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High community dissimilarity at low productivity causes the productivity-richness relation to vary with observational scale

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Abstract: It is widely reported that the productivity-richness relation (PRR) is highly variable, and several field studies suggest that the PRR varies with observational scale. Here we provide the first experimental study to test whether the PRR is scale-dependent when all replicate ecosystems have similar initial conditions. We also test the relation between productivity and compositional dissimilarity, and whether the PRR varies with ecosystem size. Moderately complex replicated microcosms were assembled consisting of a range of protozoa, algae, and a diverse bacterial flora. We found that the PRR of protozoan and algal communities varied with observational scale, but was unrelated to ecosystem size. Specifically, protozoan and algal richness increased monotonically with productivity at the local scale, but became flattened at the regional scale. This varying PRR at different scales occurred because dissimilarity among replicates decreased with productivity. Thus, in this model system, our experimental approach found a different form of scale dependence than previous field research. We speculate that this difference results from different processes governing extinctions at low levels of productivity.

Introduction

Ecologists generally agree that productivity influences species richness (e.g., Rosenzweig and Abramsky 1993, Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001). It is also clear that the patterns of species richness along productivity gradients are highly variable (Waide et al. 1999, Mittelbach et al. 2001). Thus the influence of productivity on species richness is highly variable, and recent efforts have been made attempting to determine factors controlling this variation, including the impact of disturbance (Huston 1994, Kondoh 2001), niche specialization (Kassen et al. 2000), and the sequence of community assembly (Fukami and Morin 2003).

Recent studies indicate that the shape of the productivity-richness relation (PRR) varies with observational scale (Chase and Leibold 2002, Chase and Ryberg 2004). For example, Chase and Leibold (2002) defined individual ponds as the local observational scale, and pooled subsets of ponds into watersheds as the regional scale. They used these groupings to show a hump-shaped PRR from the local scale, but a positive PRR from the regional scale. Studies from Chase and colleagues further showed that compositional dissimilarity among local ponds increased along the productivity gradient, which could contribute to this scale dependence of the PRR, and they suggested that alternate states were more likely to occur at high productivity.

Although community assembly sequence and other historical artifacts could contribute to these alternate states (Drake 1991, Law and Morton 1993, Luh and Pimm 1993, Price and Morin 2004), they are difficult to assess in most observational studies due to a general lack of information regarding the history of natural communities. Also, research on the PRR has historically focused on community assembly mechanisms at high productivity, and research exploring scale-dependence in the PRR exhibited this same historical legacy or bias toward mechanisms at high productivity. By contrast, we know little about the contributions of community assembly at low productivity levels to patterns of scale-dependence in the PRR. If a few specialized species are adapted to sustain populations at low productivity levels, one would expect this set of species to occur in low-productivity communities, whereas other less adaptive species should be entirely absent. Here we suggest that dissimilarity among localities could also exist at low productivity levels, because species with small population sizes are more likely subject to stochastic extinctions (Lande 1993, Reed et al. 2003). Consequently, the stochastic extinctions at low productivity could cause stochastic variation, and potentially increase dissimilarity in community composition among similar localities. To the best of our knowledge, however, no studies have tested this possibility. We further suggest that the relation between dissimilarity and productivity may not necessarily be positive if the historical effect is minimized to reduce the possibilities of seeing alternate states at high productivity communities.

We built moderately complex replicate microcosms with diverse bacterial flora, and a range of green algae and heterotrophic protozoa. The experimental design was similar to that of Chase and Leibold's field study in terms of how we defined local and regional scale. However, we reduced variation in community assembly sequences by starting all replicates with similar initial conditions. By minimizing historical effects such as variation in assembly sequences among replicate communities, our experimental approach could provide a test that complements past observational approaches in natural systems (Gross et al. 2000, Chase and Leibold 2002, Chase and Ryberg 2004, Chalcraft et al. 2004). Also, we varied culture dish sizes because in Chase and Leibold's field study, total pond size increased with increasing observational scale. Since ecosystem size itself may affect the PRR (Thompson and Townsend 2005, McCann et al. 2005), our design could help us separate the confounding effects of observational scale from ecosystem size in affecting the PRR. We specifically addressed the following questions: 1) Is the PRR scale-dependent when all replicate ecosystems are known to have similar initial conditions? 2) Is high dissimilarity possible among replicates with low-productivity? 3) Does the PRR vary with ecosystem size?

