the number of end states.

The rate of external dispersal was assumed to be infinitely small in Morton and Law (1997), whereas it was once in every 10 or 1000 days in this study. Population dynamics suggest that it often took longer than 1000 days for populations to reach equilibrium (Figs. 2 and 3). Therefore, local communities were frequently receiving species before they entered into equilibrium in this study, whereas they were forced always to reach equilibrium before each species introduction occurred in Morton and Law (1997). It is therefore conceivable that the difference was partly caused by this difference in dispersal rate (Law and Morton 1993: 1358, 1996: 771, Lockwood et al. 1997, Warren et al. 2003). Interestingly, the two studies taken together may suggest that between-community diversity generated and maintained by variation in dispersal history ($n_{BM} - \overline{n_{BL}}$ and $n_{CM} - \overline{n_{CL}}$) is greatest at an intermediate rate of external dispersal. This possibility seems worthy of further investigation.

The difference is unlikely to be an artifact. It may be argued that it has to do with how species composition is determined. Morton and Law used the permanence criterion except for the rare cases in which the criterion could not be used and was replaced with numerical integration, whereas this study used numerical integration throughout. However, the numerical integration used in this study can reproduce most of the results presented in Morton and Law (1997), at least qualitatively, when lower dispersal rates than used here are used (T. F., unpublished data). Therefore, the difference is unlikely to be a mathematical artifact caused by errors in numerical integration or the extinction threshold arbitrarily set in this study (Law and Morton 1993: 1358, 1996: 771). It may also be argued that the assembly process of local communities was not given enough time to reach equilibrium in this study, whereas it was in Morton and Law (1997). However, I simulated the assembly for up to two million days, during which species introductions from the species pool were attempted 2×10^5 or 2×10^3 times (see *Termination of simulations* in Methods). Two million days, or approximately 5,500 years, did appear sufficient for community dynamics to reach equilibrium (which could be a stable point or a more complex attractor) (Figs. 2 and 3). Even if it were not sufficient, given this unusually long period for an ecological process, it would appear that the transient dynamics were so long as to be indistinguishable from equilibrium. Recent theory shows that transient dynamics of models where there are no stable persistent solutions are a reasonable explanation of persistence, changing the role of transient dynamics from minor to central in understanding natural systems (Hastings 2001).

This study is only a first step to explore joint effects of external and internal dispersal on species diversity. Many related issues remain to be examined. For example, the manner in which dispersal was simulated in this study may be a rather restricted representation of what can occur in natural systems. Specifically, the implicit assumption that species have an equal chance of being chosen as the immigrant from the species pool may not apply to real-world situations where species vary considerably in their dispersal ability, regional abundance, or both. Here, I used this conventional assumption for simplicity and to make results from this study comparable to those of prior studies on community assembly (e.g., Post and Pimm 1983, Drake 1990, Morton and Law 1997, Lockwood et al. 1997). Similarly, the rate of internal dispersal may vary more greatly, or less, among species than was assumed in this study. These assumptions can be relaxed in future research to examine the sensitivity of the results presented here to them.

Another simplifying assumption of this study is the deliberate omission of environmental heterogeneity to focus on the role of dispersal. Many prior studies have shown that heterogeneity both in space (see, e.g., Tilman and Pacala 1993, McLaughlin and Roughgarden 1993, Amarasekare and Nisbet 2001, Snyder and Chesson 2003) and time (see, e.g., Chesson 1994, 2000, Holt and Barfield 2003) can alter the role of internal dispersal in species coexistence. It remains to be seen to what extent dispersal alters this interaction between internal dispersal and environmental heterogeneity. Likewise, there is a long history of internal-dispersal research on the role that various tradeoffs in species' traits and their interaction with environmental heterogeneity play in maintaining species diversity. Examples include tradeoffs between colonization ability, competitive ability, reproductive rate, and predation resistance (see, e.g., Levins and Culver 1971, Amarasekare and Nisbet 2001, Kisdi and Geritz 2003, Kondoh 2003). Impacts of external dispersal on the role of these tradeoffs are another unexplored important issue. Conversely, it would also be interesting to examine whether the assembly of local communities and metacommunities by random internal and external dispersal leads to inverse relations between these traits among species coexisting in the communities and whether the relations vary with spatial scale.

One possible reason for the paucity of prior studies that incorporate external dispersal into internal-dispersal models is the view that "nothing is learned about diversity maintenance beginning with the assumption that migration rates into local areas are constant (Chesson 2000: 344)." Researchers who hold this view argue that treating external dispersal as an explanation of species coexistence is circular; it merely transfers the problem of the maintenance of diversity to the species pool (Loreau and Mouquet 1999: 437). Consequently, for understanding species diversity, "the area addressed must be large enough that population dynamics within the area are not too greatly affected by migration across its boundary (Chesson 2000: 344)." This argument is important for theoretical understanding of species coexistence. However, many practical questions that ecologists face today, especially from conservation perspectives, concern explanations of species diversity in a limited area that does not meet the assumption of no significant immigration across its boundary (Lockwood 1997, Mack et al. 2000, Young et al. 2000). At a time when anthropogenic biological invasions is a pervasive problem at the global scale (Vitousek et al. 1997), the smallest and only scale that satisfies the above assumption could be the scale of the whole planet. By contrast, ecologists are frequently interested in explaining species diversity at much smaller scales as well. For this reason and because of the interactive effects suggested here, external dispersal can be as useful as a determinant of species diversity as internal dispersal is.

In conclusion, this study has shown that the effects of internal dispersal on species diversity can crucially depend on external dispersal, and vice versa. The two types of dispersal reciprocally provide the context in which each influences species diversity. Furthermore, the magnitude and direction of their interactive effects can depend on the scale of observation, i.e., local communities vs. metacommunities. In the simulations, this scale dependence of diversity patterns resulted because internal and external dispersal interactively determined the extent to which variation in dispersal history translated into variation in species composition among local communities. In a way, this study complements Gotelli (1991, Gotelli and Kelley 1993) by extending the model of single-species metapopulations to multiple-species metacommunities. Unifying

the two types of dispersal in a coherent framework of species diversity remains a rewarding challenge for both basic and applied ecology.

