

Species richness–variability relationships in multi-trophic aquatic microcosms

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While species loss may affect the temporal variability of populations and communities differently in multi- versus single-trophic level communities, the nature of these differences are poorly understood. Here, we report on an experiment where we manipulated species richness of multi-trophic rock pool invertebrate communities to determine the effects of species richness, *S*, on the temporal variability of communities, populations, and individual species. As in single-trophic level studies, temporal variability in community abundance decreased with increasing species richness. However, in contrast to most studies in single-trophic level systems, temporal variability of populations also decreased as species richness increased. Furthermore, the variability of the constituent populations strongly correlated with variability of community abundance suggesting that, in rock pools, *S* affects community variability through its stabilizing effect on component populations. Our results suggest that species loss may affect population and community variability differently in multi-trophic versus single trophic level communities. If this is so, then the mechanisms proposed to underlie the effects of *S* on community variability in single-trophic communities may have to be supplemented by those that describe contributions to population stability in order to fully describe the patterns observed in multi-trophic communities.

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Empirical studies generally show that combined abundance of all species, or community abundance, in species-rich communities is less variable than in species-poor communities (Tilman 1996, McGrady-Steed and Morin 2000, Romanuk and Kolasa 2002). In contrast, the responses of populations to increasing species richness are much less clear. Variability of population abundances have been shown to increase (Tilman 1996), decrease (Romanuk 2002, Kolasa and Li 2003, Valone and Hoffman 2003), and be unaffected by increasing species richness (McGrady-Steed and Morin 2000). Theoretical predictions are also idiosyncratic, with models predicting that species richness can increase (May 1973, Lehman and Tilman 2000), decrease (Ives

et al. 1999, 2000, Li and Charnov 2001, DeWoody et al. 2003) or have no effect on population variability (Tilman 1999), depending on model construction.

Whenever species richness reduces community variability and this reduction is not a result of statistical averaging, richness must also affect the variability of the constituent species (Doak et al. 1998). This proviso helps emphasize that populations should also be stabilized under some conditions. In a long-term observational study of zooplankton and benthic invertebrates inhabiting natural aquatic rock pools, both aggregate community abundances (Romanuk and Kolasa 2002) and population abundances became less variable as species richness increased. However, this effect was apparent

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only after the confounding effects of the increased variability of specialists (Kolasa and Li 2003) or local differences in environmental and biotic conditions were factored out (Romanuk and Kolasa 2004). These earlier indications that richness reduces variability of populations need confirmation and, more importantly, mechanistic explanation.

Multi-trophic communities may differ from single trophic level communities in their responses to species loss in a number of ways (Petchey et al. 2004a). First, indirect interactions are more likely in multi-trophic systems where predation mediates competition. Such mediation may stabilize populations directly and indirectly (Galkovskaya 1996). Second, in a multi-trophic system, resource use occurs as a chain of processes (i.e. resource-use complementarity, Worm and Duffy 2003), where the presence of one species can facilitate access to resources for other species (Hooper 1998, Loreau 1998, Díaz and Cabido 2001, Tilman et al. 2001, Hector et al. 2002, Naeem 2002, Petchey et al. 2002, Petchey 2003). Third, in reticulate webs, there is a greater probability that species will have access to multiple resources, which may also be stabilizing (MacArthur 1955, Kondoh 2003, T. N. Romanuk, unpubl.). Even without specific knowledge of such interactions, however, we may reasonably assume that such situations arise more often at higher rather than lower S and where resource use and processing partially overlap among some species. Li and Charnov (2001) derived a model from energetic and thermodynamic arguments that converges with this line of reasoning, which predicts stabilizing effects of S on populations in multi-trophic communities. Whether these proposed differences are sufficient to affect a general response of multi-trophic communities to increasing richness requires laboratory and field tests.

Indeed, the mechanisms by which S can stabilize community abundance (statistical averaging, competition, overyielding) interact and their effects differ depending on their specific configurations. These are quantitatively linked in Tilman (1999) who sums up variances of individual populations and covariances between pairs of species to examine the behaviour of this sum in contrast to the behaviour of a single species. We briefly review several situations, each leading to testable empirical expectations:

- 1) If all species have equal abundance, $N_1 = N_2 = \dots, N_S$ and interspecific covariances are absent (no effects of species interactions), summed variances of the community are given by (Tilman 1999):

$$\text{Var}_{\text{com}} = \sum_{i=1}^S c \times N_i^z \text{ or, alternatively,}$$

$$\text{Var}_{\text{com}} = \sum_{i=1}^S \text{var}(N_i)$$

where c is a constant, z is a scaling coefficient, and N_i is abundance of i^{th} species. The scaling coefficient z refers to how the variance in abundance of a species increases with its mean abundance. Values of z determine empirical expectations such that $z < 1$ implies community stability increasing with S, $z > 1$ implies a decline in community stability, $z = 1$ implies no effect of S on community stability. Analogously, $z < 2$ implies decrease in population stability, $z > 2$ implies stabilizing effect of S on populations, and $z = 2$ implies no effect.