Methods

Laboratory scale

All communities were established in tissue culture dishes. The PRR was measured at different observational scale: 1) at the local scale of each individual culture dish, where species could potentially interact with each other through local dispersal; 2) at the regional scale of a set of three replicated dishes with same treatment (same dish size and productivity level), where species within each culture dish were still dispersal linked, but regional dispersal among replicated dishes was virtually absent due to physical barriers (Fig. 1). Although replicated dishes in different regions were isolated from each other, they all had the same species pool at the start of the experiment. We used culture dishes with four different sizes (9 cm^2, 21 cm^2, 154 cm^2 and 500 cm^2) so that at the local scale, the total area varied from 9 cm^2 to 500 cm^2, while at the regional scale, it varied from 27 cm^2 to 1500 cm^2 (Fig. 1). Specifically, our experimental design allowed us to compare PRR when data were observed at the local and the regional scale with approximately equal total area (e.g., 21 cm^2 at the local scale vs. 27 cm^2 at the regional scale, or 500 cm^2 at the local scale vs. 462 cm^2 at the regional scale (Fig. 1).

Experimental design

Microcosms were assembled with six green algal species (*Volvox carteri, Micrasterias rotata, Scenedesmus opoliensis, Closterium libellula, Cosmarium sportella* and *Pandorina morum*), and six protozoan species (*Paramecium aurelia, Paramecium bursaria, Arcella vulgaris, Euplotes eurystomus, Spirostomum ambiguum* and *Blepharisma americanum*; Carolina Biological Supply). The soil water medium (Fukami and Morin 2003) for the lowest productivity level consisted of 0.013 g protozoan pellet, 0.01 g soil, and 0.001 g vitamin supplement in each liter of DI water. The media for the other productivity levels consisted of 0.025, 0.05, 0.09, 0.183, 0.367 and 0.733 g of the pellet per liter of DI water, respectively, from the second lowest to the highest levels. At the highest productivity level, the medium contained approximately NO_3 and PO_4 at 4.7 μmol l^{-1} and 0.17 μmol l^{-1}, respectively (Hulot et al. 2001). Tissue culture dishes of four different size were used to vary area (areas: 9 cm^2, 21 cm^2, 154 cm^2 and 500 cm^2), and we kept the depth of medium 1