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Part 5

Species pool size and community assembly history: implications for relating and partitioning species diversity at multiple spatial scales

Abstract

Many ecological variables have been invoked to explain the relationships and partitioning of species diversity at multiple spatial scales. However, implications of a potentially important process, community assembly, remain largely unexplored. Community assembly is defined here as the construction and maintenance of local communities and metacommunities by sequential dispersal of potential colonists from an external species pool. I examined the effect of community assembly in generating multi-scale diversity patterns using a simulation model in a gradient of species pool size. The simulation results show that, depending on dispersal rate and trophic level, community assembly can interact with species pool size to affect not only local species diversity, but also among-community variation in species composition. Specifically, the among-community diversity maintained by assembly can increase linearly with species pool size, while local species richness becomes decoupled from pool size. This result has two implications for multi-scale patterns in diversity. First, community assembly may explain scale-dependent relationships between local and regional species diversity; the relationship can be curvilinear at the scale of the local community, while, at the same time, being linear at the scale of the metacommunity. Second, community assembly can affect the partitioning of γ-diversity into α- and β-diversity; the relative contribution of β-diversity created by assembly increases considerably with species pool size, especially when dispersal rate is low. Overall, these results demonstrate previously overlooked interactive effects of species pool size and community assembly on the relationship and partitioning of species diversity at multiple scales.

Introduction

Species diversity is a result of various processes operating at multiple spatial scales (Ricklefs and Schluter 1993). The relative importance of these processes operating at different scales has been a central subject of ecological and evolutionary research, especially during the past decade. One popular approach to examining the relative importance of local versus regional 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) and Hillebrand and Blenckner (2002). 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 arose 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 for local-regional plots to be useful for detecting species saturation (Westoby 1998, Huston 1999, Rosenzweig and Ziv 1999, Loreau 2000, Godfray and Lawton 2001). Consequently, Loreau (2000), among others, forcibly argued that the use

of local-regional plots to infer the relative importance of local and regional processes is no longer warranted. 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 revival of an old one (e.g., Whittaker 1972) that has received little attention until it was recently given new conceptual importance (Veech et al. 2002). The question in its new context has already proven useful in some recent empirical studies (Fourier and Loreau 2001, Gering and Crist 2002).

A number of variables have been linked to how diversities at multiple scales are related to one another, from species interactions to environmental heterogeneity, to dispersal, and to speciation. Despite this near complete coverage of variables examined, one potentially important issue, the process of community assembly, has not been explicitly considered in relation to multi-scale diversity patterns (but see Morton and Law 1997). Here I define community assembly as the construction and maintenance of local communities through partly stochastic sequential dispersal of potential colonists from an external species pool (Drake 1990, Warren et al. 2003). A key feature of community assembly is the stochastic nature of dispersal history, reflected in variation in the sequence and timing of dispersal. It is well established that assembly history can in some cases greatly affect species diversity in local communities (Drake 1990, 1991). If this sequence effect interacts with the size of species pool to influence local species diversity, community assembly can have important implications for understanding diversity at multiple scales (Wilson 1992). In practice, however, ecologists usually have to regard the dynamics of community assembly as a black box, because it is difficult to reconstruct in specific detail. For example, in previous studies that used local-regional plots, local scale was often defined so broadly that it most likely contained multiple local communities that were each undergoing community assembly (e.g., Caley and Schluter 1997, Bini et al. 2000).

In this paper, I examine the role of community assembly in producing multi-scale diversity patterns. I do this by modeling the assembly of local communities and metacommunities that are structured by competition and predation. The model used here is based on general Lotka-Volterra systems that have been extensively used for studying community assembly. The model is, however, different from most prior models of community assembly in one important respect: it assembles not only local communities, but also metacommunities, through dispersal of species both from the species pool and among local communities (Fig. 1, see Drake 1990, Wilson 1992 for similar approaches). Hence, in the simulations, there were three ecologically distinct spatial scales at which species diversity could be measured: local community, metacommunity, and external species pool.

Methods

I modeled the assembly of local communities and metacommunities with independently created replicates of species pools of differing size. In each simulation, each local community was assembled through dispersal of species from a common

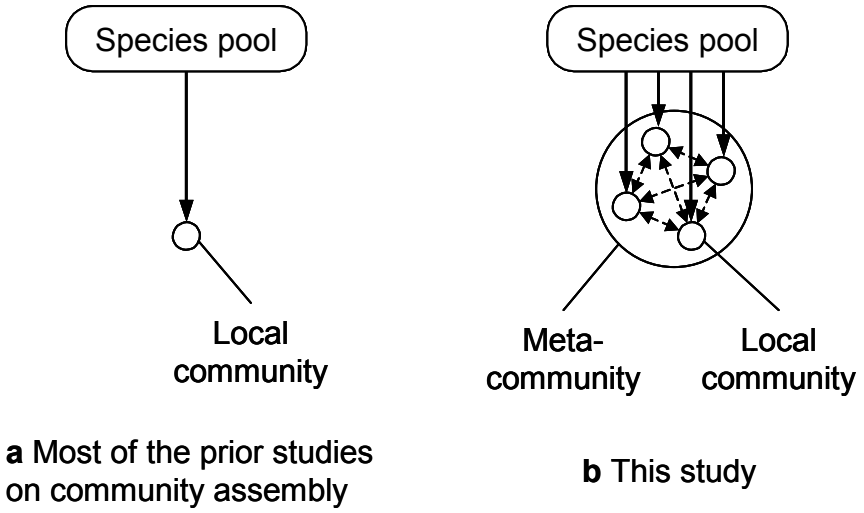


Figure 1. Schematic representation of models of community assembly. Solid and dashed arrows show external and internal dispersal, respectively

species pool (hereafter called external dispersal) and dispersal of species among local communities within the metacommunity (hereafter called internal dispersal) (Fig. 1b). Spatial and temporal heterogeneity of abiotic variables across local communities is deliberately omitted from the model, not because heterogeneity is absent in natural systems, but because removing it allows one to focus on the effects of assembly history. In total, I assembled 340 local communities, i.e., 17 independently created species pools x 2 rates of external dispersal x 2 rates of internal dispersal x 5 local communities within each metacommunity. Below I first describe how I constructed the species pools from which to assemble local communities and metacommunities. Next, I explain how I manipulated the size of species pool and how I simulated, under each pool size, external and internal dispersal and local community dynamics. Lastly, I explain the statistical analyses performed.

Construction of species pools

I assumed that the dynamics of populations within each local community constructed from the same species pool are governed by general Lotka-Volterra equations defining population growths and intra- and inter-specific interactions:

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

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 they disperse to local communities.