- 2) With interspecific interactions such as competition present, negative covariances may additionally stabilize a community although the effect is not straightforward (Tilman 1999). Thus, both the summed variances and covariances need to be considered:

$$\text{Var}_{\text{com}} = \sum_{i=1}^S c \times N_i^z + 2 \left(\sum_{i=1, S-1}^S \sum_{j=i+1, S}^S \text{cov ar}(N_i, N_j) \right)$$

where N_i and N_j are abundances of a pair of interacting species. The expected effect of S on total variation would be stronger if the summed covariances were more negative, for any given z value. However, large negative covariances lead to a reduction of the effect exerted by z.

- 3) Overyielding (Tilman 1999, Eq. 6) – an increase in population and community abundance due to better use of resources when S is higher – can stabilize N_{com} such that:

$$\frac{K_S}{K_1} = S^{1-x-(1-xz)/2}$$

where K_S is stability of a community composed of S species, K_1 is stability of a community composed of one species, and x is the overyielding parameter (a coefficient defining how the mean size of each species decreases with S). Three potential results are of interest: $x < 0$ implies a lesser reduction of mean N_i with S and thus a stabilizing effect of S on CV_{com} , $x = 1$ means no overyielding and $x > 1$ decreases community stability.

When abundances are not equal among species, some of the expected trends will change. Decreasing evenness, E, partially reverses the effect of z: stability increases less than in an even community when $z > 1$ and stability declines less compared to an even community when $z < 1$. Furthermore, parameter x, by increasing abundances of individual species compared to a community

with no overyielding but the same S , increases stability of communities for $z < 1$ but is not affected by evenness as long as all the species experience the same overyielding (unpubl.). Doak et al. (1998) provide a complementary discussion of how unevenness affects community stability (evaluated as CV_{com}), with the main point worth repeating: in the absence of correlated responses to environment, increasing unevenness will negate any effects S may have on stabilization of community variation. However, in most natural communities S is positively correlated with E . Consequently, in a typical natural situation, S should stabilize CV_{com} irrespective of E .

Here, we report on an experiment where we manipulated species richness of multi-trophic rock pool invertebrate communities to determine the effects of S on the temporal variability of communities, populations, and individual species (regional populations). We tested the hypothesis that species richness reduces population and community variability. In addition, we asked whether mechanisms proposed to underlie the negative relationship between species richness and community variability in single-trophic systems also operate in multi-trophic communities. Specifically, we hypothesized that if S reduces variability of populations, we would not find strong support for statistical averaging (Doak et al. 1998), insurance effects (Tilman 1996, Yachi and Loreau 1999), and mean–variance scaling relationships (Tilman 1999) as these mechanisms imply either a destabilizing effect of S on constituent populations or no effect at all.

System and methods

Rock pool meiofaunal communities

In this study we used the naturally occurring species assemblages of meiofauna inhabiting tropical rock pools at Discovery Bay Marine Laboratory (18°28'N/77°25'W) on the northern coast of Jamaica from October 2000 to January 2001 (Romanuk and Kolasa 2001, 2002, Kolasa and Romanuk 2005). In 15 years of sampling 49 natural rock pools, 71 species of small invertebrates have been identified, consisting primarily of copepods, cladocerans, ostracods, worms, and insect larvae. The 25 most common species in the rock pools account for 99.9% of individuals and the five most common species account for 75.6% of individuals: *Nitocra spinipes* (Boeck), a harpacticoid copepod (46%), *Orthocyclops modestus* (Herrick), a cyclopoid copepod (10%), the ostracods *Potamocypis* sp. (10%) and *Cypridopsis cf. mariae* Rome (10%), and *Ceriodaphnia* sp., a cladoceran (9%).

Trophic habits of the species used in the experiments include detritivores (e.g. worms, harpacticoid copepods), algal-filterers (e.g. cladocerans), detritivores–omnivores (e.g. ostracods, insect larvae), and predators (e.g. cyclo-

poid copepods). Rock pool communities also contain a diverse suite of microbes, protists, and rotifers. Leaf litter from the surrounding mangrove trees, detritus, phytoplankton, and periphyton form the base of this predominantly detrital food web (see Beisner and Romanuk 2005 for examples of structural rock pool food webs). Stable isotope analysis of rock pool meiofauna has shown that the majority of rock pool species are detritivore–omnivores, however carbon and nitrogen signatures differ significantly across species suggesting that many rock pool species, and in particular ostracods and worms, may partition detrital resources according to size and source of detrital particles (T. Romanuk, unpubl.).

