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How enrichment, ecosystem size, and their effects on species richness co-determine the stability of microcosm communities

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Nutrient enrichment, ecosystem size, and richness each may directly affect the stability of both populations and communities. Alternatively, nutrient enrichment and ecosystem size each may directly affect richness, which in turn may affect stability. No previous studies, however, have tested empirically how these three factors interact and co-determine stability. We manipulated nutrient input and ecosystem size in replicate microcosms containing a diverse bacterial flora, and a range of green algae and heterotrophic protozoa, and used these manipulations and the resulting variation in species richness to measure their combined effects on temporal stability of both populations and communities. Results showed that nutrient enrichment and ecosystem size controlled protist richness, and their effects on stability could be mediated by richness. In addition, both community-level and population-level stability increased with protist richness. Furthermore, mean species evenness and mean species richness was negatively related. Effects of statistical averaging, overyielding, and component population stability were identified as possible mechanisms involved explaini ng the stabilizing effects of richness on community stability. Their relative strength in influencing stability, however, is likely to change as mean evenness decreased with increasing richness. This decrease in evenness would tend to weaken the strength of the statistic averaging effect, but increase the strength of the other two mechanisms due to relatively lower population variability (component population stability) and higher mean biovolumes of dominant protists (overyielding).

What determines the stability of populations and communities has been a central topic of ecological research for over fifty years (Odum 1953, May 1973, Post and Pimm 1983, DeAngelis et al. 1989, McCann et al. 1998). Since the numerous definitions of stability have caused fundamental problems (Pimm 1991, Ives and Carpenter 2007), here we focus on one type of stability, the relative lack of temporal variability of populations and communities. We quantified and analyzed variability with the coefficient of variation of biomass production of populations and communities (CV, the ratio of the standard deviation to the mean; Gaston and McArdle 1994).

Nutrient enrichment has been regarded as one important factor affecting stability (Rosenzweig 1971, DeAngelis et al. 1989). The paradox of enrichment hypothesis, developed from simple predator–prey models, predicts that enrichment causes population oscillations, and even leads to species extinctions (Rosenzweig 1971). A great number of empirical tests, however, found no support for it (McCauley and Murdoch 1990, Kirk 1998, Murdoch et al. 1998, Steiner et al. 2005). Failure to consider biological complexity in simple models may account for this discrepancy between theory and experiments. For instance, the presence of inedible prey with increasing food web complexity may function as the 'nutrient sponge', sequestering resources away from more susceptible prey (Grover 1995), or function as stabilizing 'weak interactors', since weak trophic interactions may help stabilize ecological communities (McCann et al. 1998). In addition, inducible defenses could prevent strong population fluctuations by nutrient enrichment (Verschoor et al. 2004). Alternatively, the process of predation can be modulated by other predators via modifying functional responses (i.e. from type II to more stabilizing type III functional responses; Fussmann and Blasius 2005, Rall et al. 2008), via balancing flexible and inflexible interaction links (i.e. specialist and generalist predators; Mougi and Nishimura 2007), and via introducing predator interference (Skalski and Gilliam 2001, Rall et al. 2008). In sum, the potentially destabilizing effect of enrichment can be reduced or eliminated by increasing food-web complexity (Trzcinski et al. 2005, Rall et al. 2008).

Ecosystem size may also affect stability via its effects on food web structure and trophic interactions (Luckinbill 1974, Post and Pimm 1983, Post et al. 2000, McCann et al. 2005). For instance, predator capture efficiency could decrease with increasing ecosystem size (Luckinbill 1974). Furthermore, predators in large habitats could have more flexibility in prey preference, thereby imposing less pressure on preys in small population size (McCann et al. 2005). However, the lack of theory incorporating sufficient biological details, together with the absence of empirical tests, severely hinder our understanding of the general effect of ecosystem size on stability.

The linkage between richness and stability has been of long-standing interest (Tilman and Downing 1994, Cottingham et al. 2001). Different mechanisms may account for the stabilizing effect of richness, such as high levels of prey heterogeneity, high numbers of weak trophic interactions, and high nutrient uptake efficiency in a richness-high system. Models of single trophic level communities further predict that richness can increase stability via statistical averaging, covariance, overyielding (Doak et al. 1998, Tilman et al. 1998, Lehman and Tilman 2000), and possibly by a stabilizing effect of component populations (Ives et al. 1999, DeWoody et al. 2003). Briefly, statistical averaging occurs when the variability of aggregate community properties decreases with increasing richness, because asynchronous fluctuations among species tend to offset each other. For this to occur, the log(variance) – log(mean) relation should have a scaling coefficient greater than 1 (Doak et al. 1998, Tilman et al. 1998). The strength of the statistical averaging effect is greatest when all species are equally abundant and weakens as community evenness decreases (Cottingham et al. 2001). Covariance indicates the relation among interacting species. Zero covariance indicates that species respond independently to the environment. Positive covariance indicates that species facilitate each other, or respond synchronously to the environment. Negative covariance indicates that species compensations exist due to competition or predation, or species respond asynchronously to the environment. If covariance summed across species becomes more negative with increasing richness, then this negative covariance should be stabilizing (Tilman et al. 1998). Overyielding refers to an increase in community biomass with richness, which tends to stabilize community fluctuations (Lehman and Tilman 2000). Lastly, richness may stabilize community fluctuation via its stabilizing effect on component populations, especially in communities with low evenness (equitability of species abundances). Since dominant species could have disproportionate influences on the dynamics of community properties, dominant species with less variable populations tend to lead to less variable communities (Ives et al. 1999, DeWoody et al. 2003).