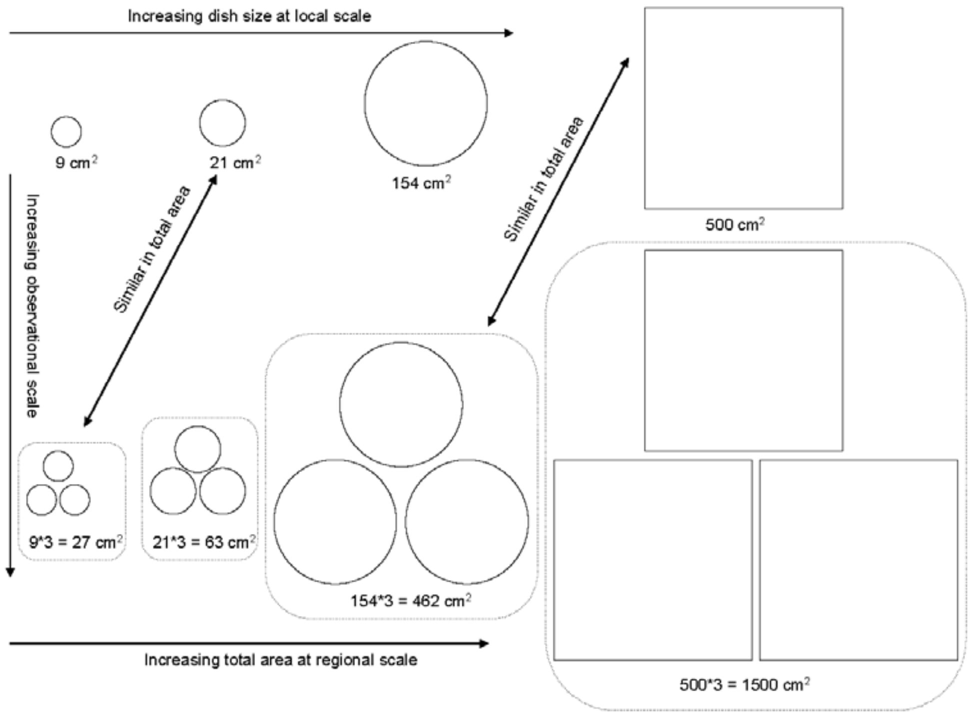


Figure 1. Schematic figure of the experimental design. Culture dishes with four different sizes, 9 cm^2, 21 cm^2, 154 cm^2 and 500 cm^{2,} were used. At the local scale of each individual dish, dish size varied between 9 cm^2 and 500 cm^2. By contrast, at the regional scale of a set of three replicated dishes, dish size varied between 27 cm^2 and 1500 cm^2.

cm in all dishes to minimize artifactual differences among dishes. Three replicates for each treatment combination were assembled. After autoclaving, the sterile medium was inoculated with *Bacillus subtilis*, *Serratia marcescens*, and filtrates from stock cultures and water samples from a local pond. Algal species were added 24 h after bacterial addition, and protozoan species were added 2 days after algal addition. We distributed volumes of medium containing protozoan and algal species from stock culture to each culture dish in proportional to the area of the culture dish. We scanned each dish and found that all protozoan and algal species were present in every dish during the first two weeks. All cultures were maintained in programmable Percival incubators at 21.4 ^{o}C with controlled light-dark cycles (12 h day and 12 h night). Positions of microcosms were alternated weekly in each incubator to minimize positional effects.

The first sampling took place 5 days later after protozoan addition, and we allowed the experiment to run for 35 days afterward, during which we sampled microcosms every 7 days up to the final day of the experiment (totally 6 sampling dates). The data presented here were from week 6 samplings (similar results were retained from either week 4 or 5 samplings, and microbial communities should have been stable since week 4). On each sampling day, we mixed culture medium gently, and withdrew a total of 10% of the volume with five widely spaced subsamples. These subsamples were mixed well, from which 300 μL was used for protist count (also see Fukami 2004). Weekly, 10% of the medium in each microcosm was replaced with fresh medium to replenish nutrients and reduce the accumulation of metabolic wastes.

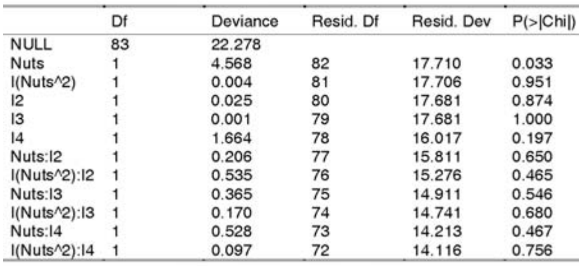
Data analysis

Dissimilarities of protozoan and algal communities were calculated among each pair

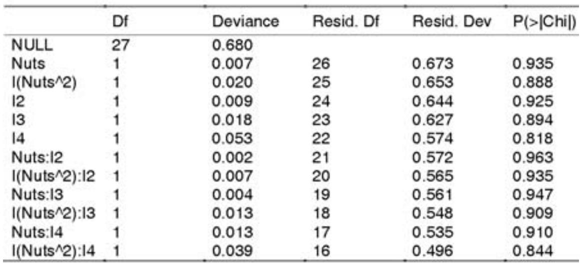
Dissimilarities of protozoan and algal communities were calculated among each pair of three replicates within each treatment as the complement of Jaccard's index of similarity (Chase and Leibold 2002), that is, 1 – [a/(a+b+c)], where a is the number of species in common between two dishes, b is the number of species unique to dish 1, and c is the number of species unique to dish 2. After we calculated each pairwise dissimilarity, we averaged them to get the average species dissimilarity among replicates.