I used 17 species pools, each of which was created independently using a method similar to that of Law and Morton (1996: 775) and Morton and Law (1997: 323-325). Morton and Law's method remains a biologically sound one for modeling community assembly. Most other assembly models have been based on an assumption that is not empirically realistic, though argued to be a starting point to investigate general properties of Lotka-Volterra and other systems in the absence of reliable empirical data at the time. Namely, they assumed that the intrinsic rates of growth, b_i's, and the strength of interactions among species, a_{ij}'s, are distributed uniform randomly (Post and Pimm 1983, Case 1990, Drake 1990, Lockwood et al. 1997, Lundberg et al. 2000, Wilmers et al. 2002). Values assigned this way are inconsistent with the recent finding that, in natural communities, most interactions are weak and only a small fraction of them are strong (Paine 1992, Berlow et al. 1999, McCann 2000, but see Abrams 2001, Sala and Graham 2002). Of course, this fact does not weaken the heuristic importance of these prior assembly studies. Nonetheless, the b_i and a_{ij} values used in them are in sharp contrast with those created by Morton and Law's (1997) empirically derived method, which gives values more consistent with the likely presence of many weak and a few strong interactions in natural communities (see also Huisman et al. 2001). Below I explain the method used in this study by modifying Morton and Law's method.

Number of species – The set of m species that constitute a given species pool are divided into m_1 basal species and m_2 consumer species. A basal species is able to grow in

the absence of any other species from the species pool and does not eat other species from the pool. A consumer species eats some of the other species from the pool and cannot sustain its population in local communities without them.

Assigning body sizes – The method begins with assigning a body size, s_i, to each species i in the species pool. The logarithm of body size of species i, $\log_{10}(s_i)$, is drawn at random from a uniform distribution over the range [-2, -1] for basal species and [-1, 1] for consumer species. Here, the unit for s_i is g. It is assumed that, if $s_i < s_j$, then species i may be eaten by species j, but not vise versa.

Assigning a_{ij} *between consumers and victims* – The strength of the interaction between a consumer and a victim is determined based on the assumption of 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 is given as:

$$\begin{aligned} \overline{a_{ij}} &= -0.1 * \exp\left\{-\left(\log_{10}\left(10 * s_i / s_j\right) * c_1\right)^2\right\} && s_i < s_j \\ a_{ij} &= 0 && s_i \geq s_j . \end{aligned} \qquad (2)$$

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, 10. 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 is given as:

$$\begin{aligned} \overline{a_{ji}} &= -\overline{a_{ij}} * c_2 * s_i / s_j && s_i < s_j \\ a_{ij} &= 0 && s_i \geq s_j . \end{aligned} \qquad (3)$$

The parameter c_2 measures conversion efficiency. I use $c_1 = 0.05$, which lies within the biologically feasible range (Humphreys 1979). Note that, with this method of defining consumer-victim interactions, not only basal species, but also consumer species, i.e., those from m_2 species, can be victims of other consumer species, depending on their body size.

Assigning a_{ij} *between basal species* – The method assumes an upper limit to total biomass, or the carrying capacity K_i, of basal species within a local community. Assuming that the limit, K_i, is 100 biomass units for each basal species i, the self-limitation term for basal species i is:

$$\overline{a_{ii}} = -b_i * s_i / 100 . \qquad (4)$$

(In Morton and Law [1997: 324], the corresponding equation, their equation 5, does not have the negative sign, most likely owing to a typographical error.) 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:

$$\overline{a_{ij}} = -c_3 * b_i * s_j / 100 . \quad (5)$$

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 used $c_3 = 0.9$, as in Morton and Law (1997). Consumers are limited only by victim density, and their self-limitation term is zero.

Assigning b_i – Based on an empirical relationship between body size and the per capita intrinsic rate of increase, b_i, of basal species (Fenchel 1974, Blueweiss et al. 1978), it is assumed that:

$$\log_{10} \overline{b_i} = -1 - 0.25 * \log_{10} s_i . \quad (6)$$

Here, units are d^{-1} for b_i and g for s_i. It is less clear how b_i of consumers should be scaled with body size. Following Morton and Law (1997), I assume it is constant, with units of d^{-1}:

$$\overline{b_i} = -0.1 . \quad (7)$$

Allowing random variation around means – The above ecological parameters, a_{ij} and b_i, are unlikely to be determined solely by body size. Morton and Law (1997) assume that there are random variables with mean values set by equations 2 to 7, and I follow this approach. Thus, if $\overline{p}$ = the mean value of a given parameter from equations 2 to 7, the parameter p itself is taken as a random variable from a normal distribution $N\left(\overline{p}, 0.1 * \overline{p}\right)$, with the distribution truncated to ensure that p has the same sign as $\overline{p}$.

Manipulation of the number of species in species pools

I used a gradient of species pool size with a total of 17 pools each consisting of an equal number of basal and consumer species. The smallest species pool used contained m_1 =2 and m_2 =2 species, and the largest m_1 =50 and m_2 =50 species. Every species pool was independently created to avoid pseudo-replication (Srivastava 1999, Fox et al. 2000). However, the results presented in this paper qualitatively hold for pool size gradients that are created as follows: first make the largest species 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 (T.F., unpublished data).

Assembly of local communities and metacommunities

External dispersal – I initiated the simulations by randomly choosing, for each local community in the metacommunity, a species from the species pool and simultaneously introducing it to the corresponding local community (i.e., external dispersal). If the first species for a given local community were a basal species, the population would start to grow according to the Lotka-Volterra equations (equations 1). If the first species were a consumer species, its population would start to decline according, again, to the Lotka-Volterra equations. When a predetermined period of time had passed since the first species introduction, a second species was chosen randomly

from the species pool for each local community and introduced to the corresponding community. This process of dispersal from the species pool was repeated for a million days. For each species pool, I used two rates of external dispersal: once in 10 days and once in 100 days. Invading species were introduced with a low abundance (x_{ik} = 1.0 x 10^{-3}). This initial abundance is significantly low relative to the mean carrying capacity of a basal species in a local community, which could range between 9.09 x 10^3 (i.e., 100 biomass units divided by the maximum body size possible = 100/(0.1x1.1)) and 1.11 x 10^4 (i.e., 100 biomass units divided by the minimum body size possible = 100/(0.01x0.9)). In keeping with the methods in pervious assembly modeling (e.g., Law and Morton 1996, Morton and Law 1997), the species already present at a given time in a given local community were not allowed to be chosen as the newly invading species for that community at that time.