In addition to directly affecting stability, nutrient enrichment and ecosystem size could directly control richness, which in turn influences stability. No previous studies, however, have tested empirically how these factors interact and co-determine stability. We manipulated nutrient input levels and ecosystem size in replicate microcosms containing diverse bacterial flora, and a range of green algae and heterotrophic protozoa. We did not manipulate richness directly. Instead, variation in richness was caused by direct manipulations of nutrient input and ecosystem size. The rationale for this is that most past empirical studies testing the effects of richness per se on stability manipulated richness, independent of variation in other factors. Such manipulations are useful for identifying independent effects of richness. However, the same environmental factors that influence stability are also likely to exert strong effects on richness (Worm and Duffy 2003, Ives and Carpenter 2007). Therefore we designed our experiment to include this realism, wherein richness could be determined by nutrient enrichment and ecosystem size, while all three factors could co-affect system stability. We addressed the following questions: 1) Do nutrients and ecosystem size affect richness? 2) Do nutrients, ecosystem size and richness co-affect stability, or are the effects of nutrients or ecosystem size only indirect and acting through richness? 3) Do different levels of biological organization (i.e. population versus community level) respond to treatments in a similar fashion? 4) What are the possible mechanisms for the observed relation between richness and community stability?

Methods

Microcosms were assembled with six protozoan species (*Paramecium aurelia, Paramecium bursaria, Arcella vulgaris, Euplotes eurystomus, Spirostomum ambiguum* and *Blepharisma americanum*), and six green algal species (*Volvox carteri, Micrasterias rotata, Scenedesmus opoliensis, Closterium libellula, Cosmarium sportella* and *Pandorina morum*) (Carolina Biological Supply). The advantage of laboratory microcosms comes at the sacrifice of a natural context, but all scientific endeavors make these tradeoffs (Morin 1998).

We used seven levels of productivity. 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. Tissue culture dishes of four different sizes 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 cm in all dishes to minimize artifactual differences among different 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 two days after algal addition. We distributed volumes of medium from stock culture to each culture dish in proportional to the area of that culture dish. All cultures were maintained in programmable incubators at 21.4°C with controlled light-dark cycles (12 h day / 12 h night). Positions of microcosms were alternated weekly to minimize positional effects.

The first sampling took place five days later after protozoan addition, and we allowed the experiment to run for 35 days afterward, during which we sampled microcosms every seven days up to the final day of the experiment (totally six sampling dates). On each sampling day, we mixed culture medium gently, and withdrew a total of 10% of the volume with five widely spaced subsamples (we performed 10% medium replacement after each sampling to replenish nutrients). These subsamples were mixed well, from which 300 μl was used for count. We recorded the density of each protist species as the number of individuals per milliliter, and estimated its biovolume from standard geometrical shapes (Wetzel and Likens 2000; also refer to <http://protist.i.hosei.ac.jp/pdb/images/menu.html>). Total biovolume of each species was calculated by multiplying specific biovolume of that species by its density. Lastly, evenness was calculated by dividing the reciprocal of Simpson's index by richness.

We used temporal variability to assess stability. Therefore, by definition, the smaller the temporal variability is, the greater the temporal stability is. Specifically, community variability was measured as the standard deviation in total protozoan (or algal) biovolume divided by mean biovolume taken over the six sampling dates. Population variability was measured as the standard deviation of biovolume divided by the mean biovolume for that species. We also averaged across populations to obtain a single measure of mean population variability for each microcosm. We assessed protozoa separately from algae for several reasons: 1) they represent different functional groups, 2) theoretical mechanisms for the stabilizing effect of richness by Tilman and colleagues (Tilman et al. 1998, Lehman and Tilman 2000) are based on single trophic level, 3) the combined high richness levels could be above the saturating point of the effect of richness on stability.

Our statistical analyses included several steps. For each group of eukaryotes, we first performed MANOVA to test the effects of nutrients and ecosystem size (independent categorical variables) on community stability and richness together. Given that they had significant effects on the multivariate response, we then performed an ANOVA to test whether these independent variables showed significant effects on richness alone. If so, we then used ANCOVA to test the effects of nutrient level, ecosystem size and richness (the former two were categorical variables while the last one was the continuous variable).

Our model of temporal variability, y, was:

$$y_{ijkl} \sim \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \epsilon_{ijkl} \tag{1}$$

where α_i was ecosystem size, β_j was nutrient level, γ_k was log(richness), and ϵ_{ijkl} was residual variation. The interactions included only ecosystem size × nutrient, and ecosystem × logarithmic richness. We could not include richness × nutrient interactions because the strong effect of nutrients on richness would violate assumptions of ANCOVA. We used AIC-based model selection to create a final parsimonious model.