The use of natural aquatic microcosms such as rock pool communities is particularly useful in studies of the effects of biodiversity loss on stability (Srivastava et al. 2004). The majority of previous studies have been conducted in single trophic level terrestrial plant communities (Tilman 1996, Pfisterer and Schmid 2002), and those that have used food webs (Naeem and Li 1997, Petchey 2000, Gonzalez and Descamps-Julien 2004, Steiner et al. 2005) often consist of artificially constructed collections of organisms that may not necessarily co-exist in nature in the same species combinations that are used in experimental treatments (but see McGrady-Steed and Morin 2000, Downing and Leibold 2002). The natural rock pool microcosms from which the experimental communities were assembled are small in size, easily manipulated, contain organisms that have fast generation times, and are located within close enough proximity to ensure uniform exposure to major sources of environmental variability. By constructing our experimental systems from natural assemblages, our experiment benefits from the versatility afforded by many artificially constructed systems, but retains the integrity of their natural analogues, making them suitable for representing natural systems (Srivastava et al. 2004). We perform statistical comparisons of the community structure in natural rock pools and experimental microcosms to determine whether the experimental system falls within the range of communities normally observed in nature.

Experimental design

We created experimental microcosms in plastic cups, 8 cm in diameter and 15 cm deep. The microcosms were filled to a depth of 10 cm (volume 500 ml) with water and were kept in the laboratory under constant conditions. To assemble the experimental communities, water was collected from five freshwater rock pools. Every invertebrate species that was present in the rock pool water was used in the experiment. The initial experimental communities consisted of nine species retained

on a 63 μm mesh net: three species of ostracods (*Candona* sp., *Cypridopsis* sp., *Potamocypris* sp.), two species of copepods (*Nitocra spinipes*, *Orthocyclops modestus*), two species of chydorids (*Leidigia leidigi*, *Alona davidii*), one species of daphnid (*Ceriodaphnia* sp.), and one species of nematode worm. Generation times for these taxa are short due to high water temperature (Gillooly 2000). For example, based on Gillooly (2000), zooplankton of similar sizes would have generation times ranging from ~ 8 –20 days at 20°C. At $\sim 27^\circ$, which was the average water temperature of the microcosms (T. Romanuk, unpubl.) these generation times would decrease substantially. For example *Alona affinis* 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).

Diversity was manipulated using a dilution method (Franklin et al. 2001, Giller et al. 2004, Romanuk and Kolasa 2005). Dilution methods have been successfully used to manipulate bacterial (Garland and Lehman 1999, Franklin et al. 2001, Kisand and Wickner 2003), fungal (Taylor and Bruns 1999), plant (Goldberg et al. 2001) and rock pool meiofaunal (Romanuk and Kolasa 2005) diversity. 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 of the initial species. Thus, it is necessary to allow for the mixtures to rebuild their biomass levels following the initial manipulation. However, as long as regrowth occurs, the method should reveal how extinctions alter ecosystem functioning (Naeem et al. 1995).

To manipulate diversity experimentally, 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 to produce 15 liters of filtered rock pool water (from which all organisms larger than the mesh size had been removed), and 15 liters of natural rock pool water with all the organisms in natural proportions. The diversity treatments (DT) were obtained by mixing the filtered water and the unfiltered water together in five combinations and six replicates (a total of 30 microcosms), with unfiltered water added in the following proportions: 0%, 25%, 50%, 75%, and 100%. For example, the DT = 0% level was composed entirely of filtered water and constituted the control treatment.

The DT = 25% level contained $\frac{1}{4}$ unfiltered water and $\frac{3}{4}$ filtered water. This procedure effectively manipulated the abundance and richness of the target communities, however organisms smaller than 63 μm such as rotifers, protozoans, and the juvenile stages of ostracods and copepods (i.e. nauplii) would not have been affected.

Samples of 30 ml were collected from each microcosm weekly from October 2000 to January of 2001. Before sampling, a microcosm was gently stirred to homogenize its contents. The water removed was replaced with filtered rock pool water. Samples were filtered through a 63 μm mesh, preserved in 50% ethanol, and sorted. For this analysis, we processed samples taken at three intervals during the eight week experiment (on week two, five, and seven). Ninety samples were sorted in total: six for each of the five initial diversity treatments for each of the three weeks. Samples were sorted to taxa and abundance of each taxon counted using a dissecting microscope. Where a taxon is not identified to species, the taxon represents one species only and not a number of different species in the same genus.

Data analysis

Observed richness, S_{obs} , is the number of species in a microcosm on a particular sampling date. Mean species richness, S_{mean} , is the mean of the three S_{obs} (one for each sampling date). Temporal variability, variability from now 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_{com} , is a standard deviation in total microcosm abundance (all species combined, N_{com}) divided by mean N_{com} taken over three sampling dates. We represented population variability in two ways: we calculated CV for each population, CV_{pop} , individually as the standard deviation of N_{pop} divided by the mean of each population (sensu Tilman 1996). We also used mean CV_{pop} of all populations. This method yields a single measure of population variability per microcosm. This is convenient if one wishes to compare or relate community and population variability directly (Romanuk 2002, Steiner et al. 2005).

