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ASSEMBLY HISTORY INTERACTS WITH ECOSYSTEM SIZE TO INFLUENCE SPECIES DIVERSITY

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Abstract. Although species diversity is often correlated with ecosystem size in a consistent manner, mechanistic explanations of when and why diversity is related to size remain elusive. Rarely considered in understanding size–diversity relationships is 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 species diversity. The experiment used a two-way factorial design with four assembly sequences and four ecosystem sizes as treatments. Community dynamics were monitored for about 50–100 generations. The results show that history affected diversity more strongly in smaller ecosystems, presumably owing to greater priority effects. Consequently, history determined when diversity was significantly related to ecosystem size. The results also suggest that long-term transient community dynamics can make assembly history important for community structuring even in the absence of alternative stable states. Because species immigration is essentially stochastic, ecosystem size is variable, and priority effects can be strong in many natural systems, the history × size interaction revealed in this study also has the potential to shape natural size–diversity patterns.

Key words: alternative stable states; area effects; community assembly history; community convergence; ecosystem size; freshwater protists and rotifers; invasion history; microcosms; priority effects; species diversity; transient dynamics.

INTRODUCTION

Species diversity is often correlated with ecosystem size in a consistent manner. For example, the relationship between area and species richness 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 many other factors including disturbance frequency, habitat diversity, extinction rate, speciation rate, and the ratio of edge to interior habitats (Rosenzweig 1995, Gotelli and Graves 1996). The relationship between size and diversity can depend on geographical location (Rosenzweig 1995), trophic rank (Holt et al. 1999), and spatial scale (MacArthur and Wilson 1967, Losos and Schluter 2000, Crawley and Harral 2001), suggesting site-, taxa-, and scale-dependent mechanisms. Moreover, species diversity is not just species richness, but also encompasses species evenness, how the total abundance or biomass of a community is distributed among species (Magurran 1988). Although biodiversity theory has recently begun to unify richness, evenness, and ecosystem size (Hubbell 2001, Olszewski 2004), much remains unclear about how species diversity is related to ecosystem size when both richness and evenness are considered. 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 history of community assembly. Community assembly, which involves the sequential immigration of species from a pool of potential community members, can greatly influence species diversity (Post and Pimm 1983, Drake 1990, Law and Morton 1996). Furthermore, a few studies suggest that the importance of assembly history in community structuring may change with ecosystem size. For example, Drake (1991) showed that assembly history affected community structure more greatly in large aquatic microcosms than in small ones. He postulated that the difference was due to greater habitat heterogeneity in larger systems. However, mainly because assembly history is difficult to manipulate or reconstruct, little is known about how history may regulate relationships between ecosystem size and species diversity. Several experiments have manipulated ecosystem size and assembly history (Dickerson and Robinson 1985, 1986, Drake 1991, Petraitis and Latham 1999, Dudgeon and Petraitis 2001), but their primary purposes were not to examine interactive effects. Most of these studies did not manipulate assembly history directly, did not have a gradient of ecosystem size, or lacked control over habitat quality variables that were likely to be correlated with ecosystem size.

In this study, I conducted a laboratory microcosm experiment with freshwater protists and rotifers to test

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TABLE 1. Introduction sequences and set composition used to assemble communities.

Introduction	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

Note: See Table 2 for species composition of the three sets.

for interactive effects of assembly history and ecosystem size on species diversity. Laboratory microcosms are well suited for this purpose. They allowed rigorous control over assembly history, ecosystem size, and other factors. They also enabled me to monitor long-term community dynamics for about 50–100 generations of the species involved. These advantages of laboratory microcosms come at the sacrifice of a natural context (Carpenter 1996, Morin 1998). However, they are useful for refining the hypotheses to test in more natural, but longer, larger scale, and more expensive field experiments (Lawler 1998, Morin 1998, Cadotte et al. 2004).