Statistical analyses varied by response variable and taxon measured. Productivity was considered a continuous variable, and dish size was considered a categorical variable. Effects of productivity and dish size on the density of each protist species were tested with general linear models with productivity × size interactions. Log transformation was not applied because the variances were homogeneous. Protozoan and algal proportional richness versus productivity and dish size were tested with generalized linear models with quasibinomial error and a logit link function. We used proportional richness because species richness was low for both protozoan and algal species, bounded between 0 and 6. Sequential deviances for treatment effects were tested with a χ^2 distribution.

Table 1. a) The analysis of deviance table for the effects of productivity and ecosystem size on algal richness at the local scale. Indicator variables of each level of size were created, and I2, I3 and I4 referred to culture dishes with size 21 cm^2, 154 cm^2 and 500 cm^2, respectively. Quadratic relations between richness and productivity were also included. **b)** The analysis of deviance table for the effects of productivity and ecosystem size on algal richness at the regional scale. Indicator variables of each level of size were created, and I2, I3 and I4 referred to culture dishes with size 21 cm^2, 154 cm^2 and 500 cm^2, respectively. Quadratic relations between richness and productivity were also included.



	Df	Deviance	Resid. Df	Resid. Dev	P(>|Chi|)
NULL	83	22.278			
Nuts	1	4.568	82	17.710	0.033
I(Nuts^2)	1	0.004	81	17.706	0.951
I2	1	0.025	80	17.681	0.874
I3	1	0.001	79	17.681	1.000
I4	1	1.664	78	16.017	0.197
Nuts:I2	1	0.206	77	15.811	0.650
I(Nuts^2):I2	1	0.535	76	15.276	0.465
Nuts:I3	1	0.365	75	14.911	0.546
I(Nuts^2):I3	1	0.170	74	14.741	0.680
Nuts:I4	1	0.528	73	14.213	0.467
I(Nuts^2):I4	1	0.097	72	14.116	0.756



	Df	Deviance	Resid. Df	Resid. Dev	P(>|Chi|)
NULL	27	0.680			
Nuts	1	0.007	26	0.673	0.935
I(Nuts^2)	1	0.020	25	0.653	0.888
I2	1	0.009	24	0.644	0.925
I3	1	0.018	23	0.627	0.894
I4	1	0.053	22	0.574	0.818
Nuts:I2	1	0.002	21	0.572	0.963
I(Nuts^2):I2	1	0.007	20	0.565	0.935
Nuts:I3	1	0.004	19	0.561	0.947
I(Nuts^2):I3	1	0.013	18	0.548	0.909
Nuts:I4	1	0.013	17	0.535	0.910
I(Nuts^2):I4	1	0.039	16	0.496	0.844

Effects of productivity on dissimilarity were tested first with general linear models, but dissimilarities took on a limited number of values, and the errors were highly nonnormal. We therefore checked the significance of our model coefficients against bootstrapped confidence intervals for these coefficients. We used observation-resampling and 1000 samples to generate adjusted bootstrap percentile confidence intervals. In all cases, our parametric significance tests agreed with bootstrapped confidence intervals, and so we reported only the results of the parametric linear models. Lastly, quadratic relations between richness and productivity levels were included in all initial models, and final analyses were based on the minimally adequate models after model simplification procedures (Crawley 2002). All statistical analyses were performed using R (v. 2.7.0) (R Development Core Team 2008).

