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Nutrient enrichment weakens the stabilizing effect of species richness

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With global freshwater biodiversity declining at an even faster rate than in the most disturbed terrestrial ecosystems, understanding the effects of changing environmental conditions on relationships between biodiversity and the variability of community and population processes in aquatic ecosystems is of significant interest. Evidence is accumulating that biodiversity loss results in more variable communities; however, the mechanisms underlying this effect have been the subject of considerable debate. We manipulated species richness and nutrients in outdoor aquatic microcosms composed of naturally occurring assemblages of zooplankton and benthic invertebrates to determine how the relationship between species richness and variability might change under different nutrient conditions. Temporal variability of populations and communities decreased with increasing species richness in low nutrient microcosms. In contrast, we found no relationship between species richness and either population or community variability in nutrient enriched microcosms. Of the different mechanisms we investigated (e.g. overyielding, statistical averaging, insurance effects, and the stabilizing effect of species richness on populations) the only one that was consistent with our results was that increases in species richness led to more stable community abundances through the stabilizing effect of species richness on the component populations. While we cannot conclusively determine the mechanism(s) by which species richness stabilized populations, our results suggest that more complete resource-use in the more species-rich low nutrient communities may have dampened population fluctuations.

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While freshwaters are currently losing species as rapidly as tropical forests (Ricciardi and Rasmussen 1999), and anthropogenic eutrophication is expected to increase nearly 3-fold by 2050, resulting in unprecedented species extinctions (Tilman 1999a), the consequences of species loss on the stability of freshwater ecosystems are largely unknown. Species richness has been suggested to reduce temporal variability in community abundance (reviewed by McCann 2000, Cottingham et al. 2001, Loreau et al. 2001) through a wide range of processes including overyielding (Tilman 1999b), insurance and competition effects (Petchey et al. 1999, Tilman 1999b, Yachi and Loreau 1999), statistical averaging (Doak et al. 1998, Tilman et al. 1998), and the effects of species richness on population level variability (Ives et al. 1999, Petchey 2000, Petchey et al. 2002, Romanuk 2002, DeWoody et al. 2003, Romanuk and Kolasa 2004, Vogt et al. 2006). However, in contrast to previous studies that have reported a destabilizing effect of increasing species richness on population abundances, particularly in plant communities (Tilman 1996, Caldeira et al. 2005), species richness appears to stabilize both community and

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population abundances in some multi-trophic aquatic communities (Romanuk 2002, Romanuk and Kolasa 2002a, Kolasa and Li 2003, Romanuk and Kolasa 2004, Steiner et al. 2005, Vogt et al. 2006). These results suggests that the above mechanisms that have been previously proposed to underlie the stabilizing effect of species richness on community abundances may not be sufficient for systems whose constituent populations are at different trophic levels and are forced to interact (Petchey et al. 2004).

In this paper we report on the results of an experiment designed to determine whether nutrients and increasing species richness affected the temporal variability of both population and community abundances in multi-trophic meiofaunal communities assembled from tropical coastal rock pools (Romanuk and Kolasa 2002a, Srivastava et al. 2004, Kolasa and Romanuk 2005). We use the results of this experiment to explore four classes of mechanisms by which species richness has been hypothesized to stabilize temporal variability in aggregate community abundance: overyielding (Tilman 1999b), statistical averaging (Doak et al. 1998, Tilman et al. 1998), competition or insurance effects (Tilman 1999b, Yachi and Loreau 1999), and a stabilizing effect of species richness on component populations (Petchey et al. 2002, Romanuk 2002).

Briefly, overyielding refers to an increase in mean community abundance with increasing species richness, which tends to stabilize community fluctuations (Tilman 1999b). Statistical averaging, or the portfolio effect, occurs when the variability of an aggregate community property, such as abundance, declines with increased species richness even in the absence of any strong species interactions (Doak et al. 1998, Tilman et al. 1998, Ives et al. 1999, 2000). Statistical averaging should be stabilizing if the mean-variance relation of population abundance has a slope greater than 1 and should be destabilizing if it has a slope less than 1 (Petchey et al. 2002). Insurance or competitive effects, such as different responses to environmental fluctuations or strong interspecific interactions, can be stabilizing if populations fluctuate asynchronously (Tilman 1999b, Ives et al. 2000). Lastly, species richness may stabilize community fluctuations through a stabilizing effect on component populations, i.e. less variable populations will lead to less variable communities (Petchey et al. 2002, Romanuk 2002, Romanuk and Kolasa 2004, Vogt et al. 2006).

Methods

Experimental design

We conducted this experiment on the grounds of the Discovery Bay Marine Laboratory (DBML) on the north coast of Jamaica (18°28′N/77°25′W) from 27 September to 5 November 2001. Descriptions of the site, rock pools, species, and sampling methods have been published previously (Kolasa et al. 1996, 1998, Romanuk and Kolasa 2001, 2002a, 2002b, Kolasa and Romanuk 2005). We used a 5×3 factorial design with five initial levels of diversity and three levels of nutrients (Romanuk and Kolasa 2005). Each of the 15 treatment combinations was replicated three times for a total of 45 microcosms. Artificial 'rock pools', hereafter called microcosms, were plastic cups, 8 cm in diameter and 15 cm deep. The microcosms were filled to a depth of 10 cm (volume 500 ml) with rock pool water (below) and were set up outdoors $\sim$25 m from the natural rock pools on 27 September 2001. The microcosms were placed on a 3×1 m table that was 1 m in height and were covered loosely with a 2 mm mesh fiberglass screening. The size of the microcosms was representative of smaller sized natural rock pools, which range in volume from $\sim$250 ml to 115 l.