METHODS

Microcosms were initially sterile glass containers kept in the laboratory at 20–23°C. Sterilized lids loosely covering the containers minimized contamination and evaporation while allowing sufficient air exchange. I filled the containers with a sterile medium made of 0.55 g of crushed protozoan pellet (Carolina Biological Supply, Burlington, North Carolina, USA) and 0.10 g of Herpetivite powdered vitamin supplement (Rep-Cal Research Labs, Los Gatos, California, USA) per 1.5 L of commercially available spring water (Crystal Springs, Chicago, Illinois, USA). I inoculated the medium with bacteria (*Bacillus subtilis*, *Bacillus cereus*, *Proteus vulgaris*, and *Serratia marcescens*, purchased from Carolina Biological Supply) and, two days later, with unidentified microflagellates and associated bacteria (isolated from ponds in New Brunswick, New Jersey, USA). I distributed the medium to microcosms six days after microflagellate introduction. Bacteria and microflagellates served as food for the protozoa and rotifer species later introduced. The microcosms were semi-continuous batch cultures: I renewed nutrients once a week by gently mixing and homogenizing the medium and then removing and replacing 10% of the volume with fresh sterile medium. Medium replacement occurred four days after each introduction event during the initial phase of the experiment.

Natural history and the knowledge gained through laboratory culturing indicate that all of the protozoa and rotifer species used here can sustain their populations by feeding on bacteria and microflagellates, although one of them, *Euplotes* sp., also eats small ciliates. These species are known to compete with one another for bacteria and microflagellates 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 freshwater habitats in New Brunswick, New Jersey, USA, or purchased from Carolina Biological Supply, and each had been separately cultured for many generations under conditions similar to those of the experiment.

I used a two-way factorial design with four ecosystem sizes and four assembly sequences as treatments. Each of the 16 treatments (four sequences $\times$ four sizes) had five replicates, resulting in 80 microcosms. I manipulated ecosystem size by using containers of four different sizes. The treatments consisted of 5, 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 minimized variation in spatial heterogeneity and oxygen availability across size treatments, as in Dickerson and Robinson (1986), Holyoak and Lawler (1996), Spencer and Warren (1996), Warren (1996), and Holyoak (2000).

I introduced 14 protozoan and rotifer species to the microcosms sequentially according to predetermined schedules, with four sequence treatments (Tables 1 and 2). I used a set of four or five species for each introduction. First, second, and third sets of species were introduced 7, 14, and 21 days after the microflagellate inoculation, respectively. I introduced a small number of individuals compared to the maximum densities realized, but no fewer than 15 individuals per species to reduce trivial extinction by chance. I standardized the initial number of individuals of each species across introduction events by estimating population densities in stock cultures and, if necessary, by diluting them before introductions. I also standardized the age of the stock cultures at the time of introductions: the stock cultures were 12 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 events. The experimental design also standardized the total biomass introduced over time across treatments. This standardization of initial total biomass allowed me to assess interactive

TABLE 2. Set composition used to assemble communities.

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

Note: Rotifers are denoted by ''(r).''

effects of assembly history and ecosystem size in the absence of differences in initial total biomass. In natural systems, however, immigration rate may increase with ecosystem size because of a target effect (Coleman et al. 1982, Lomolino 1990), resulting in greater initial total biomass in larger systems (see also Petraitis and Latham 1999). In the *Results and Discussion* section, I will discuss implications of such differential immigration rate, based on the results from this study.

The four assembly sequences used here comprise only a small fraction of all of the possible sequences that could have been used with the species pool. I did not use all possible sequences for logistical reasons. For the purpose of this study, it was essential to minimize physiological variation in each species among introductions and among treatments and to minimize contamination by unwanted species (no contamination was detected in this experiment). More than four assembly sequences would have been too time-consuming to ensure adequate experimental control for a strong test of assembly history $\times$ ecosystem size interactions on species diversity.

I monitored the abundance of each protozoa and rotifer species in each microcosm for 109 days past the last introduction (see Fig. 1 for the timing of sampling). This 109-day duration corresponds to roughly 50–100 generations of the protozoa and rotifer species. This period was sufficient for comparable microcosm communities to reach persistent species composition (Weatherby et al. 1998, Law et al. 2000, Warren et al. 2003). For each replicate, I estimated densities by gently mixing the medium removed for nutrient replacement to homogenize the content and counted live individuals in several separate pipette drops of a 0.2-mL subsample. When species were too abundant to count reliably, I diluted the sample and counted individuals of these species in a 0.2-mL subsample of the dilution.

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 10 individuals of that species (Table 2). Cell mass was estimated based on cell volume, which, in turn, was estimated using equations that approximate cell shapes (Wetzel and Likens 1991).