Internal dispersal – Species in local communities were also allowed to disperse among the local communities within a metacommunity (i.e., internal dispersal). Once in 10 days, total abundance summed across the five local communities in the metacommunity was measured for each species present in the metacommunity. For each species and for each local community, whether the species disperses to the community was determined probabilistically as a linear function of its total abundance in the metacommunity. For basal species, the dispersal probability was set so that a species that had the maximum total abundance possible would have a dispersal probability of 1. The maximum total abundance possible was calculated as follows: the number of local communities in a metacommunity (5) x the maximum biomass units possible in a local community (100) / the minimum body size possible (0.01 x 0.9) = 5.556 x 10^4. For consumer species, the dispersal probability was set out so that a species that had 5 % of the maximum total abundance possible for basal species would have a dispersal probability of 1. Placing the 5 % (same as the value of conversion efficiency, c_2) here was done on the assumption that consumers should tend to be better able to disperse between local communities than basal species do, so that consumers can efficiently forage basal species within a metacommunity. Species dispersing among local communities were introduced to the target communities with the same abundance as for those dispersing from the species pool (x_{ik} = 1.0 x 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 probability specified above.

Local community dynamics – Throughout the simulation, the abundance of each species in each local community was calculated by numerically integrating the Lotka-Volterra equations (equations 1) using the commercially available algorithm, "d02ejc" (Numerical Algorithm Group 2002), which implements Backward Differentiation Formulae (see Hall and Watt 1976). This method more accurately tracks population dynamics than do other methods used in earlier assembly studies, including those based on 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 for more detailed discussion on these important technical issues). Species went extinct if their abundance fell below a threshold, x_{ik} = 1.0 x 10^{-3}, which is the same as the initial density of dispersing species (see above).

Measures of species richness and invasion resistance

For each metacommunity replicate, the following six measures of species diversity and relative abundance were obtained at the end of the simulation, i.e., a million days after the first species introduction: (1) mean number of basal species in a local community, averaged over the four local communities in the metacommunity, (2) number of basal species in the metacommunity, (3) basal species richness found among the local communities (i.e., (3) equals (2)-(1)), (4) mean number of consumer species in a local community, averaged over the five local communities in the metacommunity, (5) number of consumer species in the metacommunity, (6) consumer species richness found among the local communities (i.e., (6) equals (5)-(4)). Additionally, for each metacommunity at the end of the simulation, I also determined the mean number of potentially colonizing species. This measure of invasion resistance was the number of species absent from a local community, but present in the species pool, which would remain in the local community after a certain time interval (1.0×10^3 days) had passed if they were introduced to the community, averaged over the five local communities in the metacommunity. Thus, the greater this number is, the less resistant the local communities are to invasion by species in the pool. Obtaining species richness and invasion resistance separately for basal and consumer species allowed clearer ecological interpretation of patterns in species diversity. Although these measures were examined only at a single time, they constitute a result of long-term community dynamics, for a million days. Equally importantly, the robustness, both in statistical and ecological senses, of the results from this single point was ensured by a relatively large number of data points, with a total of 17 independently created species pools. Finally, the same results can be obtained by using overlapping species pools, as described above.

Statistical analyses

I used simple linear regressions to examine the relationships between the size of species pool and each of the above measures of species richness and invasion resistance, with the former as the independent variable and the latter as the dependent variable. I examined curvilinearity of each of these 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. If there was not a significant relation, I concluded that the relationship was flat. All statistical analyses were conducted using the software SYSTAT version 10 (SPSS 2000).

Some limitations exist with this method of examining significant relationships. A quadratic function can result in a prediction of an unrealistic decrease in species richness with species pool size. However, the significance of the inclusion of the quadratic term provides a convenient statistical test for curvilinearity (Shurin et al. 2000). A quadratic function also has the assumption that the independent variable, species pool size, is measured without error, which is not met by field data. In these cases, the slope of log-log regressions can be a better index to test for curvilinearity (Hillebrand and

Blenckner 2002). However, this assumption is met in the simulations conducted in this study.

Results

Community dynamics

Visual inspection of temporal changes in species richness in several replicates of metacommunities indicated that the communities had reached equilibrium in terms of species richness when the simulations were terminated (Figs. 2 and 3). Under the infrequent external dispersal (once in 100 days), indications of equilibrium were not clear; with large species pools, local communities and metacommunities continued to fluctuate widely in species richness throughout the course of the simulation (Fig. 2). However, there were no overall trends of increase or decrease in species richness over time. Under the frequent external dispersal (once in 10 days), local communities converged to a similar state in terms of species richness by the time the simulations were terminated (Fig. 3).

Species richness and invasion resistance under infrequent external dispersal

In basal species, species richness in metacommunities increased linearly with the size of species pool (Fig. 4a, Table 1). In contrast, species richness in local communities increased curvilinearly with it (Fig. 4b, Table 1). Species richness found among local communities increased linearly with pool size, starting from the pool containing 14 species (Fig. 4c, Table 1). With the pools smaller than this, local communities showed convergence leading to no among-community diversity. Similarly, the number of potentially colonizing species also increased linearly with pool size (Fig. 4d, Table 1).

In consumer species, species richness did not show any significant relations with pool size (Fig. 4e-g, Table 1), although the number of potential colonizers increased linearly with pool size (Fig. 4h, Table 1).

Species richness and invasion resistance under frequent external dispersal

In basal species, species richness in both local communities and metacommunities increased linearly with the size of species pool (Fig. 5a, b, Table 2). Species richness found among local communities was zero or near zero regardless of pool size and did not show a significant relation with it (Fig. 5c, Table 2). The number of potential colonizers was also zero in most cases regardless of pool size, although the regression analysis found a significant linear relation (Fig. 5d, Table 2).