In 15 years of sampling 49 of the natural rock pools on a yearly basis we have identified 75 different species of micro- and meio-invertebrates with species richness in any one pool ranging from 0–16 species (Romanuk and Kolasa 2002b). Experimental communities reflected this range and consisted of mixtures of 11 of these species that were retained on a 63 μm mesh net: three species of ostracods (*Candona* sp., *Cypridopsis* sp., *Potamocypris* sp.), a chydorid (*Alona davidii*), a daphnid (*Ceriodaphnia* sp.), a copepod (*Orthocyclops modestus* Herrick), a larval decapod (*Armases miersii* Rathbun), two worms (one species of Nematode and one species of Oligochaete), and two dipteran larvae (*Culex* sp. and *Dasyhelea* sp.). Every species that was present in the rock pool water was used in the experiment.

Generation times for these taxa were short due to high water temperature (up to $\sim$33°C). Zooplankton that are sized similarly to those found in our communities have generation times ranging from $\sim$8–20 days at 20°C (Gillooly 2000). These generation times would be substantially reduced at the average water temperature measured in our microcosms ($\sim$27°C; T. N. Romanuk, unpubl.). For example, *Alona affinis*, which is a similar to our *Alona davidii*, has a generation time of 73 days at 5°C, 39 days at 10°C, 26 days at 15°C and 17 days at 20°C (Gillooly 2000). Based on Gillooly (2000) the generation time for species in our microcosms would have ranged from $\sim$2–14 days. Population growth curves are shown in Fig. 1 for the seven most abundant species.

To manipulate species richness we collected 30 liters of rock pool water with a standard salinity of 0 ppt and filtered half of the water through a 63 μm mesh filter. Species smaller than 63 μm such as rotifers, protozoans, and the juvenile stages of the target communities (e.g. copepod nauplii) would not have been affected by this manipulation. This manipulation resulted in 15 liters of "filtered" rock pool water from which all organisms

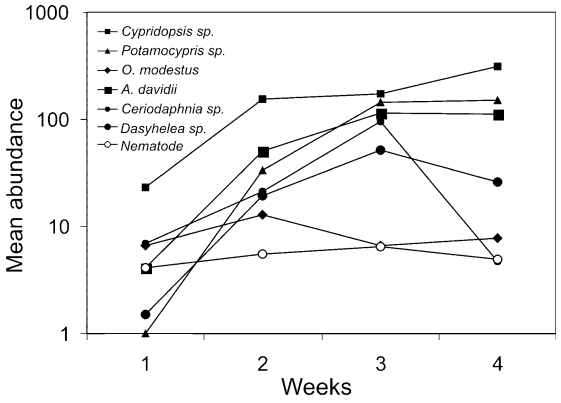

Fig. 1. Population growth (log scale) for the seven most abundant species from week 1 to week 4. Note that only the last three weeks of samples were used in the analysis.

larger than the mesh size had been removed, and 15 liters of "natural" rock pool water with all the invertebrates in natural proportions. The initial diversity treatments (DT) were created by mixing the "filtered" water and the "natural" water together to create five diversity levels (DT = 0%, 25%, 50%, 75% and 100%). The percent given represents the amount of natural 'unfiltered' water in each diversity level. For example, the DT = 0% level was composed of only filtered water (i.e. control), and the DT = 25% level contained ¼ "natural" water and ¾ "filtered" water. This procedure effectively manipulated the abundance and richness of the target communities (Romanuk and Kolasa 2005).

This type of diversity manipulation is called a dilution series (Franklin et al. 2001, Goldberg et al. 2001, Giller et al. 2004, Romanuk and Kolasa 2005, Vogt et al. 2006). The premise behind using a dilution series to manipulate diversity is that dilution of a diverse community will result in the exclusion of rarer species as the dilution progresses. Subsequent re-growth of diluted mixtures should then result in cultures of differing species richness that retain roughly the same biomass or abundance (Franklin et al. 2001). Recently, Giller et al. (2004) discussed the potential of using dilution series to manipulate species richness in diversity-ecosystem function experiments in aquatic systems. They concluded that dilution experiments may be preferable to random loss methods with multiple comparisons per diversity level. One potential problem with using dilution series is that dilution can also affect abundance. Thus it is necessary to allow the mixtures to rebuild their abundance following the initial manipulation; otherwise, differences in species richness will be confounded with differences in abundance. However, as long as re-growth occurs, the method should reveal how extinctions alter ecosystem functioning (Naeem et al. 1995). To determine the effectiveness of the diversity manipulation we used linear regression and ANOVA with Tukey post-hoc tests.

The microcosms were fertilized on 27 September with soluble phosphorus (KH_2PO_4) and nitrogen (NH_4NO_3) with an N:P ratio of 20:1. Low nutrient microcosms had no nutrients added and served as controls for the nutrient manipulations. The intermediate nutrient treatment had nutrients added once at the start of the experiment (n = 15). The high nutrient microcosms had nutrients added at the start of the experiment and again after the first week (n = 15). Nutrients were measured on 5 November for one of each DT/NT combination. Differences in N, P and the N:P ratios across nutrient levels (NT) were assessed using t-tests.

Overall, five weekly samples were taken including a set of baseline samples to determine the species composition and effectiveness of the dilution series. Microcosms were sampled weekly by gently stirring the water with a glass stirrer and using a 50 ml dip container to collect 30 ml of water. This water was sieved through a 63 μm mesh sieve and then stored in a centrifuge tube in 50%–70% ethanol. The volume of water removed was replaced with filtered rock pool water following sampling. Only the last three weeks of samples were analyzed to allow for re-growth to similar density levels across all microcosms (Fig. 1; also Romanuk and Kolasa 2005). Samples were enumerated using a dissecting microscope and individuals were identified to species or genus. Where we identify a taxon to genus level, that genus represents one species only and not a number of different species.