I used two measures of species diversity: species richness and Simpson diversity. Species richness is the number of species observed in the 0.2-mL sample. Simpson diversity is the complement of Simpson's (1949) index, $1 - \Sigma\, p_i^2$, where p_i is the relative frequency of species i in terms of biomass. Because the fundamental measure of competitive success is how much of the available resource a species sequesters in its biomass, biomass is a suitable unit for expressing the diversity of a competitive community. Simpson diversity was originally devised to describe the probability that two randomly chosen individuals from a community are different species (Magurran 1988). However, one can apply this measure to describe biomass-based diversity by considering that it describes the probability that two sufficiently small units of biomass randomly chosen from a community belong to different species (Krebs 1999, Ricklefs and Lovette 1999). I used Simpson diversity because it is the least biased of the most commonly used measures of species diversity with respect to sample size (Lande 1996).

I used repeated-measures ANOVAs to determine whether effects of assembly history on diversity varied among ecosystem sizes and sampling days. Diversity measures on different sampling days were the repeated measures. I did not use data prior to day 41, because populations had not achieved their maximal size (see Appendices A, B, and C). To aid interpretation of the repeated-measures ANOVAs, I also used ANOVAs separately for each day, with a Bonferroni correction to account for conducting the same tests for multiple days ($\alpha = 0.05/6$ sampling days $= 0.0083$). Because data indicated that interactions between particular sets of species potentially caused differences among history treatments (see *Results and Discussion*), I further performed linear regressions for each sequence and for each day starting at day 41 to assess whether size–diversity relationships depended on assembly sequence and time, using the same Bonferroni correction as previously noted. In the regressions, ecosystem size and species diversity were the independent and dependent variables, respectively. Ecosystem size and species richness were log-transformed to follow the convention in species–area studies, whereas Simpson diversity was

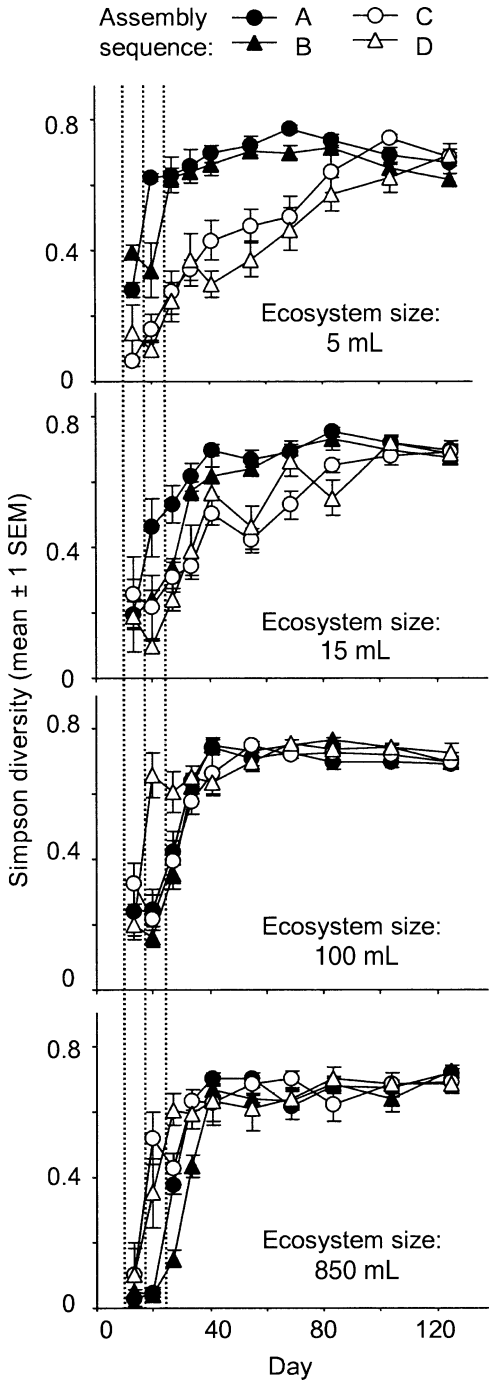

FIG. 1. Temporal changes in Simpson diversity. Microcosms received bacteria on day 0, microflagellates on day 2, and protozoa and rotifer species on days 9, 16, and 23 (indicated by dashed lines). See Table 1 for sequences A–D.

power-transformed (from Y to Y^4). These transformations helped the data to meet the assumption of homogeneity of variances required for ANOVAs and regressions (O'Brien's test and the Brown-Forsythe test, $P > 0.05$). I did all analyses with SYSTAT version 10 (SPSS 2000), except for the homogeneity of variances tests, for which JMP version 5 was used (SAS Institute 2003).