Summed variances, covariances, and abundances were calculated to test for portfolio effects (summed variances), insurance effects (summed covariances), and overyielding effects (summed abundances) according to the procedures outlined in Tilman (1999). Mean–variance relationships for each species were calculated for each species according to Tilman (1999). There, S is stabilizing if the slope of the mean–variance scaling relationship is $z > 2$ (Table 1). One way ANOVA was used to determine the effects of initial diversity level on community abundance and species richness. Post-hoc Tukey tests were used to determine whether significant

Table 1. Summary of the mechanisms that can generate or modify relations between aggregate community variability and species richness that were tested in this study. Note that the mechanisms differ in the number of components (see formulae after Tilman 1999) and that the existence of those clear differences makes their empirical separation feasible.

Mechanism	Prediction	References	Test	Result	Conclusion
Statistical averaging; community variance	Summed variances will decrease as S increases because the sum of random variables deviates less than the mean variable	Doak et al. 1998, Tilman et al. 1998	Relationship between S and summed variances	S and summed variances are unrelated for DT = 0–100 ($r^2 = 0.01$, $p = 0.607$). Negative relationship between S and summed variances for DT = 25–100 ($r^2 = 0.297$, $p = 0.007$).	Only important when communities with low N_{com} were excluded
Competition, predation, and indirect interactions	Antagonistic interactions will produce negative covariances between species (a condition stabilizing N_{com})	Tilman 1999, Petchey et al. 2002	S and summed covariances are related	No significant relationship for DT = 0–100 ($r^2 = 0.06$, $p = 0.211$) or for DT = 25–100 ($r^2 = 0.05$, $p = 0.306$).	Not important
Population and community abundance	Abundance will increase with species richness due to overyielding, resource-use complementarity etc.	Tilman 1999, Hughes and Roughgarden 2000, Petchey et al. 2002	S and population or community abundance should be correlated	Abundance increases with S for DT = 0–100 ($r^2 = 0.713$, $p < 0.001$), but is unrelated for DT = 25–100 ($r^2 = 0.097$, $p = 0.148$). S and N_{pop} are positively related for 4 of 9 species (Table 2)	S was only important for N_{com} when communities with low N_{com} were included. S affected some population abundances
Population variability	<ol style="list-style-type: none"> Increased population stability will lead to community stability if individual populations vary less with increases in S. S is stabilizing if the slope of the mean–variance scaling relationship is $z > 2$ 	Tilman 1999, Petchey et al. 2002	<ol style="list-style-type: none"> Relationship between S and CV_{pop}. Slope of the mean–variance scaling relationship $s = cm^z$ 	<ol style="list-style-type: none"> S and CV_{pop} are negatively related for DT = 0–100 ($r^2 = 0.765$, $p < 0.001$) and for DT = 25–100 ($r^2 = 0.488$, $p < 0.001$). Mean of z-values are less than 2. 	Important, but mean–variance scaling was not as predicted

differences in species richness and community abundance occurred between the different diversity conditions. Linear regression was used to determine 1) the relationship between S and variability in N_{com} and N_{pop} of individual taxa, 2) the relationship between S and summed variances, covariances, and abundance, 3) the relationship between mean population (mean CV_{pop}) and community variability (CV_{com}), 4) the relationship between species abundances, CV_{com} , and CV_{pop} , 5) the relationship between S and CV of individual species, and 6) the relationship between a species' mean N and its variance in abundance (i.e. mean–variance scaling relationship). All analyses were conducted across all DT (0–100) as well as with the DT = 0 removed from the dataset. This contrast served to determine whether patterns were driven by higher CV's at low abundances and whether S affected patterns at very low levels of species richness only.

We also compared species composition of our experimental communities to the species composition of natural rock pool communities characterized in Theriault and Kolasa (1999) and Romanuk and Kolasa (2005). Evenness in the experimental communities mimicked natural conditions and was far from the conditions examined by Tilman (1999). To determine the similarity of the experimental communities to natural rock pool communities we considered two aspects of

community structure. First, we compared rank–abundance curves between the experimental microcosms and the natural rock pools from which the experimental communities were assembled ($n = 41$). Second, we tested whether the experimental communities reflected the natural range of species richness values by comparing species richness–rank distributions for both the experimental microcosms and natural rock pools. For both of these analyses we used data from the five pools from which the experimental communities were assembled. Yearly samples were collected from these pools for nine years. Natural rock pools that were dry at the time of sampling ($n = 4$) were excluded from the analysis.

Results

Comparisons between experimental communities and natural rock pools

The experimental assemblages successfully imitated the species assemblage patterns in the natural rock pools. Prior to the experiment, we obtained 41 samples from the five pools used to assemble experimental assemblages (species source pools). Less than 1% of total abundance in these natural pools included species that were not included in the experimental treatments.

Present in the natural rock pools but excluded from the experimental treatments were insect larvae (e.g. *Culex* sp. and *Dasyhelea* sp.), two species of ostracods, one cyclopoid copepod, a species of crab (larval *Armases miersii*), and two oligochaete species.