Data analysis

Mean species richness is the average of microcosm species richness across the three sampling dates. Temporal variability, variability from here on, was evaluated as coefficients of variation (CV). We used CV because they standardize for differences in abundance (Cottingham et al. 2001). Community variability, CV_C, is the standard deviation in total microcosm abundance (all species combined) divided by mean abundance taken over the three sampling dates. Population variability was calculated in two ways: 1) we calculated CV for each species across all microcosms, $CV_{species}$, as the standard deviation of abundance divided by the mean abundance for each species, 2) we calculated the mean variability of all populations in each microcosm, CV_{POP}, as the standard deviation of mean population variability for each microcosms divided by the mean variability for each microcosm. This latter method yields a single measure of population variability per microcosm and can be used to relate community and population variability directly (Romanuk 2002, Steiner et al. 2005, Vogt et al. 2006).

Statistical averaging was assessed by determining the relationship between species richness and summed variances (Tilman 1999b). If statistical averaging is occurring increased species richness should decrease the summed variances and the slope of the corresponding mean-variance relation should be greater than 1 (Petchey et al. 2002). Mean-variance scaling relationships were assessed according to Tilman (1999b) where $s = cm^z$ (s is the variance, c is a constant, m is the mean and z is the scaling coefficient). We calculated mean-variance scaling relationships for individual species. Competitive effects and insurance effects were assessed by determining the relationship between species richness and summed covariances (Tilman 1999b). If competitive or insurance effects underlie the stabilizing effect of species richness on community abundances then summed covariances should become more negative as species richness increases. Overyielding was assessed by determining the relationship between species richness and summed abundances (Tilman 1999b), where a positive relationship would suggest a contribution of overyielding to a reduction in community variability with increasing species richness.

The effect of nutrients (NT, low nutrient, intermediate nutrient, high nutrient) and mean species richness (species richness) on CV_C, CV_{POP}, $CV_{species}$, summed variances (log_{10}), summed covariances, summed abundances (log_{10}), and mean-variance scaling z-values were assessed using GLM in Statistica 6.0 (Statsoft 2004). First, we tested for significant differences in slopes based on NT using a "homogeneity of slopes model" (HOM). Where significant differences in slopes were present, we used a 'separate slopes model' (SSM)-otherwise we used analysis of covariance (ANCOVA). The one exception to the above procedure was for the effects of mean species richness and NT on CV_C where we used both models (i.e. ANCOVA and the SSM) because the interaction term in the 'homogeneity of slopes model' was only marginally insignificant (Table 1). The separate slopes model was used because the traditional analysis of covariance (ANCOVA) design for categorical and continuous predictor variables is inappropriate when the categorical

Table 1. General linear models for effects of mean species richness and nutrient treatment, NT, on a) community variability, CV_C and b) population variability, CV_{POP}.

	SS	df	MS	F	P
a) Community variability					
Homogeneity of slopes model					
Intercept	4.986	1	4.986	51.906	>0.001
NT	0.576	2	0.288	2.999	0.061
Mean species richness	0.583	1	0.583	6.065	0.018
NT × mean species richness	0.518	2	0.259	2.697	0.080
Error	3.747	39	0.096		
ANCOVA					
Intercept	5.023	1	5.023	48.289	>0.001
Mean species richness	0.548	1	0.548	5.271	0.027
NT	0.258	2	0.129	1.241	0.300
Error	4.265	41	0.104		
Separate slopes model					
Intercept	4.986	1	4.986	51.906	>0.001
NT × mean species richness	1.066	3	0.355	3.700	0.020
NT	0.576	2	0.288	2.999	0.061
Error	3.747	39	0.096		
b) Mean population variability					
Homogeneity of slopes model					
Intercept	12.180	1	12.180	444.628	>0.001
NT	0.254	2	0.127	4.628	0.016
Mean species richness	0.644	1	0.644	23.507	>0.001
NT × mean species richness	0.326	2	0.163	5.959	0.006
Error	1.068	39	0.027		
Separate slopes model					
Intercept	12.180	1	12.180	444.628	>0.001
NT × mean species richness	0.912	3	0.304	11.101	>0.001
NT	0.254	2	0.127	4.628	0.016
Error	1.068	39	0.027		

A 'homogeneity of slopes' (HOM) model was used first to determine interactions between species richness and nutrient treatment, NT. ANCOVA was used if slopes between species richness and species variability did not differ based on NT. A separate slopes model was used if the slope between species richness and species variability differed significantly according to NT. We used both ANCOVA and a SSM for community variability as the result of the species richness × NT interaction in the HOM model was only marginally insignificant.

and continuous predictors interact in influencing the outcome. The primary difference between ANCOVA and the separate slope designs is that separate slopes design omits the main effects for continuous predictors (Statsoft 2004).

Linear regression was used to determine whether there was a relationship between CV_{POP} and CV_C. Backward multiple stepwise regressions were used to determine whether CV_{POP}, species richness, and mean abundance explained more variability in CV_C than species richness alone across all nutrient treatments and within each nutrient treatment. For all analyses comparing the effects of the nutrient treatment on patterns at the individual species level we only considered the six species that were present in at least three replicates in all three nutrient conditions.

Results

Nutrient treatment manipulation

Nutrient concentrations were significantly different across low, intermediate, and high nutrient microcosms ($P < 0.001$). Mean total phosphorus (P) and nitrate+nitrite (N) were 0.105 μg l^{-1} P (SD 0.015) and 1.61 μg l^{-1} N (SD 0.426) in low nutrient microcosms, 3.35 μg l^{-1} P (SD 0.225) and 11.83 μg l^{-1} N (SD 0.752) in intermediate nutrient microcosms, and 5.483 μg l^{-1} P (SD 0.923) and 26.5 μg l^{-1} N (SD 1.87) in high nutrient microcosms. The N:P ratio averaged 16.8, 3.45 and 4.48 for low, intermediate and high nutrient microcosms respectively, with ratios being significantly different at $P < 0.001$. These values were representative of N and P in the natural pools which ranged from 0.02 to 12.1 μg l^{-1} P (mean 0.356 ± SD 2.57) and 5.89 to 102.23 μg l^{-1} N (mean 38.92 ± SD 25.46).