When the sums of squares in the above model are partitioned sequentially (i.e. effects of nutrients before effects of richness), the resulting analysis provides us with an estimate of the amount of variation in variability explained uniquely by richness which could not be explained by the main effect of nutrients. Thus, this model provided us with a minimum effect of richness on stability.

We compared model (1) to an alternative (2), which accounts for the effects of richness first,

$$y_{ijkl} \sim \gamma_k + \alpha_i + \beta_j + \alpha\gamma_{ik} + \alpha\beta_{ij} + \epsilon_{ijkl} \tag{2}$$

and thereby provides us with a maximum effect of richness on variability. Given that the relation between richness and variability could be curvilinear, we also included quadratic terms for richness in the relevant sequences.

Statistical averaging was assessed by determining the relationship between summed variances and mean of community biovolume. We regressed the logarithms of the mean biovolume against the logarithms of summed variances. If the slope was greater than 1, this indicated that increasing richness reduced the summed variance, and thus stabilized the community. We then tested the relation between richness and evenness to check whether the effect of statistical averaging might be affected by unevenness. We calculated the summed covariances for each culture dish as the difference between the variances of community biovolumes and the sum of variances of individual species. Overyielding was assessed by checking the relationship between richness and mean biovolume, and a positive relationship would suggest

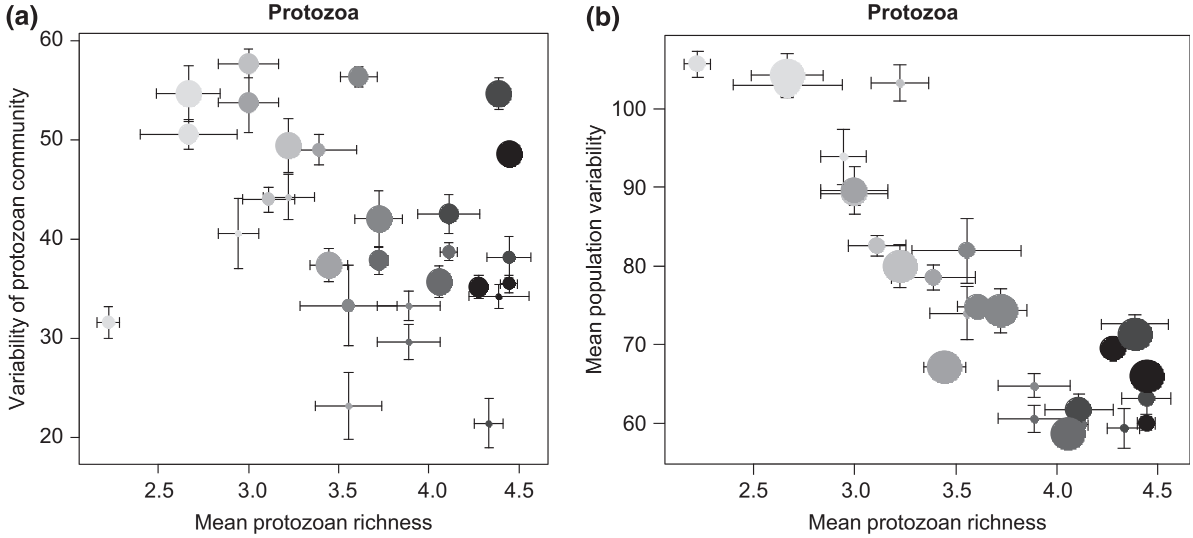

Figure 1. Effects of nutrient input and ecosystem size on protozoan richness and variability at different organization levels. (a) Joint response of protozoan community variability and protozoan richness to increased levels of nutrient input and ecosystem size. (b) Joint response of mean population variability and protozoan richness to increased levels of nutrient input and ecosystem size. Circles with different shades of grey represent different nutrient levels, with the darkest corresponding to the highest nutrient. Variation in circle size represents different ecosystem size. Results are shown as means ± CI.