In consumer species, species richness in both local communities and metacommunities increased curvilinearly with the size of species pool (Fig. 5e, f, Table 2). However, the model selection was ambiguous: the linear regressions (adjusted R^2 = 0.857 and 0.847 for local communities and metacommunities, respectively) explained the relationships almost as well as did the quadratic regressions (adjusted R^2 = 0.883 and 0.874) (Table 2). Species richness and the number of potential colonizers showed the same trend as in basal species richness: they were zero or near zero regardless of pool

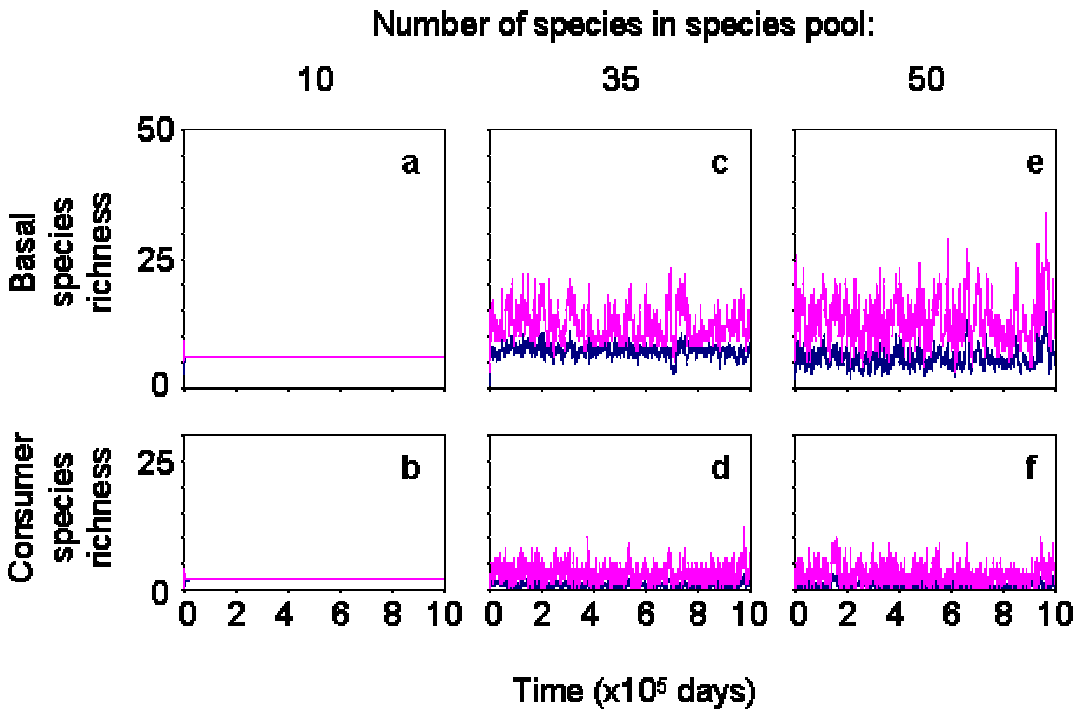


Figure 2. Representative examples of community dynamics in the simulations under infrequent external dispersal (once in 100 days). For each panel, red and blue lines represent species richness in metacommunities and in local communities, respectively. Because red lines are drawn on top of blue lines, blue lines are hidden when the two overlap. Results in a and b, in c and d, and in e and f are each from the same simulation.

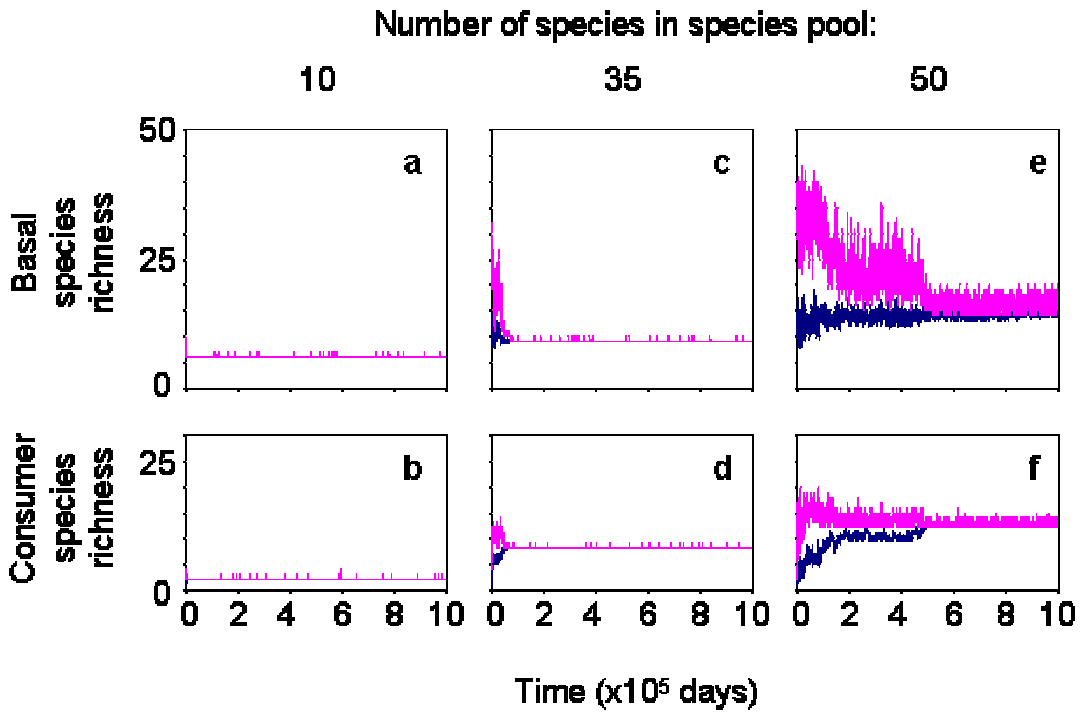


Figure 3. Representative examples of community dynamics in the simulations under frequent external dispersal (once in 10 days). Red and blue lines are as in Fig. 2. Results in a and b, in c and d, and in e and f are each from the same simulation. For each pair, the same species pool was used as in the corresponding pair in Fig. 2.