Species richness manipulation

The dilution series significantly affected initial species richness and abundance, and the general trend of higher species richness and abundance in less diluted treatments was retained throughout the experiment (Romanuk and Kolasa 2005). However, mean abundance was only significantly different between DT = 0 and the other DT's ($P < 0.05$; Romanuk and Kolasa 2005). In contrast, mean species richness differed significantly between DT = 0 and all other DT levels as well as between DT = 25 and DT = 50 ($P < 0.05$; Romanuk and Kolasa 2005). Initial species richness in the microcosms (week 1) ranged from 0 to 8 species (mean 4.15 ± 2.39 SD) and decreased over time. Initial mean abundance ranged from 0 to 159 (mean 30.47 ± 30.95 SD) and increased over time. Similar sets of species were present in all three nutrient conditions and the three most abundant species in the low nutrient microcosms (*Cypridopsis* sp., *Potamocypris* sp. and *O. modestus*), which comprised 89% of the total abundance, were also the three most abundant in the intermediate (79%) and high nutrient microcosms (76%). The three most abundant species were also present in at least one replicate from DT = 0 and were present in 35 of 35 (*Cypridopsis* sp. and *O. modestus*) or 30 of 35 (*Potamocypris* sp.) replicates from DT = 25–100 during week 2. This pattern indicates that dominant species were lost from the sampling counts of higher species richness replicates in less than 4% of the cases.

Effects of nutrient enrichment on species richness and N

Nutrient additions had no significant effect on mean species richness ($F_{2,42} = 0.108$, $P = 0.347$), while mean abundance increased with nutrient enrichment ($F_{2,42} = 5.169$, $P = 0.001$).

Community and population variability

CV_C declined with increasing species richness, albeit weakly, when data were pooled across NT ($r^2 = 0.074$, $P = 0.039$). However, within NT, species richness only significantly decreased CV_C under low nutrient conditions ($F_{3,39} = 3.7$, $P = 0.02$; Fig. 2a, Table 1). In the low nutrient microcosms species richness explained 36% of the variance in CV_C ($P = 0.019$, $n = 15$) whereas under nutrient enriched conditions species richness had no impact on CV_C (intermediate, $P = 0.875$, $n = 15$; high, $P = 0.117$, $n = 15$).

CV_{POP} also declined with increasing species richness when data was pooled across NT ($r^2 = 0.272$, $P < 0.001$). Similar to the pattern for CV_C, however, species richness only significantly decreased CV_{POP} in low nutrient microcosms ($F_{2,39} = 5.958$, $P = 0.006$; Fig. 2b, Table 1) explaining 72.4% of the variance in CV_{POP} (CV_{POP}, $r^2 = 0.724$, $P < 0.001$). In the nutrient enriched microcosms, species richness did not significantly affect CV_{POP} (intermediate $r^2 = 0.195$, $P = 0.056$; high $P = 0.579$). CV_{POP} was highest in the high nutrient microcosms ($F_{2,39} = 11.101$, $P < 0.001$).

Effect of species richness on summed variances, covariances, abundances, and mean-variance scaling

Species richness increased summed abundances in the low nutrient microcosms but not in the intermediate or high nutrient microcosms ($F_{3,39} = 7.48$, $P < 0.001$; Fig. 3a). However, when the three replicates with mean species richness of less than 1.5 were removed from the analysis for the low nutrient microcosms, species richness was shown to be unrelated to summed