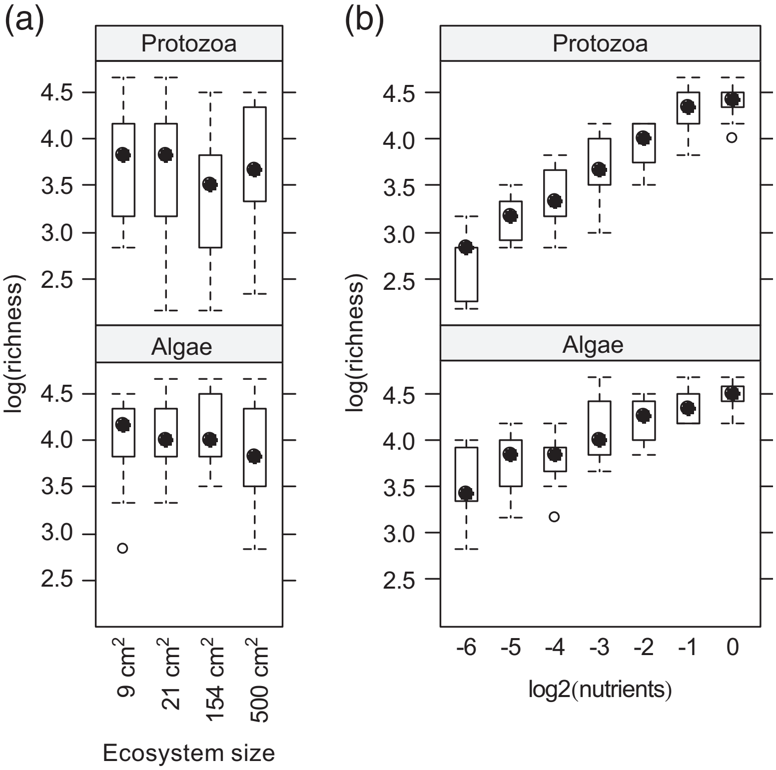

Figure 2. Weak effects of ecosystem size and strong effects of nutrients on richness. (a) Protozoa richness is lowest at intermediate ecosystem sizes (quadratic polynomial contrast $b = 0.057$, $t_{56} = 3.34$, $p = 0.001$); algae richness declined linearly with increasing size (linear polynomial contrast $b = -0.034$, $t_{56} = -2.28$, $p = 0.026$). (b) Both protozoa and algae richness increase strongly with increasing nutrient levels (linear contrasts $b_{\text{protozoa}} = 0.449$, $b_{\text{algae}} = 0.224$, both $p < 0.001$; quadratic contrast $b_{\text{protozoa}} = -0.083$, $p < 0.001$).

a contribution of overyielding to a reduction in community variability with increasing richness. Lastly, the correlation between community variability and mean population variability was calculated to test the hypothesis that richness stabilizes community fluctuation via its stabilizing effect on component populations. All statistical analyses were performed using R (ver. 2.7.0, R Development Core Team 2008).

Results

For protozoan communities, MANOVA showed significant main effects of nutrient and ecosystem size on community variability and richness ($F_{12,112} = 8.62$, $p < 0.001$; $F_{6,112} = 4.41$, $p < 0.001$, respectively; Fig. 1a). Univariate ANOVA showed that increasing nutrients increased richness ($F_{6,56} = 71.91$, $p < 0.001$), while ecosystem size had weak idiosyncratic

Table 1. ANCOVA tested for effects of nutrient input, ecosystem size, and richness on the variability of protozoan community in both (a) model 1 (a minimum effect of richness on variability) and (b) model 2 (a maximum effect of richness on variability). Retained variables in both models were based on the AIC criterion. R^2 provided an estimate of the amount of variation in variability explained by each corresponding variable.

(a) Model 1	DF	SS	MS	F	p	R^2
Size	3	3167.4	1055.8	7.08	<0.001	0.18
Richness	1	1211.2	1211.2	8.12	0.005	0.07
Richness^2	1	10.0	10.0	0.07	0.796	0.00
Size × richness	3	653.8	217.9	1.46	0.232	0.04
Size × richness^2	3	1807.6	602.5	4.04	0.010	0.10
Error	72	10742.8	149.2			

(b) Model 2	DF	SS	MS	F	p	R^2
Richness	1	1586.1	1586.1	9.37	0.003	0.09
Richness^2	1	24.0	24.0	0.14	0.708	0.00
Size	3	2778.5	926.2	5.47	0.002	0.16
Error	78	13204.2	169.3			