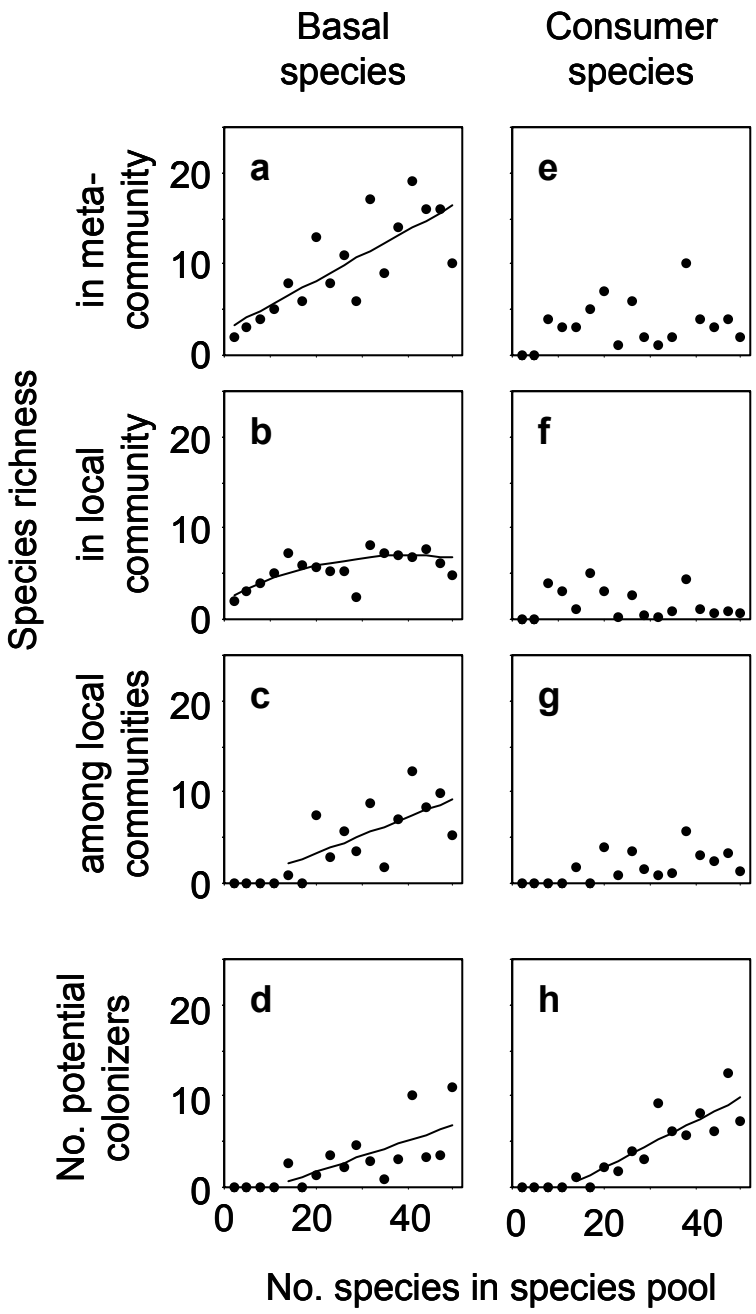


Figure 4. Relationships between species pool size and species richness (a-c and e-g) and invasion resistance (d and h) under infrequent external dispersal (once in 100 days). Data are fitted to regression models where significant (Table 1). Note that species pool size is the number of basal (a-d) or consumer (e-h) species only; species pools also had equal numbers of basal or consumer species.

Table 1. Regression equations under frequent dispersal, corresponding to data presented in Fig. 4.

Dependent variable	Model	Regression parameter estimates (*P* values) *a*	*b*	*c*	Adj. R^2
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
Species richness found among local communities	**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
Species richness found among local communities	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

Notes: 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 shown in bold. The range of X used was 2-50 for species richness in local communities and metacommunities and 14-50 for species richness found among local communities and the number of potential colonizers. See Methods for model selection method.

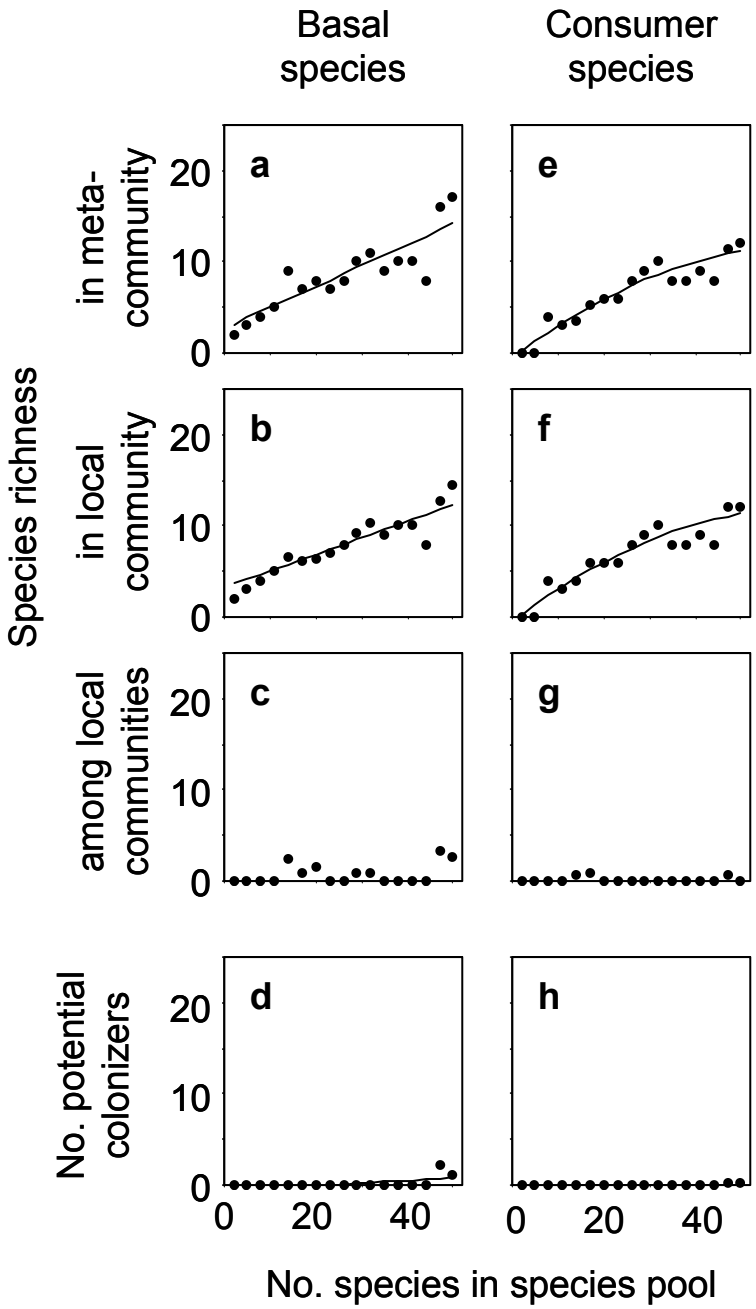


Figure 5. Relationships between species pool size and species richness (a-c and e-g) and invasion resistance (d and h) under frequent external dispersal (once in 10 days). Data are fitted to regression models where significant (Table 2). Note that species pool size is the number of basal (a-d) or consumer (e-h) species only; species pools also had equal numbers of basal or consumer species.