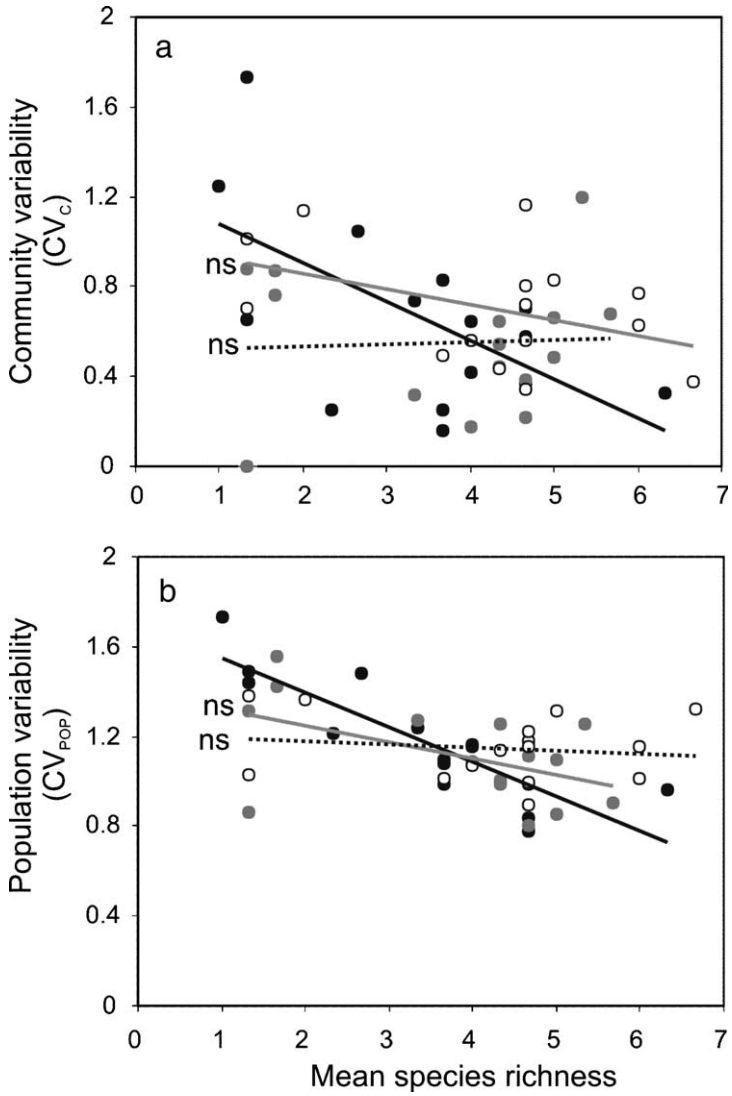

Fig. 2. Effect of species richness on (a) temporal variability in community abundance (CV_C,) and (b) temporal variability in mean population abundance (CV_{POP}) for low nutrient (black circles, black line), intermediate nutrient (grey circles, grey line), and high nutrient (open circles, dotted line) microcosms. All regression lines are shown (ns denotes an insignificant relationship).

abundances ($P = 0.595$). Summed abundances were highest in the high nutrient microcosms ($F_{2,39} = 17.05$, $P < 0.001$).

Species richness significantly increased summed variances under all three nutrient conditions; however, the effect of species richness on the summed variances was strongest in the low nutrient microcosms ($F_{3,39} = 29.801$, $P < 0.001$; Fig. 3b, Table 2). Summed variance were highest in the high nutrient microcosms ($F_{2,39} = 8.336$, $P < 0.001$). The slope of the mean-variance scaling relationship averaged across all species was greatest in low nutrient microcosms (slope = 1.14; Table 3); however the slope did not differ according to NT ($P = 0.234$). Likewise, there were no significant differences in z-values for individual species according to NT. $z < 1$ for all species except for nematodes (slope = 1.66) in the low nutrient microcosms (Table 2). Neither species richness nor nutrients had an effect on summed covariances (Fig. 3c).

Species variability and abundance effects

Species richness stabilized abundances ($CV_{species}$) for four of the six species in the low nutrient microcosms and three of the six species in the intermediate nutrient microcosms (Fig. 4, Table 4). $CV_{species}$ was not affected by species richness for any species in the high nutrient microcosms and $CV_{species}$ did not increase significantly with species richness under any nutrient condition. Three of six species in the low nutrient microcosms and one of the six species in the intermediate nutrient microcosms showed higher abundance as a function of species richness (Table 5). Species richness had no effect

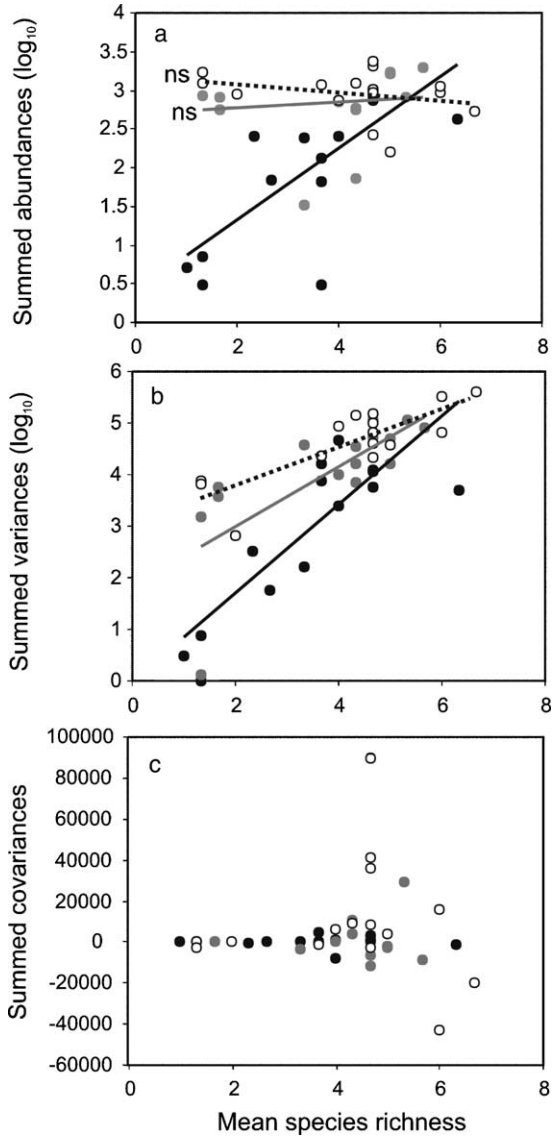

Fig. 3. (a-c) Three mechanisms by which species richness can affect community variability in experimental microcosms: (a) summed abundances (log_{10}), (b) summed variances (log_{10}) and (c) summed covariances. See Fig. 1 for descriptions of symbols and lines.

on abundance for any species in the high nutrient microcosms (Table 5). The abundance of *Dasyhelea* sp. declined with increasing species richness in the intermediate nutrient microcosms.

Effect of population variability on community variability

CV_C positively correlated with CV_{POP} across all nutrient conditions ($r^2 = 0.36$, $P < 0.001$, Fig. 5). However, CV_{POP} explained less variability in CV_C in the high nutrient microcosms ($r^2 = 0.19$, $P = 0.059$) than in either the intermediate nutrient (CV_{POP} $r^2 = 0.303$, $P = 0.033$) or low nutrient (CV_{POP} $r^2 = 0.446$, $P = 0.006$) microcosms. In a series of backward stepwise multiple regressions for CV_C, with mean species richness, mean abundance, and CV_{POP} as independent variables, only CV_{POP} was retained in the model across all nutrient conditions ($R = 0.6$, $P < 0.001$, $n = 45$). CV_{POP} was also the only variable retained in the model for CV_C in low nutrient microcosms ($R = 0.677$, $P = 0.006$, $n = 15$). For the intermediate and high nutrient microcosms none of the independent variables were retained in the model for CV_C.