RESULTS AND DISCUSSION

The results for species richness yielded only weak evidence for interactive effects of assembly history and ecosystem size on diversity. Although the ANOVAs detected a significant interaction (Table 3), species richness varied little after day 55 (mean 7–8 species), and history did not strongly affect size–richness relationships (regressions: highest $F_{1,18} = 7.29$, highest $R^2 = 0.29$, lowest $P > 0.015$, note that Bonferroni-corrected $\alpha = 0.0083$). The Bonferroni correction may, however, unreasonably inflate Type II error (Cabin and Mitchell 2000), so I report the regressions that had a P value < 0.05: $y = 0.84 + 0.03x$ ($F_{1,18} = 5.82$ and 7.03, $R^2 = 0.24$ and 0.28, $P < 0.027$ and 0.016) on days 41 and 55, respectively, under sequence A, and $y = 0.91 - 0.02x$ ($F_{1,18} = 7.29$, $R^2 = 0.29$, $P < 0.015$) on day 125 under sequence C (x and y are ecosystem size and species richness, respectively, both log-transformed). The positive relationship under sequence A was caused mainly by two species, *Paramecium caudatum* and *Colpidium striatum*, which persisted until these sampling days only in the largest system. The negative relationship under sequence C reflects one species, *Spirostomum* sp., which was absent only in the second largest system (see Appendices A, B, and C). Overall, however, effects of assembly history and ecosystem size were weak, although significant, on species richness. The absence of strong effects may have been because the relatively small set of species used in this experiment made it harder to observe changes in species richness.

In contrast, the results for Simpson diversity provide strong support for a history × size interaction. History affected diversity in smaller systems to a greater extent and for a longer time than in larger systems (Fig. 1). Interactive effects were sufficiently strong that history determined whether and when the size–diversity relationship was significant: of the six sampling days for regression analyses, the regression was significant on day 69 under sequence A ($y = 0.80 - 0.06x$, $F_{1,18} = 11.82$, $R^2 = 0.40$, $P < 0.003$), on day 125 under sequence B ($y = 0.60 + 0.05x$, $F_{1,18} = 14.67$, $R^2 = 0.45$, $P < 0.001$), on days 55 and 69 under sequence C ($y = 0.37 + 0.13x$ and $y = 0.44 + 0.10x$, $F_{1,18} = 17.12$ and 15.0, $R^2 = 0.49$ and 0.46, respectively, $P < 0.001$), and on days 41 and 55 under sequence D ($y = 0.31 + 0.13x$ and $y = 0.33 + 0.12x$, $F_{1,18} = 9.72$ and 9.76; for both days, $R^2 = 0.35$, $P < 0.006$). (Here, x and y are log-transformed ecosystem size and Simpson diversity, respectively. These results qualitatively hold when Simpson diversity is power-transformed.) Considering the possibility that the Bonferroni correction may unreasonably inflate Type II error, I also report that P values were smaller than 0.05 on day 83 under sequence A ($y = 0.77 - 0.03x$, $F_{1,18} = 6.98$, $R^2 = 0.28$, $P <$

TABLE 3. Summary of ANOVAs.