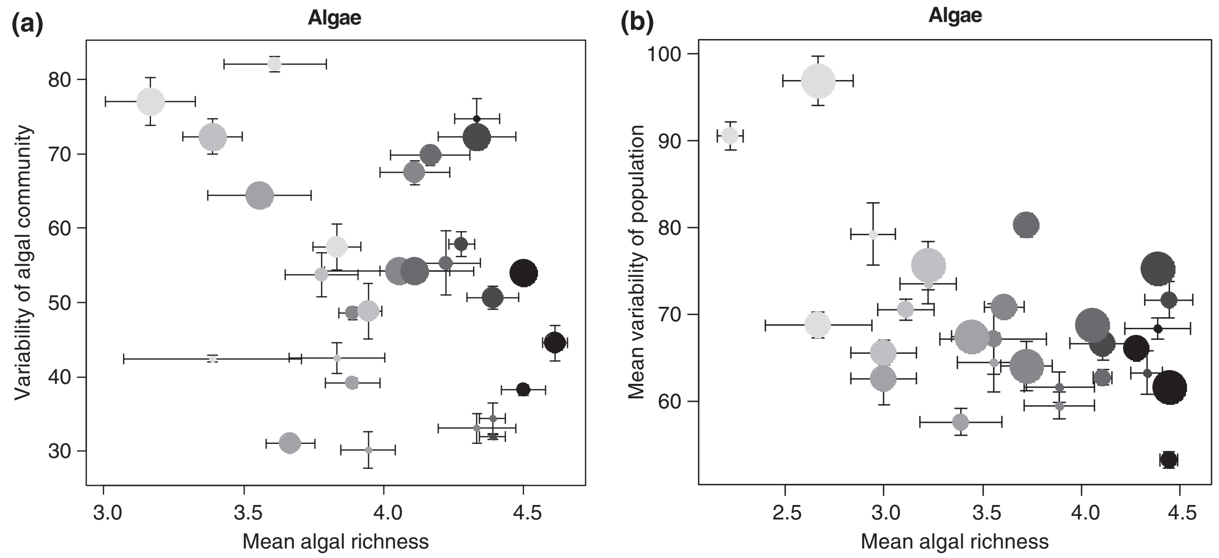

Figure 3. Effects of nutrient input and ecosystem size on algal richness and variability at different organization levels. (a) Joint response of algal community variability and algal richness to increased levels of nutrient input and ecosystem size. (b) Joint response of mean population variability and algal richness to increased levels of nutrient input and ecosystem size. Circles with different shades of grey represent different nutrient levels, with the darkest corresponding to the highest nutrient input. Variation in circle size represents different ecosystem size. Results are shown as means ± CI.

effects on richness (i.e. quadratic concave relation between richness and ecosystem size) ($F_{3,56} = 4.13$, $p = 0.010$) (Fig. 2). Two ANCOVAs differed only in whether richness was fitted to models before or after other factors, measuring the maximum or minimum variation in variability predicted by richness. In both models, the AIC criterion supported retaining only ecosystem size and richness, and not nutrients (Table 1). These final models showed that community variability decreased with richness (partial $R^2 = 0.07$ and 0.09), but increased with ecosystem size (partial $R^2 = 0.16$ and 0.18).

For algal communities, MANOVA showed the combined response of community variability and richness depended on the interaction of nutrients and ecosystem size ($F_{36,112} = 1.64$, $p = 0.027$; Fig. 3a), with variability positively related to nutrients in smallest ecosystem size, but the pattern reversed in other ecosystem sizes. Univariate ANOVA showed that increasing nutrient increased richness ($F_{6,56} = 23.35$, $p < 0.001$), while increasing ecosystem size decreased richness ($F_{3,56} = 3.43$, $p = 0.023$; Fig. 2). The AIC criterion for ANCOVA supported retaining all terms in the model (Table 2). Community variability decreased linearly with

Table 2. ANCOVA tested for effects of nutrient input, ecosystem size, and richness on the variability of algal community in both (a) model 1 (a minimum effect of richness on variability) and (b) model 2 (a maximum effect of richness on variability).

(a) Model 1	DF	SS	MS	F	p	R^2
Size	3	5437.8	1812.6	9.57	<0.001	0.17
Nutrient	6	3409.4	568.2	3.00	0.015	0.11
Richness	1	625.4	625.4	3.30	0.076	0.02
Richness^2	1	316.7	316.7	1.67	0.202	0.01
Size × nutrient	18	10572.6	587.4	3.10	<0.001	0.33
Size × richness	3	1065.8	355.3	1.88	0.147	0.03
Size × richness^2	3	1364.0	341.0	1.80	0.145	0.04
Error	47	8903.9	189.4			

(b) Model 2	DF	SS	MS	F	P	R^2
Richness	1	1476.8	1476.8	7.80	0.008	0.05
Richness^2	1	1615.6	1615.6	8.53	0.005	0.05
Size	3	4312.9	1437.6	7.59	<0.001	0.14
Nutrient	6	2384.0	397.3	2.10	0.071	0.08
Richness × size	3	1664.6	554.9	2.93	0.043	0.05
Size × richness^2	3	944.7	236.2	1.25	0.304	0.03
Size × nutrient	18	10393.0	577.4	3.05	0.001	0.33
Error	47	8903.9	189.4			

Table 3. ANCOVA tested for effects of nutrient input, ecosystem size, and richness on the mean protozoan population variability in both (a) model 1 (a minimum effect of richness on variability) and (b) model 2 (a maximum effect of richness on variability).

(a) Model 1	DF	SS	MS	F	p	R^2
Nutrient	6	14612.4	2435.4	16.24	<0.001	0.47
Richness	1	5053.9	5053.9	33.71	<0.001	0.16
Error	76	11394.9	149.9			

(b) Model 2	DF	SS	MS	F	p	R^2
Richness	1	17703.0	17703.0	118.07	<0.001	0.57
Nutrient	6	1963.3	327.2	2.18	0.053	0.06
Error	76	11394.9	149.9			

richness to only a small degree (partial $R^2 = 0.02$ and 0.05) and nutrients (partial $R^2 = 0.08$ and 0.11), but increased with ecosystem size (partial $R^2 = 0.14$ and 0.17).

At population level, MANOVA showed significant main effects of nutrients and ecosystem size on protozoan population variability ($F_{36,336} = 1.80$, p = 0.004; $F_{18,159} = 2.53$, p = 0.001, respectively; Fig. 1b). The AIC criterion supported retaining only nutrients and richness, and not ecosystem size (Table 3). Protozoan population variability decreased with nutrients (partial $R^2 = 0.06$ and 0.47) and richness (partial $R^2 = 0.16$ and 0.57). For algae, MANOVA showed significant main effects of nutrients and ecosystem size on algal population variability ($F_{36,336} = 2.30$, $p < 0.001$; $F_{18,159} = 3.53$, $p < 0.001$, respectively; Fig. 3b). The AIC criterion supported retaining only nutrients and richness, and not ecosystem size (Table 4). Algal population variability decreased with nutrients (partial $R^2 = 0.11$ and 0.23) and richness (partial $R^2 = 0.31$ and 0.45). Lastly, the relative importance of nutrients, ecosystem size, and richness in affecting population stability of individual species was species-specific (Supplementary material Appendix 1 Table S1, S2).