Results

Algal richness increased monotonically with productivity at the local scale (the main effect of productivity P = 0.033; Fig. 2a, Table 1a). Dish size had no influence on the curvilinearity, slope, or intercept of the PRR (the main effect of size and the productivity × size interaction were both insignificant at P > 0.05; Fig. 2a, Table 1a). At the regional

Table 2. a) The analysis of deviance table for the effects of productivity and ecosystem size on protozoan richness at the local scale. Indicator variables of each level of size were created, and I2, I3 and I4 referred to culture dishes with size 21 cm^2, 154 cm^2 and 500 cm^2, respectively. Quadratic relations between richness and productivity were also included. **b)** The analysis of deviance table for the effects of productivity and ecosystem size on protozoan richness at the regional scale. Indicator variables of each level of size were created, and I2, I3 and I4 referred to culture dishes with size 21 cm^2, 154 cm^2 and 500 cm^2, respectively. Quadratic terms for productivity were also included.

	Df	Deviance	Resid. Df	Resid. Dev	P(>|Chi|)
NULL	83	49.420			
Nuts	1	18.912	82	30.508	<0.001
I(Nuts^2)	1	0.482	81	30.026	0.487
I2	1	0.025	80	30.001	0.875
I3	1	2.439	79	27.562	0.118
I4	1	2.001	78	25.562	0.157
Nuts:I2	1	0.487	77	25.075	0.485
I(Nuts^2):I2	1	0.097	76	24.978	0.756
Nuts:I3	1	0.270	75	24.708	0.603
I(Nuts^2):I3	1	0.090	74	24.618	0.764
Nuts:I4	1	0.326	73	24.292	0.568
I(Nuts^2):I4	1	0.205	72	24.087	0.650

	Df	Deviance	Resid. Df	Resid. Dev	P(>|Chi|)
NULL	27	6.100			
Nuts	1	2.482	26	3.618	0.115
I(Nuts^2)	1	0.627	25	2.991	0.428
I2	1	0.135	24	2.856	0.713
I3	1	0.067	23	2.790	0.796
I4	1	0.001	22	2.790	1.000
Nuts:I2	1	0.001	21	2.789	0.989
I(Nuts^2):I2	1	0.003	20	2.786	0.955
Nuts:I3	1	0.040	19	2.746	0.841
I(Nuts^2):I3	1	0.496	18	2.250	0.481
Nuts:I4	1	0.313	17	1.937	0.576
I(Nuts^2):I4	1	0.104	16	1.833	0.747

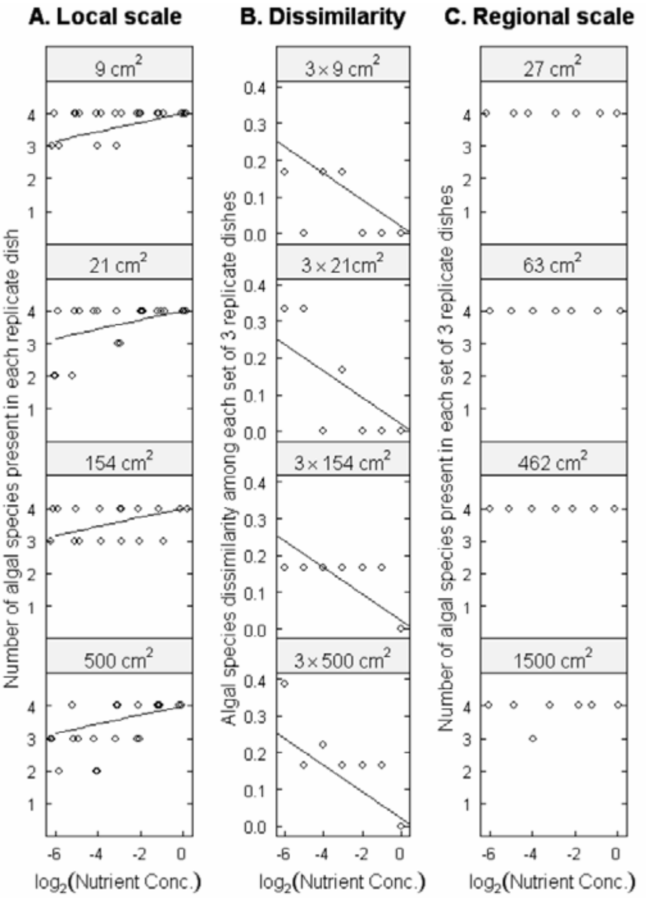


Figure 2. The effect of productivity on algal richness and dissimilarity at the local and the regional scale. Regression lines show relations estimated by models; only statistically significant relations are shown.