Source of variation	df	Response variable: Species richness *F*	Species richness *P*	Simpson diversity *F*	Simpson diversity *P*
Repeated-measures ANOVAs					
Between subjects					
Assembly history (H)	3	15.620	<**0.001**	13.938	<**0.001**
Ecosystem size (S)	3	15.100	<**0.001**	25.004	<**0.001**
H × S	9	3.078	<**0.005**	5.529	<**0.001**
Within subjects					
Day	5	8.180	<**0.001**	9.795	<**0.001**
Day × H	15	1.190	>0.287	4.231	<**0.001**
Day × S	15	2.378	<**0.006**	3.203	<**0.001**
Day × H × S	45	1.313	>0.113	2.342	<**0.001**
ANOVAs performed separately for each sampling day					
Day 41					
Assembly history (H)	3	1.249	>0.299	10.359	<**0.001**
Ecosystem size (S)	3	5.125	>0.024	6.048	>0.015
H × S	9	2.139	>0.039	1.504	>0.166
Day 55					
Assembly history (H)	3	7.515	<**0.001**	13.298	<**0.001**
Ecosystem size (S)	3	3.19	>0.077	3.928	>0.048
H × S	9	2.152	>0.037	5.207	<**0.001**
Day 69					
Assembly history (H)	3	9.507	<**0.001**	6.822	<**0.001**
Ecosystem size (S)	3	6.389	>0.013	1.779	>0.221
H × S	9	1.100	>0.376	7.045	<**0.001**
Day 83					
Assembly history (H)	3	4.129	>0.010	5.348	<**0.002**
Ecosystem size (S)	3	3.39	>0.067	1.202	>0.363
H × S	9	1.575	>0.142	2.915	<**0.006**
Day 104					
Assembly history (H)	3	6.466	<**0.001**	0.809	>0.494
Ecosystem size (S)	3	4.128	>0.043	2.167	>0.162
H × S	9	1.110	>0.369	2.272	>0.028
Day 125					
Assembly history (H)	3	9.812	<**0.001**	0.541	>0.656
Ecosystem size (S)	3	0.637	>0.610	2.439	>0.131
H × S	9	2.778	<**0.008**	0.934	>0.502

Notes: *P* values in boldface indicate statistical significance ($\alpha = 0.05$ for repeated-measures ANOVAs, and Bonferroni-corrected $\alpha = 0.0083$ for ANOVAs performed separately for each sampling day). Note that the Bonferroni correction may unreasonably inflate Type II error (Cabin and Mitchell 2000). Within-subjects *P* values are Greenhouse-Geisser adjusted. Ecosystem size and species richness are log-transformed, and Simpson diversity is power-transformed (see *Methods*). Assembly history is treated as a random factor in ANOVAs performed separately. The results qualitatively hold when Simpson diversity is not transformed (statistics not shown).

0.017), on day 41 under sequence C ($y = 0.40 + 0.10x$, $F_{1,18} = 7.71$, $R^2 = 0.30$, $P < 0.012$), and on day 83 under sequence D ($y = 0.51 + 0.08x$, $F_{1,18} = 8.61$, $R^2 = 0.32$, $P < 0.009$). We can attribute this history and time dependence to a history × size interaction at least on days 55, 69, and 83 because the ANOVAs detected significant interactive effects specifically on these days (Table 3, see Fig. 2 for representative examples of the historically derived variation in size–diversity relationships).

How individual species responded to the experimental manipulations helps to explain the history × size interactive effect on Simpson diversity. A large ''priority effect'' (reviewed in Morin 1999 and Almany 2003) affected *Spirostomum* (see Appendix B). *Spirostomum* populations grew only when they were introduced first (i.e., under sequences C and D, and not under A or B). However, once they achieved high abundance, they maintained it. This effect was greatest in 5-mL and 15-mL microcosms, intermediate in 850-mL microcosms, and non-existent in 100-mL microcosms (see Appendix B). Assembly sequence affected several other species, but the effects were smaller. Because *Spirostomum* individuals are exceptionally large (Table 2), they drove patterns in Simpson diversity (Fig. 3). To illustrate the importance of this species relative to others, I performed simple linear regressions for each species, using log-transformed abundance as the independent variable and Simpson diversity (all values from day 41) as the response variable. I also performed