Discussion

Species richness and the relationship between population and community variability

Our results show that the nature of the relationship between species richness and temporal variability in abundance is dependent on the nutrient status of the system. Recent theoretical and empirical studies have suggested that populations may be stabilized by increasing species richness (Ives et al. 1999, Li and Charnov 2001, DeWoody et al. 2003, Kolasa and Li 2003, Valone and Hoffman 2003, Romanuk and Kolasa 2004, Vogt, et al. 2006). We find additional support for a stabilizing effect of species richness for populations, but only in low nutrient microcosms. Under low nutrient conditions, community variability, mean population variability, and the variability of four of the six species present in all three nutrient conditions decreased with increasing species richness. Our results also support the hypothesis that community variability declines with increasing species richness due to a stabilizing effect of species richness on the component populations, i.e. mean population variability was the only variable retained in a backward stepwise regression model for community variability in the low nutrient microcosms, which also included mean species richness and mean abundance as predictor variables. Thus, we suggest that the mechanism by which increased species richness leads to lower community variability in low nutrient rock pool communities involves reduced variability of component populations.

Other mechanisms

The relationships between species richness and summed abundances (overyielding), summed covariances (evidence of insurance or competitive effects) and summed variances (statistical averaging) have received considerable theoretical attention (Doak et al. 1998, Tilman et al.

Table 2. Effects of mean species richness and nutrient treatment, NT, on summed abundances (log_{10}), summed variances (log_{10}), summed covariances, and effect of NT on the mean-variance scaling relationship.

	SS	df	MS	F	p
Summed abundances[2]					
Intercept	302.130	1	302.130	1136.316	>0.001
NT × mean S	5.966	3	1.989	7.480	>0.001
NT	9.067	2	4.533	17.051	>0.001
Error	10.370	39	0.266		
Summed variances[2]					
Intercept	672.140	1	672.140	1174.994	>0.001
NT × mean S	51.142	3	17.047	29.801	>0.001
NT	9.538	2	4.769	8.336	0.001
Error	22.309	39	0.572		
Summed covariances[1]					
Intercept	5.446E+08	1	5.446E+08	1.619	0.210
Mean S	4.181E+07	1	4.181E+07	0.124	0.726
NT	7.505E+08	2	3.753E+08	1.115	0.338
Error	1.379E+10	41	3.364E+08		
Mean-variance scaling (z-values)[1]					
Intercept	162.112	1	162.112	3590.022	>0.001
Mean abundance (log)	16.958	1	16.958	375.550	>0.001
NT	0.032	2	0.016	0.356	0.703
Error	1.851	41	0.045		

ANCOVA[1] was used if slopes between species richness and species variability did not differ based on NT. A separate slopes model[2] was used if the slope between species richness and species variability differed significantly according to NT.

1998, Tilman 1999b, Yachi and Loreau 1999, Hughes and Roughgarden 2000). In our experiment the summed variances did not decline with species richness and species richness had similar strong positive effects on the summed variances in all three nutrient conditions. Similar results have been reported by Petchey et al. (2002) in protist microcosms. The slope of the mean-variance scaling relationship, which must be greater than 1 to be consistent with theoretical expectations for statistical averaging to occur (Doak et al. 1998, Tilman et al. 1998), was less than 1 for all species except for the nematode in the low nutrient microcosms. Thus, it is unlikely that statistical averaging effects contributed to the reduction in community variability with increased species richness. We also found no relationship between species richness and summed covariances, suggesting that mechanisms such as competitive effects or differential responses of species to environmental fluctuations were not responsible for the reduction in community variability with increasing species richness seen in the low nutrient microcosms. While it is possible that the abbreviated length of our experiment (five weeks) may not have been long enough to capture strong effects of species richness on covariances, the magnitude of covariances did differ across nutrient treatments, with a few strong positive and negative covariances in the high nutrient microcosms.

Both statistical averaging and the covariance effect assume that abundance does not vary with species richness (Doak et al. 1998, Lehman and Tilman 2000). This assumption was violated in the low nutrient microcosms suggesting an overyielding effect (Tilman 1999b, Hector et al. 1999). However, the increase in summed abundance with species richness was only seen when the three replicates with the lowest species richness were included in the analysis (Fig. 3a). When we removed the replicates with a mean species richness of less than 1.5 from the analysis, species richness was unrelated to summed abundance. Thus, we suggest that while overyielding may have been important at

Table 3. Individual and mean z-values for the mean-variance scaling relationship for the six species present in all three nutrient treatments. Also shown is the test for significant differences in slopes.