scale, the PRR flattened, and algal richness did not vary with productivity (the main effect of productivity $P = 0.935$; Fig. 2c, Table 1b). We also observed different algal PRR of compared communities within approximately equal total area but with different observational scale (e.g., 21 cm^2 at the local scale vs. 27 cm^2 at the regional scale, or 500 cm^2 at the local scale vs. 462 cm^2 at the regional scale; Fig. 2a,c). Algal dissimilarity among replicated dishes decreased significantly with productivity (Fig. 2b; $F_{1,23} = 21.960$, $P = 0.0001$), and the effect of dish size was nonsignificant ($F_{3,23} = 2.262$, $P = 0.108$).

Protozoan richness increased monotonically with productivity at the local scale (the main effect of productivity $P < 0.0001$; Fig. 3a, Table 2a). Dish size had no significant influence on the curvilinearity, slope, or intercept of the PRR (the main effect of size and the productivity × size interaction were both insignificant at $P > 0.05$; Fig. 3a, Table 2a). At the regional scale, however, the PRR flattened, and this pattern

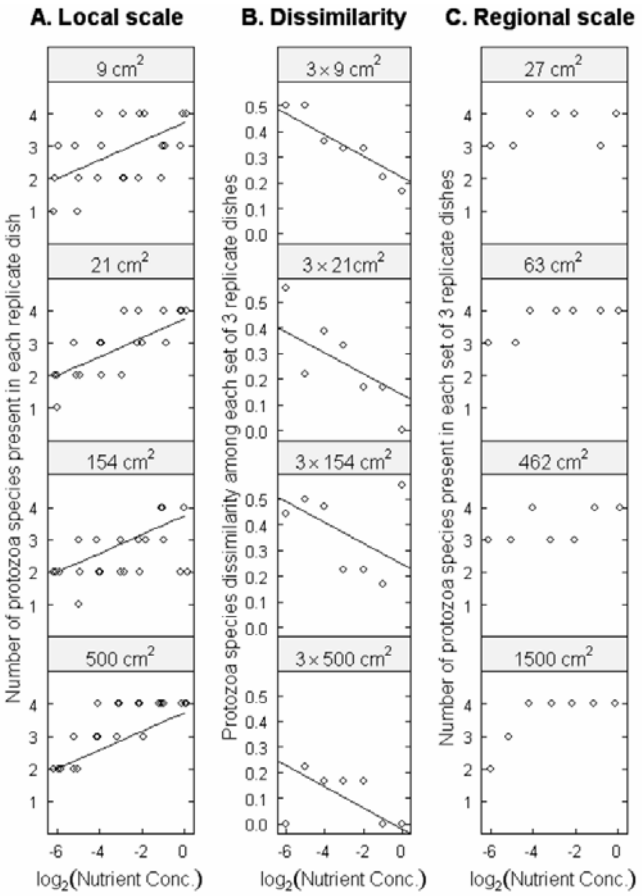


Figure 3. The effect of productivity on protozoan richness and dissimilarity at the local and the regional scale. Regression lines show relations estimated by models; only statistically significant relations are shown.