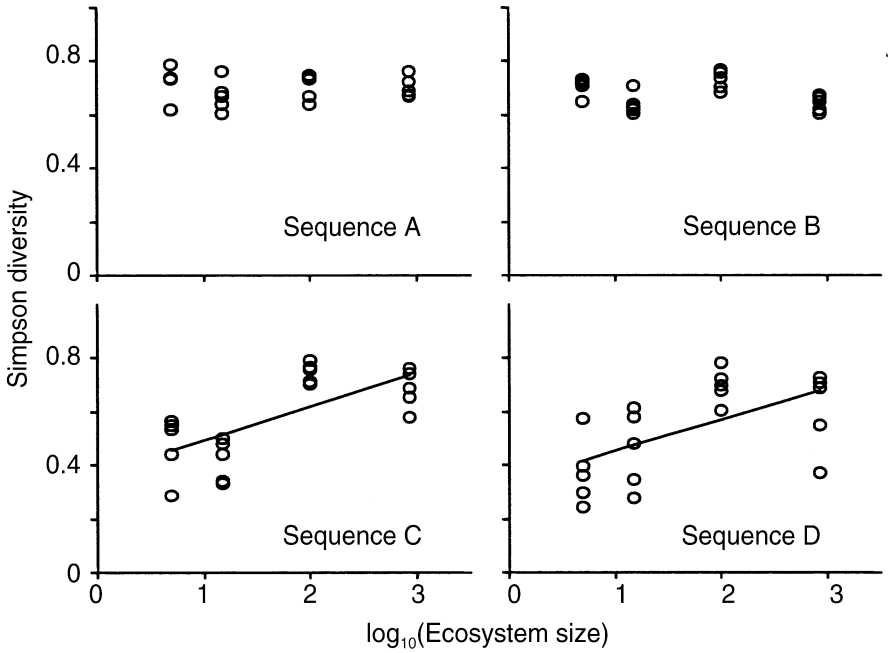

FIG. 2. Relationship between ecosystem size (measured in mL) and Simpson diversity on day 55 under different assembly sequences. Regression lines are drawn where statistically significant (see *Results and Discussion* for parameter estimates and statistics).

similar regressions with a quadratic term added as another independent variable. *Spirostomum* 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%. Consequently, the tendency for a greater priority effect on this species in smaller systems resulted in the history dependence and time dependence of size–diversity relationships.

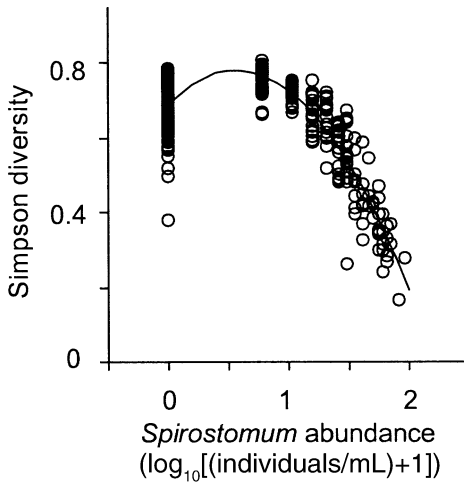

FIG. 3. Much of the variation in Simpson diversity (d) was explained by *Spirostomum* abundance, s ($d = 0.69 + 0.33s - 0.29s^2$, $F_{2, 477} = 785.56$, $P < 0.0005$, adjusted $R^2 = 0.77$).

The reason for a greater priority effect in smaller systems seems simple. I held initial population sizes constant, so initial densities were higher in smaller microcosms. As a result, generally, earlier immigrants had achieved a higher population density in smaller systems when other species were introduced (see Appendices A, B, and C). For this reason, earlier immigrants probably affected later immigrants more greatly in smaller systems, leading to the differential magnitude of the priority effect. Stronger historical effects in smaller systems observed in this study seemingly contradict the stronger historical effects in larger systems observed in Drake's (1991) aquatic microcosms. Habitat heterogeneity may explain this difference. Drake (1991) attributed stronger historical effects in larger systems to greater habitat heterogeneity caused by light gradients; larger microcosms were deeper than smaller ones. In this study, microcosm depth and other aspects of habitat heterogeneity were standardized to assess the effects of ecosystem size per se.

Because assembly treatments differed only in the order of species introduction, I can attribute among-treatment variation in *Spirostomum* to the influence of other species. Diversity patterns therefore reflect community-level biotic interactions, not the response of a single species independent of other species. Species interactions may have occurred via changes in the abundance and composition of bacteria and microflagellates, the chemical properties of the medium, or other unmonitored factors (cf. Petersen 1984, Sutherland 1990).

Priority effects lasted for as long as 20–40 generations after the last species introduction (>40 days after the last introduction; Fig. 1). The population dynamics data (Appendices A, B, and C) and previous studies (McGrady-Steed and Morin 2000, Fukami 2001, Fox 2002, Fukami and Morin 2003) indicate that 40 days is more than enough time for all species to reach carrying capacity, even in the largest microcosm used here. Therefore, the long-lasting priority effect cannot be attributed solely to the difference in starting biomass among the species sets (Table 2).

Community structure, at least in terms of species diversity, appeared to converge eventually, regardless of assembly history or ecosystem size (Fig. 1). Population densities of most species became indistinguishable among treatments by the end of the experiment (see Appendices A, B, and C). Although it is not certain whether this end state was stable (cf. Samuels and Drake 1997), I disturbed the communities weekly by replacing 10% of the medium. Low temporal variability in densities, despite these repeated disturbances, suggests local stability (see Appendices A, B, and C). Despite this eventual community convergence, however, history and size exerted significant interactive effects for more than 20–40 generations before convergence (Fig. 1).