Species rank–abundance distributions were similar between experimental communities and the natural pools (Fig. 1a). The primary differences between the experimental and natural communities was a shift in the dominant species, from *Ceriodaphnia* sp. in the natural pools to *Cypridopsis* sp. in the experimental microcosms, conforming to a shift in basal resources from a mixture of algae and detritus in the natural pools to primarily detritus in the laboratory microcosms, and the single case of one-species community in the microcosms (*Cypridopsis* sp.), which was not the case in the source pools.

Richness frequency distributions based on 41 samples taken from the natural source pools was similar to those in experimental communities (Fig. 1b). The median S was four in the microcosms and five in the natural pools and there was no significant difference in mean S between experimental and natural pools (experimental pools mean $S = 4.47$, natural pools mean $S = 4.73$, t-test $p = 0.302$). While this analysis does not address whether particular species combinations were similar between the natural rock pools and laboratory microcosms, unpublished analyses suggest that the species combinations in the laboratory microcosms were representative of the

species combinations in the natural pools (T.N. Romanuk, unpubl.).

Effectiveness of dilution series

The dilution series was effective in creating a species richness gradient, with species richness increasing with the intended diversity treatment (ANOVA: $F_{1,4} = 100.875$, $p < 0.001$; Fig. 2). The dilution series also affected community abundance (ANOVA: $F_{1,4} = 22.67$, $p = 0.0001$; Fig. 2). However, differences in community abundance were only found between communities that had extremely low abundances (DT = 0 and 25) and the higher diversity treatments. Post-hoc Tukey test showed that the only significant differences in mean abundance were between DT = 0 and DT = 25–100 ($p < 0.001$). For all other comparisons abundance was not significantly different between treatments (all $p > 0.205$) except between DT = 25 and DT = 100 ($p = 0.032$). In contrast, mean species richness was significantly different between most diversity treatments, with exception of two pairs: DT = 25 and DT = 75 ($p = 0.317$), DT = 50 and DT = 75 ($p = 0.609$).

Changes in species richness and abundance over time

Species richness ranged from zero to eight across DT (mean 4.22 ± 2.33 SD) and community abundance ranged from zero to 139 per sample across DT (mean 52.62 ± 38.11 SD; Fig. 2). Mean species richness decreased from 4.6 (± 2.56 SD) in week two to 4.3 (± 2.25 SD) in week five to 3.87 (± 2.34 SD) in week seven (Fig. 2). Community abundance fluctuated, increasing across DT from the mean of 38.77 (± 28.80 SD) in week two to 63 (± 40.71 SD) in week five, and then decreasing again to 56.1 in week seven (± 40.59 SD; Fig. 2).

Community and population variability

Diversity treatment DT = 0–100

Community variability ($CV_{\text{com}} r^2 = 0.849$, $p < 0.001$) and mean population variability (mean $CV_{\text{pop}} r^2 = 0.765$, $p < 0.001$) were both significantly lower in microcosms with higher species richness (Fig. 3a–b). S explained more variance for mean CV_{pop} than for the observed population variability ($r^2 = 0.108$, $p < 0.001$; Fig. 3c). Mean CV_{pop} explained 72% of the variance in community variability, CV_{com} ($p < 0.001$; Fig. 5).

The abundances of three of the nine species were positively correlated with community variability and the abundances of four of the nine species were positively correlated with mean population variability (Table 3). Abundances of four of the nine species increased with S (Table 2). CV_{pop} of seven of the nine species decreased

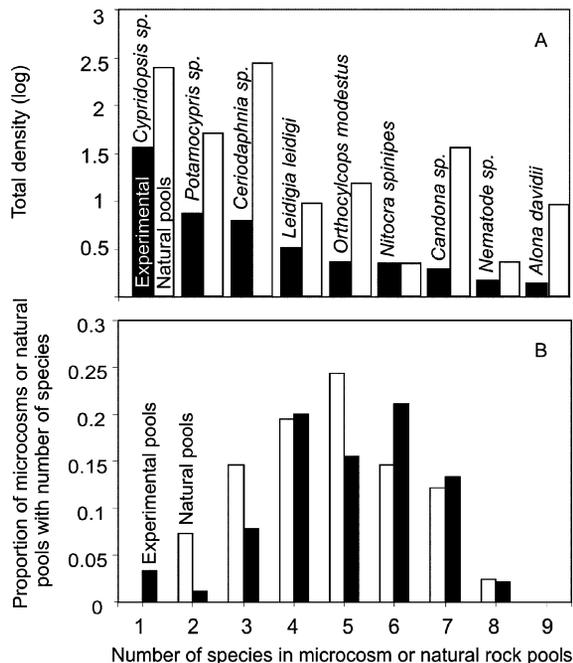
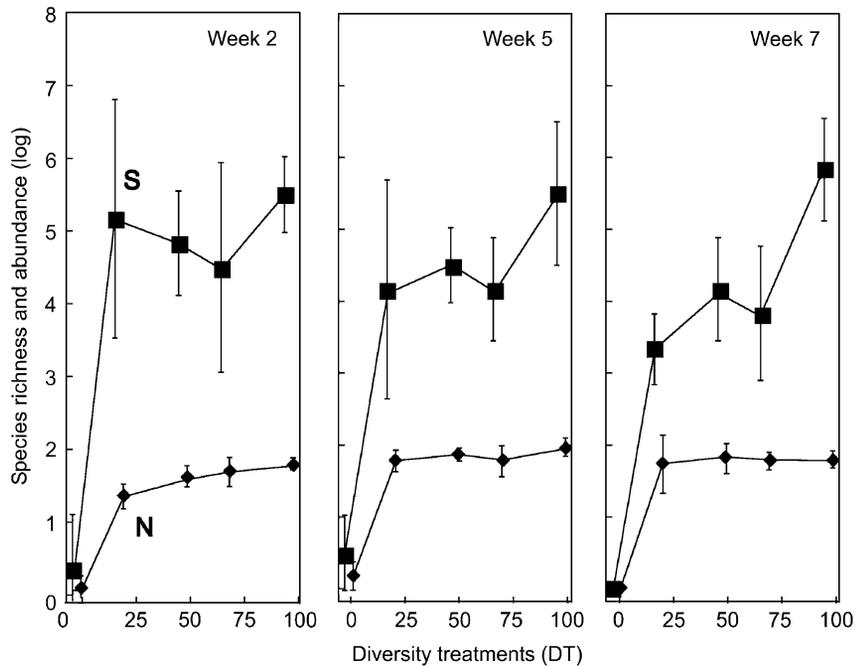