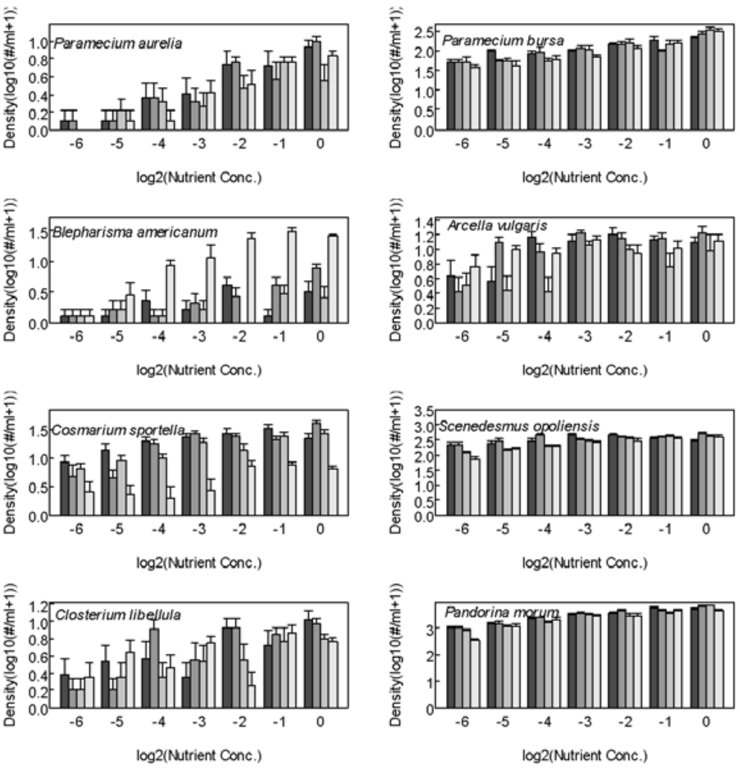
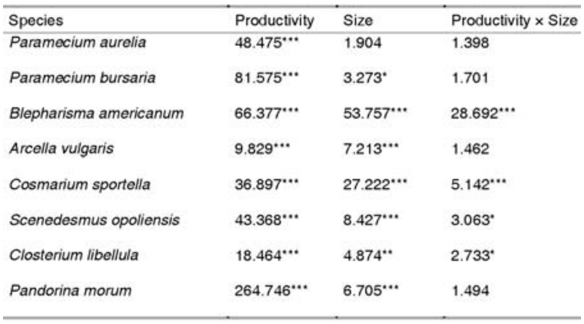


Figure 4. The effects of productivity (from the lowest to the highest) and size (from the smallest, 9 cm^2, in black, to the largest, 500 cm^2, in light grey, at each productivity level) on the abundance of 8 species present on the final sampling week.

Table 3. Response of protozoan and algal species to productivity gradient and dish size. Numbers indicate *F*-ratio (general linear models). * P < 0.05; ** P < 0.005; ***P < 0.0005. Species not listed here were below detection limits in all replicates at all productivity gradient.



Species	Productivity	Size	Productivity × Size
Paramecium aurelia	48.475***	1.904	1.398
Paramecium bursaria	81.575***	3.273*	1.701
Blepharisma americanum	66.377***	53.757***	28.692***
Arcella vulgaris	9.829***	7.213***	1.462
Cosmarium sportella	36.897***	27.222***	5.142***
Scenedesmus opoliensis	43.368***	8.427***	3.063*
Closterium libellula	18.464***	4.874**	2.733*
Pandorina morum	264.746***	6.705***	1.494

did not vary with productivity (the main effect of productivity $P = 0.115$; Fig. 3c, Table 2b). We also observed different protozoan PRR of compared communities within approximately equal total area but with different observational scale (e.g., 21 cm^2 at the local scale vs. 27 cm^2 at the regional scale, or 500 cm^2 at the local scale vs. 462 cm^2 at the regional scale; Fig. 3a,c). Protozoan dissimilarity among replicated dishes decreased significantly with productivity (Fig. 3b; $F_{1,23} = 13.949$, $P = 0.001$) and dish size ($F_{3,23} = 7.438$, $P = 0.001$), with no significant interaction ($P > 0.05$). Average dissimilarity was lower in the large (500 cm^2) dishes than in dishes with other sizes (all $P < 0.0001$).

Two protozoan species, *Spirostomum ambiguum* and *Euplotes eurystomus*, and two algal species, *Volvox carteri* and *Micrasterias rotate*, were not observed in any dishes in week 6. Among the remaining eight species, the occurrence of two protozoan species (*P. aurelia* and *Blepharisma americanum*), and two algal species (*Closterium libellula* and *Cosmarium sportella*) varied: all of them were present with higher densities in high-productivity dishes; by contrast, they were of very low densities or even died out in some low-productivity dishes, although they were not entirely absent in all low-productivity dishes (Fig. 4, Table 3).