The slope of the mean-variance scaling relationship averaged across all protozoa was 1.57 (Fig. 4a). The summed covariance had both positive and negative values, and there was no relationship between summed covariance and richness (Fig. 4b). The logarithms of the mean protozoan biovolume increased with richness significantly ($r^2 = 0.86$, $p < 0.001$; Fig. 4c). Community variability increased with increasing mean population variability ($r^2 = 0.36$, $p < 0.001$; Fig. 4d). The slope of the mean-variance scaling relationship averaged across all algae was 1.89 (Fig. 5a). The summed covariance had both positive and negative values, and there was no relationship between summed covariance and richness (Fig. 5b). The logarithms of the mean algal biovolume increased with richness significantly ($r^2 = 0.71$, $p < 0.001$; Fig. 5c). Community variability increased with increasing mean population variability ($r^2 = 0.44$, $p < 0.001$; Fig. 5d). Finally, for both protozoan and algal communities, mean evenness declined with increasing mean richness ($r^2 = 0.74$, $p < 0.001$; $r^2 = 0.62$, $p < 0.001$, respectively; Fig. 6a–b). This decrease in evenness was primarily because of increasing dominance by two consumers, *P. bursaria* and *Blepharisma* (Fig. 4a), and by two primary producers, *Scenedesmus* and *Cosmarium* (Fig. 5a). For all four dominants, time-averaged values of biovolume decreased with increasing mean evenness, but increased with increasing mean richness (Supplementary material Appendix 1 Fig. S3, S4).

Discussion

Consistent with many other studies (Tilman and Downing 1994, Caldeira et al. 2005, Steiner et al. 2005, Romanuk et al. 2006, Vogt et al. 2006), we found that community stability increased with increasing richness. We explored possible mechanisms, and found that richness increased community stability via statistical averaging, overyielding, and component population stability effects. Our results did not support the covariance effect hypothesis. The presence of both positive and negative covariances indicated that the way species interacted may change through time. Although

Table 4. ANCOVA tested for effects of nutrient input, ecosystem size, and richness on the mean algal population variability in both (a) model 1 (a minimum effect of richness on variability) and (b) model 2 (a maximum effect of richness on variability).

(a)	DF	SS	MS	F	p	R^2
Nutrient	6	3827.3	637.9	6.46	<0.001	0.23
Richness	1	4187.6	4187.6	42.42	<0.001	0.25
Richness^2	1	1035.7	1035.7	10.49	0.002	0.06
Error	69	6810.9	98.7			

(b)	DF	SS	MS	F	p	R^2
Richness	1	5339.7	5339.7	58.19	<0.001	0.32
Richness^2	1	2154.4	2154.4	23.48	<0.001	0.13
Nutrient	6	1834.6	305.8	3.33	0.008	0.11
Error	69	6810.9	98.7			