These results have implications for evaluating the importance of assembly history in community structuring. Theory suggests that local communities can assume alternative stable equilibria even if they share the same species pool and environmental conditions (MacArthur 1972:247–250, Gilpin and Case 1976). Conventionally, assembly history is considered important when it creates such alternative equilibria, but is deemed unimportant when it does not (Lewontin 1969, Sutherland 1974, Knowlton 1992, Law and Morton 1996, Samuels and Drake 1997, Petraitis and Latham 1999, Chase 2003). However, my results indicate that assembly history can be important for many generations owing to transient community dynamics, even if historical effects eventually weaken to allow convergence (Fig. 1) (see also Grover and Lawton 1994, Samuels and Drake 1997, Walker and del Moral 2003).

Similarly, conventional models for size–diversity relationships assume that diversity is near equilibrium (e.g., MacArthur and Wilson 1967, Hubbell 2001). Although this assumption is heuristically important (Brown and Lomolino 1998), we know that disturbance keeps many natural systems far from equilibrium (Pickett and White 1985). The results here support the argument that we cannot ignore non-equilibrial, transient community dynamics to explain size–diversity relationships (e.g., Holt et al. 1999). This study, which lasted for about 50–100 generations, demonstrates that long-term studies are essential for understanding ecological processes (Hastings 2001, 2004), particularly community assembly (Grover and Lawton 1994, Samuels and Drake 1997, Warren et al. 2003).

Species immigration is essentially stochastic, ecosystem size is variable, and priority effects can be strong in many natural systems. It is thus possible that the history × size interaction revealed in this study also shapes natural diversity patterns. However, it is difficult to manipulate assembly history experimentally and monitor long-term dynamics along an ecosystem size gradient in natural communities (but see Dudgeon and Petraitis 2001, Bertness et al. 2002). Laboratory microcosm experiments will remain a useful complementary approach (see also natural microcosm experiments; Srivastava et al. 2004). Factors that may influence size × history interaction, but were not manipulated in this experiment, include productivity (cf. Fukami and Morin 2003), resource diversity (cf. Long and Karel 2002), species pool size (cf. Fox et al. 2000), and immigration rate (cf. Robinson and Dickerson 1987, Spencer and Warren 1996). Microcosm experiments can readily manipulate these factors.

Immigration rate may be particularly relevant (Lockwood et al. 1997). Although held constant in this experiment, immigration rate may decrease with decreasing ecosystem size due to a target effect (Coleman et al. 1982, Lomolino 1990). Such changes in immigration rate may alter the importance of history × size interactive effects in two contrasting ways. On one hand, the smaller number of individuals arriving in smaller systems may reduce the difference in initial densities among systems of differing size. This can, in turn, reduce the difference in the strength of priority effects among different systems. Consequently, history × size interactive effects would be reduced. On the other hand, the slower immigration rate in smaller systems can mean more time available there than in larger systems for earlier immigrants to alter the environment before other species arrive. This can strengthen priority effects in smaller systems relative to larger systems, making the difference in the strength of priority effects between small and large systems more pronounced. Thus, history × size interactive effects would be intensified. The relative importance of these contrasting processes remains to be investigated.

In conclusion, this study has shown that assembly history can interact with ecosystem size to affect species diversity. Specifically, assembly history can affect diversity more strongly in smaller systems owing to greater priority effects. Through this interaction, assembly history can regulate size–diversity relationships. In this study, the interaction affected mainly a single species, but the experimental design ensured that diversity patterns resulted from community-level biotic interactions. The results also highlight the importance of long-term transient community dynamics in understanding historical effects on community structure.

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APPENDIX A

A figure showing population dynamics of the species in set 1 is available in ESA's Electronic Data Archive: *Ecological Archives* E085-110-A1.

APPENDIX B

A figure showing population dynamics of the species in set 2 is available in ESA's Electronic Data Archive: *Ecological Archives* E085-110-A2.

APPENDIX C

A figure showing population dynamics of the species in set 3 is available in ESA's Electronic Data Archive: *Ecological Archives* E085-110-A3.