Discussion

Our results showed that a few protozoan and algal species were absent from some low-productivity culture dishes, but they were not entirely absent from other replicated dishes with low productivity. In other words, the identity of these species varied among replicated dishes with low productivity, and thus our result did not support the hypothesis that dissimilarity is low at low productivity assuming that only a few specialized species are adapted to sustain populations at these conditions, but supported the alternative hypothesis that species extinctions could be stochastic at low productivity, which could then cause stochastic variation in community composition among localities. By contrast, at high productivity, all species achieved sufficiently high densities to avoid stochastic extinctions resulting in high local richness but low species dissimilarity.

We found that the high community dissimilarity at low productivity caused the PRR of protozoan and algal species to vary with observational scale. This contrasted with the positive dissimilarity-productivity pattern found in natural ponds (Chase and Leibold 2002, Chase and Ryberg 2004). The natural ponds and the laboratory microcosms are different systems, and we do not intend to make an overly simplistic comparison between these systems. However, assembly sequence and other priority effects can have profound effects on community structure (Drake 1991, Luh and Pimm 1993, Fukami and Morin 2003), but are often difficult to test. Observational studies have not intended to control for such effects, and so have currently left untested the role of priority effects in generating the observed richness and dissimilarity patterns. In contrast, an experimental microcosm system is well-suited to manipulate and test the role of priority effects on patterns of richness and dissimilarity across spatial scales. In this sense, our experimental approach provided a test that complements past observational approaches in natural systems. We note only that our study used a particular known assembly sequence, and our particular results differ from those of observational studies in ponds. It may be that a more thorough investigation of the role of priority effects, perhaps in laboratory microcosms, may reveal an important influence of history.

Chase and Leibold (2002) suggested three mechanisms for why some habitats have high dissimilarity: first, habitats with high resource heterogeneity could increase species dissimilarity; second, habitats with high variation in specie composition could increase species dissimilarity; third, habitats that are more likely to obtain multiple stable states could increase species dissimilarity. Given that laboratory microcosms were generally considered homogeneous because mixing could rapidly lead to homogenization, the first mechanism is unlikely for our system. Our results supported the second mechanism because stochastic extinction of low-abundance protist species caused stochastic variation in community, and thus raised species dissimilarity. We could not test the third mechanisms due to experimental design reason, although our results showed a diminishing effect on species dissimilarity when the possibility of obtaining multiple state states was minimized.

Positive PRR have been commonly found in both terrestrial and aquatic ecosystems (Brown 1973, Wright 1983, Srivastava and Lawton 1998, Hall et al. 2000, Kaspari et al. 2000, Mittelbach et al. 2001, Stevens and Carson 2002, Jiang and Morin 2004). This positive PRR can be explained by the “more individual hypothesis” (Abrams 1995, Srivastava and Lawton 1998), which states that the abundance of each species increases with increasing productivity because high population size may help reduce the chance of stochastic extinction. Our results seemed to support this hypothesis because high productivity dishes had high number of individuals and high richness. However, we found that large-sized dishes contained high number of individuals but were no more species-rich than small-sized dishes. Other possible mechanisms may also explain this positive PRR. Specifically, high productivity could increase the amount of rare resources or rare resource combinations for specialist species and thus promote species coexistence (Abrams 1995). This study did not evaluate specific resource utilization by each species, but certainly our abundance data are consistent with this hypothesis. In particular, *P. aurelia* and *Blepharisma* were rare at low productivity but became more common at high productivity and were important in generating the patterns of both richness and dissimilarity.

To the best of our knowledge, our study is the first to test experimentally whether the PRR of different taxonomic groups varies with observational scale and ecosystem size when all replicates start out at similar initial conditions. We found that PRR of protozoan and algal species varied with observational scale, but was unrelated to ecosystem size. Thus, in this model system, our experimental approach found a different form of scale dependence than previous field research, and this difference could result from different processes governing extinctions at low levels of productivity.

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