Fig. 1. Comparison between species proportions in natural rock pools (white bars) and in experimental rock pool microcosms (black bars). (A) Rank-abundance distribution based on species ranks. (B) Frequency distribution of species richness.

Fig. 2. Effects of dilution series manipulation on species richness (squares) and abundance (log; diamonds) in rock pool microcosms over time (week 2–7). Error bars show 95% standard deviations from the mean.



with increasing S (Table 2). CV_{pop} of four species was positively correlated with community variability, CV_{com} , and CV_{pop} of seven species was positively correlated with mean population variability, mean CV_{pop} (Table 3).

Diversity treatment $DT=25-100$

When $DT=0$ was removed from the analysis, the relationships between S and CV_{com} ($r^2=0.322$, $p=0.004$) and between S and both mean CV_{pop} ($r^2=0.488$, $p<0.001$) and observed CV_{pop} ($r^2=0.053$, $p=0.003$) weakened but remained significant. Mean CV_{pop} still explained 29% of the variance in community variability ($p=0.008$; Fig. 5).

Seven of the nine species were absent from $DT=0$. Thus, for these seven species differences between $DT=0-100$ and $DT=25-100$ could not be assessed. For *Cypridopsis* sp. and *Ceriodaphnia* sp. we found a number of differences between $DT=0-100$ and $DT=25-100$ (Table 2, 3). For *Cypridopsis* sp., removing $DT=0$ from analysis also removed the effect of S on abundance and weakened the effect of S on CV_{pop} (Table 2). Also, abundance of *Cypridopsis* sp. no longer related to CV_{com} or mean CV_{pop} (Table 3). Finally, the correlation between *Cypridopsis* sp. CV_{pop} and CV_{com} weakened and the correlation between CV_{pop} of *Cypridopsis* sp. and mean CV_{pop} strengthened (Table 3). For *Ceriodaphnia* sp., removing $DT=0$ from analysis weakened the effect of S on abundance and CV_{pop} (Table 2). Also, abundance of *Ceriodaphnia* sp. was no longer related to CV_{com} or CV_{pop} (Table 3). Finally, the correlation between CV_{pop} of *Ceriodaphnia* sp. and CV_{com} was

lost and the correlation between CV_{pop} of *Ceriodaphnia* sp. and mean CV_{pop} strengthened (Table 3).

Mean–variance scaling

The stabilizing parameter z spanned a range inclusive of the theoretically critical value $z=2$ (Tilman 1999), depending on species and scope of analysis. For $DT=0-100$ z -values ranged from 1.45 to 3.66 for the nine species (Table 2). When $DT=0$ was removed from the analysis, z increased from 1.91 to 2.11 for *Cypridopsis* sp. and decreased from 1.85 to 1.6 for *Ceriodaphnia* sp. (Table 2). These values represent a mix where mean–variance scaling can stabilize only some of the populations.

Relationships between species richness and summed variances, covariances, and abundances

We found no relationship between S and summed variances or covariances for $DT=0-100$ (Fig. 4a–b, Table 1). In contrast, S and summed abundances, N_{com} , were positively related (Fig. 4c, Table 1). While S and N_{com} were related when we included all DT, they were not when $DT=0$ was removed from analysis (Fig. 4c, Table 1). However, S and summed variances were not related when we included all DT but became negatively related when $DT=0$ was removed (i.e. for $DT=25-100$; Fig. 4a, Table 1).