Species	Low z	Intermediate z	High z	F	P
Cypridopsis sp.	0.795	0.79	0.957	2.11	0.135
Potamocypris sp.	0.897	0.892	0.806	0.44	0.649
O. modestus	0.997	0.89	0.98	0.837	0.442
A. davidii	0.761	0.759	0.91	0.909	0.412
Nematode	1.66	0.808	0.55	2.606	0.118
Dasyhelea sp.	0.927	0.846	0.874	0.151	0.861
Mean	1 (0.875[a])	0.831 (0.835[a])	0.846 (0.905[a])		

[a]Values in brackets are the mean z-values not including the nematode

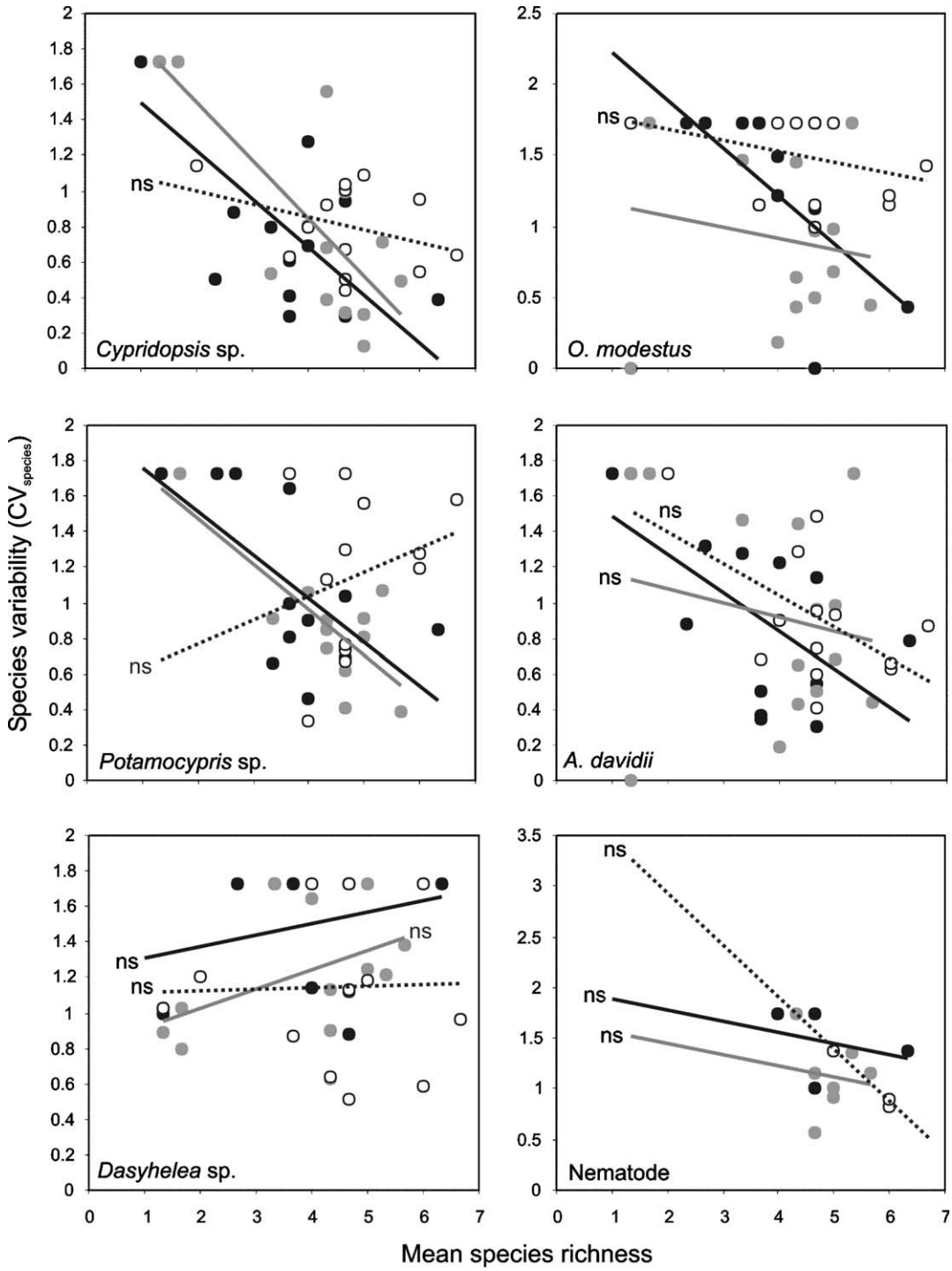

Fig. 4. Relationship between mean species richness and species variability for the six species present in at least three microcosms in all three nutrient conditions. See Fig. 1 for descriptions of symbols and lines.

very low levels of species richness in this experiment, it cannot account for the decrease in community variability across the entire range of richness values examined here.

Recently, a number of empirical studies have shown that population abundances can be stabilized by increases in species richness, at least under some environmental conditions (Petchey et al. 2002, Romanuk 2002,

Table 4. Effects of mean species richness and nutrient treatment, NT, on the temporal variability (CV) of individual species.

Species		SS	df	MS	F	P
Cypridopsis sp.[1]	Intercept	11.784	1	11.784	93.197	<0.001
	Mean species richness	3.554	1	3.554	28.106	<0.001
	NT	0.571	2	0.285	2.256	0.119
	Error	4.805	38	0.126		
Potamocypris sp.[2]	Intercept	3.689	1	3.689	27.406	<0.001
	NT × mean species richness	2.059	3	0.686	5.099	0.006
	NT	0.642	2	0.321	2.383	0.109
	Error	4.173	31	0.135		
O. modestus[1]	Intercept	13.824	1	13.824	112.443	<0.001
	Mean species richness	2.260	1	2.260	18.379	<0.001
	NT	0.855	2	0.427	3.477	0.042
	Error	4.180	34	0.123		
A. davidii[1]	Intercept	9.105	1	9.105	42.455	<0.001
	Mean species richness	1.612	1	1.612	7.515	0.009
	NT	0.145	2	0.073	0.338	0.715
	Error	7.935	37	0.214		
Nematode[1]	Intercept	0.579	1	0.579	3.618	0.080
	Mean species richness	0.001	1	0.001	0.006	0.942
	NT	0.407	2	0.203	1.270	0.313
	Error	2.082	13	0.160		
Dasyhelea sp.[1]	Intercept	4.933	1	4.933	31.734	<0.001
	Mean species richness	0.225	1	0.225	1.450	0.237
	NT	0.762	2	0.381	2.451	0.102
	Error	5.129	33	0.155		