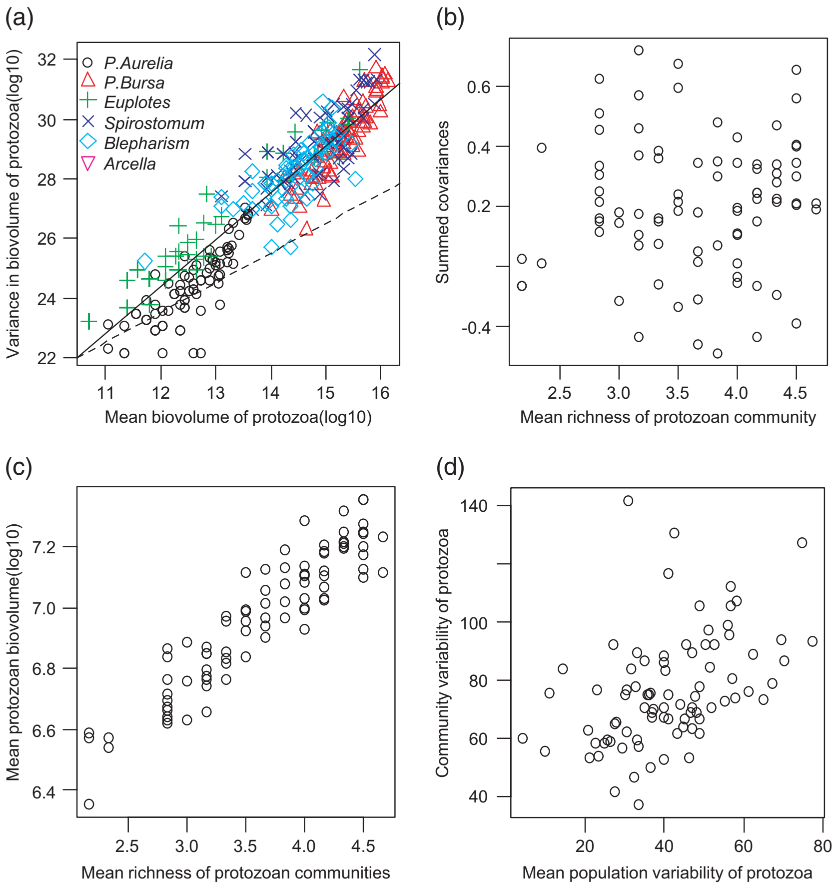

Figure 4. (a) Log-log plot of variances in the biovolume of individual protozoan species in all replicates versus the mean biovolume of each protozoan species (solid line, slope = 1.57; dotted contrast line, slope = 1). (b) Summed covariances of protozoan biovolume for all replicates vs. mean protozoan richness of the replicate. (c) The relationship between mean protozoan biovolume and mean protozoan richness ($r^2 = 0.86$, $p < 0.001$). (d) The relationship between protozoan community variability and mean population variability ($r^2 = 0.36$, $p < 0.001$).

it is difficult to estimate the relative importance of aforementioned mechanisms to each other, community evenness may affect their relative strength. On one hand, the effect of statistical averaging could be strong in communities with relatively high evenness and with the value of scaling coefficient more than 1, but the strength of this effect could weaken with an increasing unevenness (Cottingham et al. 2001). On the other hand, as unevenness increases, dominant species with relatively high biovolumes, or inherently low population variability could have significant influence on community stability. In our case, we found that increased dominance of two protozoan species, *P. bursaria* and *Blepharisma*, and two algal species, *Scenedesmus* and *Cosmarium*, with increasing richness but decreasing evenness. Interestingly, the two dominant protozoan species both have strong population buffering mechanisms. *P. bursaria* has algal endosymbionts, rendering it less dependent on bacterial or algal prey (Loefer 1936). *Blepharisma* is highly competent as an omnivore, which could be stabilizing (Morin and Lawler 1996). In addition, *Blepharisma* has cannibalistic behavior, another possible stabilizing mechanism (Rudolf 2007).

By contrast, empirical studies have documented opposite relationships between population stability and richness, such as negative relationships (Tilman and Downing 1994, Caldeira et al. 2005), and positive relationships (Romanuk et al. 2006, Vogt et al. 2006). Recent simulation and empirical studies have shown that increasing predator-prey body mass ratios could lower metabolic and consumption rates, and therefore, reduce the average interaction strength and promote stability (Emmerson and Raffaelli 2004, Brose et al. 2006, Otto et al. 2007, Rall et al. 2008). Also, populations are more stable in diverse communities due to the presence of more weak trophic links (McCann et al. 1998, Brose et al. 2006). Our experimental design did not allow us to directly test these ideas, but the high mass ratios between bacterivorous protozoa and prey bacteria in our experiment could lead to a reduction in the average interaction strength, and potentially explain why species richness and population stability were positively correlated in our study and several other microcosm experiments.

We found that nutrient enrichment promoted richness of both protozoan and algal functional groups, but we did not find direct effects of enrichment on protozoan community stability. One likely explanation is that enrichment could directly control richness, which in turn influences stability. In other words, the effect of enrichment on protozoan