The overyielding parameter x was above 1 for all species ($x_{all}=1.48$; underyielding) except one ($x_{mean} =$

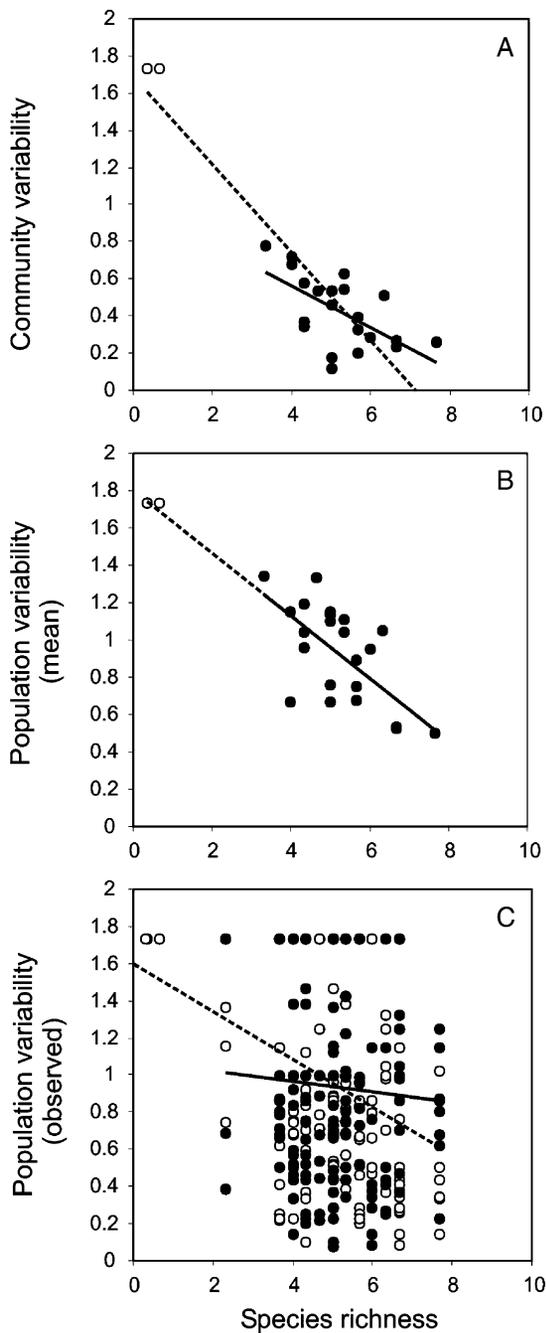


Fig. 3. Relationship between species richness (observed or mean as appropriate) and (A) community variability, (B) mean population variability, and (C) observed population variability. For each panel data are shown for DT=0 (open circles) and DT=25–100 (black circles). Regression lines are shown for DT=0–100 (hatched line) and for DT=25–100 (solid line).

0.32; overyielding). However, this low value may not indicate actual overyielding because it belongs to the smallest of ostracod species. A general trend describing scaling of density as a function of body size sufficiently explains its higher than neutral abundance.

Discussion

Stabilizing effect of increasing species richness on community and population variability

Consistent with previous studies we found that S stabilized aggregate community abundance, CV_{com} . This effect has also been shown for natural plant communities (Valone and Hoffman 2003), experimental plant communities (Tilman 1996), microbial microcosms (McGrady-Steed and Morin 2000), in natural unmanipulated rock pools with low environmental variability (Romanuk and Kolasa 2002) and for pond zooplankton (Steiner 2005). In the next section we discuss mechanisms that could produce this effect in the experimental microcosms.

Variability of populations (individual CV_{pop} , mean CV_{pop} , and CV_{pop} of seven of nine species) also decreased significantly with increasing S . This finding supports some theoretical predictions (Li and Charnov 2001) but not others (Tilman 1999). We initially reported that S had no effect on population variability in natural rock pool communities (Romanuk and Kolasa 2002). However, re-analysis of the dataset has shown that the method of calculation affects this result (Romanuk and Kolasa 2004). When CV_{pop} was calculated for each population over the whole set of pools rather than in each pool separately, CV_{pop} declined with S . Similarly, when Kolasa and Li (2003) factored out the effect of habitat specialization, S stabilized populations.

We also found a strong correlation between mean population variability and community variability. Because pure portfolio effect implies no relationship between population and community variability, a plausible interpretation is that lower variability of populations is the main cause for low aggregate variability of the whole community in the multi-trophic experimental microcosms. Furthermore, we found no evidence for overyielding – another potential stabilizing mechanism. Taken together, these results strongly support a stabilizing effect of species richness on experimental and natural rock pool communities. They further suggest that this effect arises initially from reduction of population variability, which is then passed onto the community level. Aggregated abundance, N_{com} , may be additionally stabilized by the portfolio effect.

Evidence for other mechanisms underlying a stabilizing effect of species richness on community variability

We hypothesized that mechanisms postulated to link S and variability in plant communities would be absent or weak in multi-trophic communities. In support of this, we found that S did not affect summed covariances (Tilman 1999, Yachi and Loreau 1999). While some of

Table 2. Summary of linear regressions between species richness and individual species abundances and their variability, CV_{pop} , for all diversity treatments (DT = 0–100) and for the diversity treatments excluding DT = 0 (DT = 25–100). The number of microcosms (n) with specific species and the z-value for the mean–variance scaling are also given.