ANCOVA[1] was used if slopes between species richness and species variability did not differ based on NT. A separate slopes model[2] was used if the slope between species richness and species variability differed significantly according to NT

Valone and Hoffman 2003, Kolasa and Li 2003, Romanuk and Kolasa 2004, Vogt et al., 2006). If populations are stabilized by increasing richness, they can directly reduce community variability (Petchey et al. 2002, this paper) without having to invoke more complicated mechanisms. These empirical studies have some theoretical support. Ives et al. (1999) have shown that species richness does not affect community variability directly; instead a community level relationship between species richness and stability is a direct result of the relationship between species richness and stability at the population level. Similarly, DeWoody et al. (2003) and Li and Charnov (2001) have shown that, in model communities, species richness reduces population variability. Our current results support those found previously in the natural rock pool system from which our communities were assembled (Romanuk 2002, Kolasa and Li 2003, Romanuk and Kolasa 2004) and those derived from other experimental manipulations of species richness in the same system (Vogt et al., 2006, T. N. Romanuk, pers. obs.).

The presence of a stabilizing effect of species richness on populations in the low nutrient microcosms, and the absence of any effect of species richness in nutrient enriched microcosms suggests that, in rock pools, increasing species richness may contribute to reduced population variability through a mechanism such as niche complementarity in resource-use (Norberg 2000, Loreau and Hector 2001, Cardinale et al. 2002). In microcosms with a high proportion of unused resources, the densities of populations may fluctuate more than in pools in which resource-use is more complete. As the available resources in a community decrease, fluctuations in population densities may be reduced. Our finding that population variability was greater in high nutrient microcosms is consistent with this hypothesis. Under lower nutrient conditions, the number of species in a microcosm may act to stabilize populations by

Table 5. Relationship between mean species richness and mean species abundance ($\log_{10}$) for the six species present in all three nutrient treatments.

Species	Oligotrophic			Mesotrophic			Eutrophic		
	n	r^2	P	n	r^2	P	n	r^2	P
Cypridopsis sp.	15	0.704	<0.001	14	0.718	<0.001	13	0.24	0.063
Potamocypris sp.	13	0.303	0.033	12	0.259	0.052	12	0.037	0.491
O. modestus	12	0.177	0.117	12	0.142	0.166	13	0.239	0.053
A. davidii	14	0.433	0.008	13	0.26	0.052	13	0.214	0.083
Nematode	4	0.013	0.679	7	0.004	0.824	6	0.01	0.721
Dasyhelea sp.*	9	0.002	0.957	13	0.416	0.009	15	0.139	0.14

**Dasyhelea sp.* in the intermediate nutrient treatment was the only species to show declines in abundance with increasing species richness

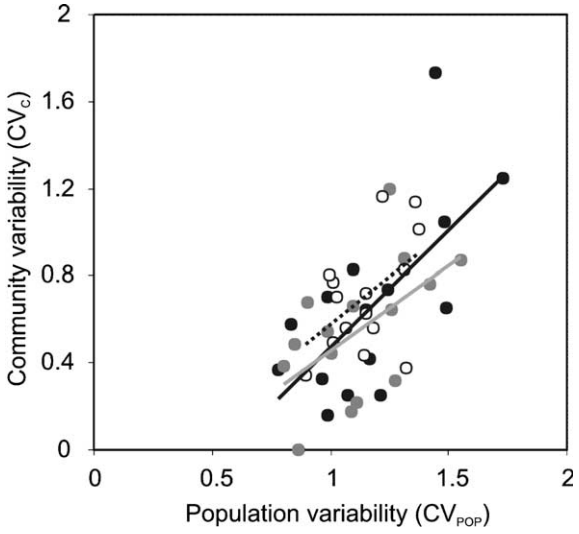

Fig. 5. Effect of population variability (CV_{POP}) on community variability (CV_C). See Fig. 1 for descriptions of symbols and lines.

facilitating access to previously available resources (through niche complementarity for instance), which would in turn lead to more complete resource-use (Cardinale et al. 2002). For example, the species richness of ostracods in any one natural rock pool can be as high as eight species. While the rock pool ostracods are all detritivores, they also have a large range of body sizes (100 μm to 5 mm) suggesting that ostracods might partition their resources according to particle size.

As far as we know, the only similar experiment to ours is Steiner et al. (2005) who manipulated diversity and productivity in laboratory protist microcosms. Steiner et al. (2005) found a stabilizing effect of species richness on community abundance and a weak and somewhat equivocal stabilizing effect of species richness on population abundance. Enrichment was somewhat stabilizing in their study, particularly at the community level; however, there were no significant interaction effects between species richness and enrichment on stability. Instead, Steiner et al. (2005) suggest that enrichment increased species richness, leading to more stable populations. This, in turn, could underlie the stabilizing effect of species richness Steiner et al. (2005) found at the community level. Thus, while the effects of enrichment on variability differed between Steiner et al. (2005) and the present study, both suggest the potential for enrichment to mediate the effects of species richness on stability as well as the potential for population stability to lead directly to more stable communities, in contrast with earlier studies (Tilman 1996). In support of the hypothesis that less variable populations lead directly to less variable communities, neither Steiner et al. (2005) or the present study find strong support for other mechanisms proposed to underlie a stabilizing effect of species richness on community abundances.

In conclusion, we found that enrichment decoupled the stabilizing effect of species richness on community and population variability. The only mechanism for how species richness stabilized community abundances that unambiguously applied given our results was that community variability arose from increased variability of component populations. While we cannot conclusively identify the mechanism(s) by which species richness stabilized population abundances, it seems likely that more complete resource-use in more diverse communities may dampen population fluctuations. This mechanism is, however, still relatively untested and warrants further attention.

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