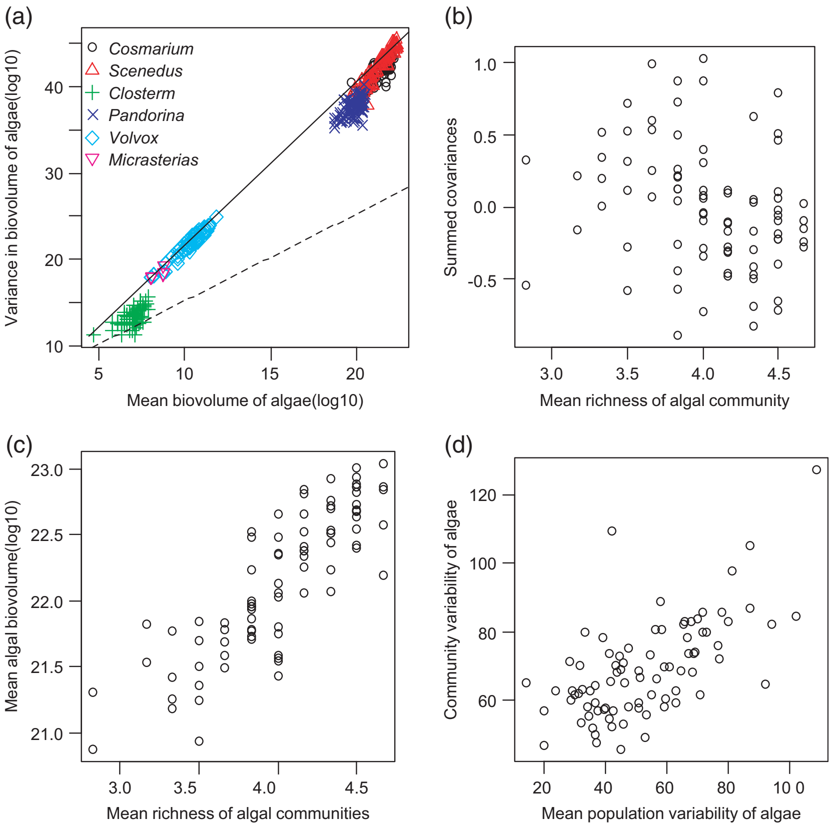

Figure 5. (a) Log-log plot of variances in the biovolume of individual algal species in all replicates vs. the mean biovolume of each algal species (solid line, slope = 1.89; dotted contrast line, slope = 1). (b) Summed covariances of algal biovolume for all replicates versus. mean algal richness of the replicate. (c) The relationship between mean algal biovolume and mean algal richness ($r^2 = 0.71$, $p < 0.001$) (d) The relationship between algal community variability and mean population variability ($r^2 = 0.44$, $p < 0.001$).

community stability could have been mediated by richness. This indirect effect of enrichment on variability has also been reported in other empirical studies (Steiner et al. 2005, Romanuk et al. 2006). Similarly, the effect of ecosystem size on protozoan and algal population stability could also have been mediated by richness.

We found no support for the theoretical prediction that community stability will increase with ecosystem size (McCann et al. 2005) because our results showed that community stability was high in small ecosystems, but low in large ecosystems. One explanation is that an increase in ecosystem size may increase prey carrying capacity or population

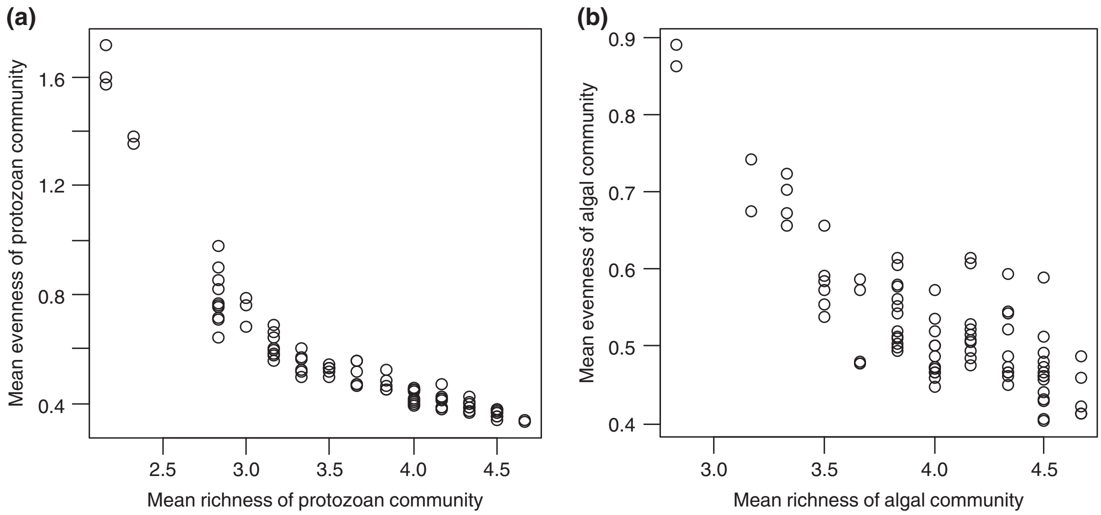

Figure 6. (a) The relationship between mean evenness and richness of protozoan community ($r^2 = 0.74$, $p < 0.001$); (b) The relationship between mean evenness and richness of algal community ($r^2 = 0.62$, $p < 0.001$).

growth rate (Griffen and Drake 2008), and thus reduce the negative-feedback mechanism of prey intraspecific competition. In this sense, increasing size could have a negative effect on stability in the same manner as nutrient enrichment does. Furthermore, it can be argued that since large ecosystems could contain more total available resources as a result of their size (Schoener 1989), stability could be lower in large ecosystems than in small ecosystems if resource enrichment has a direct destabilizing effect. Lastly, for our study, we held initial densities constant among culture dishes with different sizes. Had we held initial population sizes constant over dishes so that initial densities were higher in smaller systems than that of larger systems, we might get different results.

In our experiment, protist richness consistently increased but evenness decreased with nutrient enrichment. Since declines in evenness may lead to declines in richness (Wilsey and Polley 2004), we might expect a hump-shaped relationship between nutrient enrichment and protist richness occurring if the experiment had been carried out at higher nutrient levels. A positive relationship, however, may still persist at higher nutrient levels. A recent meta-analysis study showed that nutrient enrichment could reduce both richness and evenness in terrestrial systems, but reduce evenness and increase richness in aquatic systems (Hillebrand et al. 2007).

In conclusion, we found that both community stability and population stability increased with richness. Although we found support for three mechanisms, statistical averaging, overyielding, and component populations, their relative importance likely varied as community evenness changed. We did not find direct effects of nutrients on protozoan community stability, or direct effects of ecosystem size on protozoan and algal population stability, and their effects on stability were likely mediated by richness.

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