Table 2. Regression equations under frequent dispersal, corresponding to data presented in Fig. 5.

Dependent variable	Model	Regression parameter estimates (*P* values) *a*	*b*	*c*	Adj. R^2
Basal species					
Species richness in local communities	**Linear**	2.472 (0.001)	0.203 (0.000)		0.867
	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
Species richness found among local communities	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
Species richness found among local communities	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

Notes: All notes for Table 1 apply.

size (Fig. 5g, h, Table 2).

Effect of internal dispersal rate

The above results are for one of the two rates of internal dispersal used, i.e., potential dispersal once in 10 days. The results qualitatively hold for the other rate, i.e., potential dispersal once in 100 days (data not shown). Thus, there were no significant effects of the rate of internal dispersal.

Discussion

The simulation results show that, depending on dispersal rate (e.g., Fig. 4c vs. 5c) and trophic level (e.g., Fig. 4c vs. 4g), the role of assembly history in producing among-community variation in species composition becomes increasingly important with the size of the species pool (Fig. 4c). This result has implications for both relating and partitioning species diversity at multiple scales. Below I discuss these implications by highlighting relevant parts of the simulation results.

Implications for relating species diversity at multiple scales

The results for basal species richness under infrequent dispersal (Fig. 4a-d) show that local-regional richness relationships can be linear with no limit to local richness at the scale of the metacommunity (Fig. 4a), while, at the same time, they can be strongly curvilinear with a clear asymptote at the local community scale (Fig. 4b). This scale-dependence of the local-regional richness relationships was caused by the linear increase in the among-community diversity with species pool size (Fig. 4c). Community dynamics suggest that species richness in local communities continued to fluctuate throughout the simulations, which lasted for a million days (Fig. 2). Therefore, in this study, among-community diversity was not a result of different local communities within a metacommunity each assuming alternative stable states (Lewontin 1969, Sutherland 1974, Drake 1990, Law and Morton 1993). Local communities did not reach a stable point with a fixed species composition. Instead, they experienced continuous species turnover. Results for invasion resistance suggest that, when communities went through this turnover, the number of states that a local community could enter at the next time step increased linearly with the size of the species pool (Fig. 4d, h). This linear increase resulted in a linear local-regional relationship at the metacommunity scale (Fig. 4a), despite the leveling off of increase in species richness at the local-community scale (Fig. 4b).

These results highlight the importance of considering community assembly for understanding species richness and saturation. Assembly dynamics make communities appear unsaturated (Fig. 4a) even when local species interactions strongly limit local species coexistence (Fig. 4b). 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 diversity and automatically creates correlations with regional pool size regardless of the importance of local interactions (Fig. 4a). 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.

I emphasize that community assembly was responsible for both curvilinear and linear relationships. Curvilinear relationships resulted from local species interactions that occurred because species were being continuously introduced from the regional pool through community assembly. Linear relationships resulted from the linear increase in the possible species combinations that local communities could take in the process of community assembly. Without these effects of assembly, local-regional richness patterns would be independent of scale, always showing linear patterns as a simple sampling process, regardless of how local scale is defined.

The results demonstrate that community assembly generates scale-dependent patterns even in the absence of other confounding factors that were previously identified with local-regional plots. For example, the problem of spatio-temporal environmental heterogeneity (Cornell and Lawton 1992, Huston 1999, Loreau 2000) does not apply to the present study, because environmental conditions were homogeneous across all local communities throughout the assembly process (i.e., the same set of constant b_i and a_{ij} values governed population dynamics in all communities of a given region). 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, the measurement of species richness was based on every species present in communities regardless of their abundance. Second, the basal species' carrying capacity, which ranged from 9.09×10^3 to 1.11×10^4, was several orders of magnitude greater than the extinction threshold, 1.0×10^{-3}. Selection of comparable communities, effects of differing region size (Srivastava 1999, Ricklefs 2000, Shurin et al. 2000), and pseudo-replication (Srivastava 1999, Fox et al. 2000) are not a problem either, because the regional species pools were created independently and standardized to be comparable (i.e., each pool was created with new values of b_i and a_{ij}).

An additional implication is that the different patterns of species richness between the two external dispersal rates (Fig. 4 vs. 5) apparently contradict the widely accepted view on the effect of dispersal rate on local-regional richness relationships. It is generally thought that local diversity will be shaped mainly by local processes and will thus be decoupled with regional diversity when dispersal rate is high, whereas local diversity will be regulated by regional processes and will therefore closely reflect regional diversity when dispersal rate is low (see, e.g., Shurin 2000: 3074). The latter case is referred to as dispersal limitation. By contrast, in this simulation study, local diversity was decoupled from regional diversity when dispersal rate was low (Fig. 4b, e, f), whereas it more closely reflected regional diversity when dispersal rate was high (Fig. 5b, e, f). Another simulation study of community assembly that used an infinitely low dispersal rate also found that local and regional diversity are decoupled (Morton and Law 1997). Taken together, these results calls for reexamination of the conventional idea on dispersal limitation.

Implications for partitioning species diversity at multiple scales

The results suggest that community assembly also has implications for how regional species diversity (γ-diversity) is spatially partitioned into within- (α-diversity)

and between- (β-diversity) community components (Loreau 2000, Veech et al. 2002). There is no a priori rule to determine the scales at which these diversity components are 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 community assembly processes, the appropriate way to assign the diversity components is as follows: species richness in local communities as α-diversity, species richness in metacommunities as γ-diversity, and species richness found among local communities as β-diversity. In this case, it is convenient to draw the relationships between species pool size and local-community richness (e.g., Fig. 4a) and between species pool size and metacommunity richness (e.g., Fig. 4b) on the same graph (e.g., Fig. 6a). Further, the partitioning of γ-diversity into α- and β-diversity can be more directly visualized with the percentages of γ-diversity contributed by them (e.g., Fig. 6b).

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

These results are novel because questions addressed by most community assembly studies have previously been limited to local scales (see Samuels and Drake 1997, Law 1999 for reviews). Community assembly has rarely been investigated as a regulator of between-community diversity (but see Wilson 1992, Drake et al. 1993, Lockwood et al. 1997). It is, instead, environmental heterogeneity among local sites that has been treated as the main regulator of between-community 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 owing to environmental heterogeneity (see also Veech et al. 2002 for a historical perspective). It may also be because the effects of community assembly and environmental heterogeneity are hard to differentiate from each other in practice, which has resulted in lively discussions among ecologists (e.g., Connor and Simberloff 1979, Connell and Sousa 1983, Gilpin and Diamond 1984, Petersen 1984, Sutherland 1990, Grover and Lawton 1994). Whatever the reasons may be, the results suggest that future research on species diversity will benefit from considering the role that community assembly and its interaction with environmental heterogeneity may play in controlling the relative contribution of within- and between-community diversity to regional diversity (Wilson 1992) and ultimately to ecosystem processes as well (Grime 1998, Wardle 1999).

Notes on simulation methods

Past assembly studies that used permanence algorithms predict that, given a regional species pool, most assembly sequences will tend to a very limited number of invasion-resistant endpoints (Morton et al. 1996, Law and Morton 1996, Morton and Law 1997, Law 1999). This prediction apparently contradicts the results reported in this

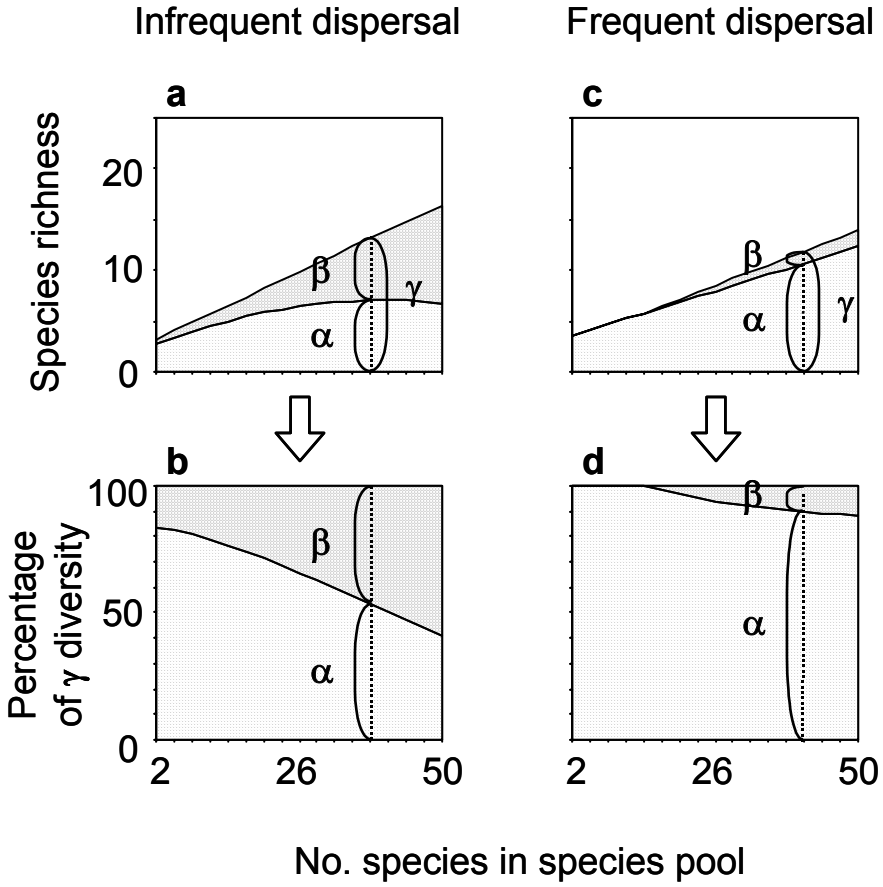


Figure 6. Relationships between α-, β-, and γ-diversity in basal species as a function of species pool size. Here, α-diversity is mean species richness in a local community, β-diversity is species richness found among local communities in a metacommunity, and γ-diversity is species richness in a metacommunity. In a and c, regression lines for species richness in metacommunities (from Fig. 4a and 5a) and in local communities (from Fig. 4b and 4b) are drawn together to show the absolute values of α-, β-, and γ-diversity. In b and d, predicted species richness in local communities (Fig. 4b and 4b) is divided by predicted species richness in metacommunities (Fig. 4a and 5a) to show the relative contributions of α- and β-diversity to γ-diversity.

paper, namely the high divergence in species composition between local communities and the general absence of invasion resistance even after local species richness has reached equilibrium. Because I used a method of constructing species pools similar to that of Law and Morton (1996) and Morton and Law (1997), this apparent contradiction warrants explanation. A most likely explanation concerns dispersal frequency. The permanence algorithm assumes that population dynamics in local communities always reach equilibrium between adjacent dispersal events. However, populations can frequently take a considerably longer time to reach equilibrium than the time allowed between adjacent introductions in this study (T. F., unpublished data). Lockwood et al. (1997) suggested that communities do not become resistant to further invasions, but continue to go through species turnover, if assembled with high dispersal rate. The dynamics observed in this study more closely represent this situation. Another possible explanation is that the results in this study are an artifact owing to unidentified errors with the numerical integration method. However, this is unlikely to be the case. The numerical integration used here can reproduce most of the results in Morton and Law (1997), at least qualitatively, if lower rates of external dispersal than used here are used (T. F., unpublished data).

Future directions

This study suggests some future research directions, both empirical and theoretical. An important direction is to test the predicted scale-sensitive 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 relatively easily 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). Laboratory microcosm experiments (Fox et al. 2000, Fukami and Morin 2003) would also be valuable as they uniquely allow for rigorous control over assembly history (Drake 1991), though in less natural settings.

Theoretically, the way that dispersal was simulated in this study is only one of many that could have been used. For example, dispersal among local communities occurred in a spatially implicit fashion in this study. However, nearest neighbor distances and the species composition and abundance in neighboring communities may be critical to local community structure (Selmi and Boulinier 2001). Also, dispersal ability may correlate with other traits of species, for example, body size, and may therefore vary more greatly among species than assumed in this study (Hillebrand and Blenckner 2002). Moreover, the implicit assumption that species have an equal chance of being chosen as the immigrant from the species pool may not apply to real-world situations where species vary considerably in their dispersal ability, regional abundance, or both. Here, I used this conventional assumption for simplicity and to make results from this study comparable to those of prior studies on community assembly (e.g., Post and Pimm 1983, Drake 1990, Morton and Law 1997, Lockwood et al. 1997). It seems worthwhile to assess the robustness of the results presented here to these possible variations in dispersal mode.

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