DT	Individual species abundance				Individual species CV				n		z-value	
	DT = 0–100		DT = 25–100		DT = 0–100		DT = 25–100		DT = 0–100	DT = 25–100	DT = 0–100	DT = 25–100
	r^2	p	r^2	p	r^2	p	r^2	p				
<i>Candona</i> sp.	0.368†	0.006			0.324	0.011			19	19	1.79	
<i>Cypridopsis</i> sp.	0.541†	<0.001	0.0048	0.747	0.867	<0.001	0.503	<0.001	26	24	1.91	2.11
<i>Potamocypris</i> sp.	0.009†	0.654			0.232	0.017			24	24	1.8	
<i>Ceriodaphnia</i> sp.	0.583†	<0.001	0.233	0.019	0.386	0.001	0.187	0.039	26	23	1.85	1.6
<i>Orthocyclops modestus</i>	0.073	0.202			0.004	0.763			24	24	1.46	
<i>Nitocra spinipes</i>	0.033†	0.665			0.741	0.006			8	8	2.92	
<i>Alona davidii</i>	0.254†	0.212			0.467	0.062			8	8	3.66	
<i>Leydigia leydigi</i>	0.341†	0.014			0.268	0.033			17	17	2.27	
<i>Nematode</i> sp.	0.09†	0.297			0.629	0.001			14	14	3.27	

Note: all slopes are negative except where indicated†.

the other three mechanisms (selection effects: Huston 1997, overyielding: Tilman 1999, and statistical averaging: Doak et al. 1998) might contribute to the stabilization of community abundance by species richness, none had significant effects across both DT = 0–100 and DT = 25–100.

Mean–variance scaling did not appear to offer a general explanation for the stabilizing effect of S on populations as scaling coefficients, z, showed values below (3 of 7 species) and above (4 of 7 species) the critical value of z = 2 and a mean of z = 1.92 (Tilman 1999). Valone and Hoffman (2003) found a similar pattern in plant communities. Thus, while mean–var-

iance scaling could explain the reduction in population variability with increasing species richness for some species, it would destabilize others. However, this argument has been developed by Tilman (1999) for species of equal abundance, which is not the case in the microcosms or natural systems. Given the difference between the model and natural communities, scaling coefficient values require cautious interpretation and may not apply to communities with uneven distribution of abundances.

Most mechanisms (Table 1) linking richness to community stability were either not applicable or applied under only one of the two analytic diversity ranges. This result warrants further comments. First, if effects of S

Table 3. Summary of linear regressions between abundance of individual species and two measures of variability (community and population) as well as between variability in individual species abundances and two measures of variability (community and population) for all diversity treatments included (DT = 0–100) and with the lowest diversity treatment excluded (DT = 25–100).

	Community variability		Community variability		Population variability		Population variability	
	DT = 0–100		DT = 25–100		DT = 0–100		DT = 25–100	
	r^2	p	r^2	p	r^2	p	r^2	p
Species abundance								
<i>Candona</i> sp.	0.497	<0.001			0.516	<0.001		
<i>Cypridopsis</i> sp.	0.703	<0.001	0.005	0.735	0.526	<0.001	0.15	0.061
<i>Potamocypris</i> sp.	0.045	0.317			0.051	0.286		
<i>Ceriodaphnia</i> sp.	0.407	<0.001	0.002	0.828	0.32	0.003	0.019	0.525
<i>Orthocyclops modestus</i>	0.001	0.938			0.011†	0.632		
<i>Nitocra spinipes</i>	0.007	0.843			0.011	0.81		
<i>Alona davidii</i>	0.08	0.497			0.122	0.395		
<i>Leydigia leydigi</i>	0.003†	0.83			0.261	0.036		
<i>Nematode</i> sp.	0.011	0.718			0.122	0.22		
Species CV								
<i>Candona</i> sp.	0.6†	<0.001			0.507†	<0.001		
<i>Cypridopsis</i> sp.	0.923†	<0.001	0.682†	<0.001	0.31†	0.005	0.614†	<0.001
<i>Potamocypris</i> sp.	0.396†	<0.001			0.383†	0.001		
<i>Ceriodaphnia</i> sp.	0.326†	0.002	0.105†	0.132	0.284†	0.009	0.464†	<0.001
<i>Orthocyclops modestus</i>	0.038†	0.363			0.147†	0.067		
<i>Nitocra spinipes</i>	0.185†	0.288			0.768†	0.004		
<i>Alona davidii</i>	0.1†	0.446			0.03†	0.683		
<i>Leydigia leydigi</i>	0.02†	0.586			0.376†	0.009		
<i>Nematode</i> sp.	0.128†	0.21			0.584†	0.001		

Note: all slopes are negative except where indicated†.

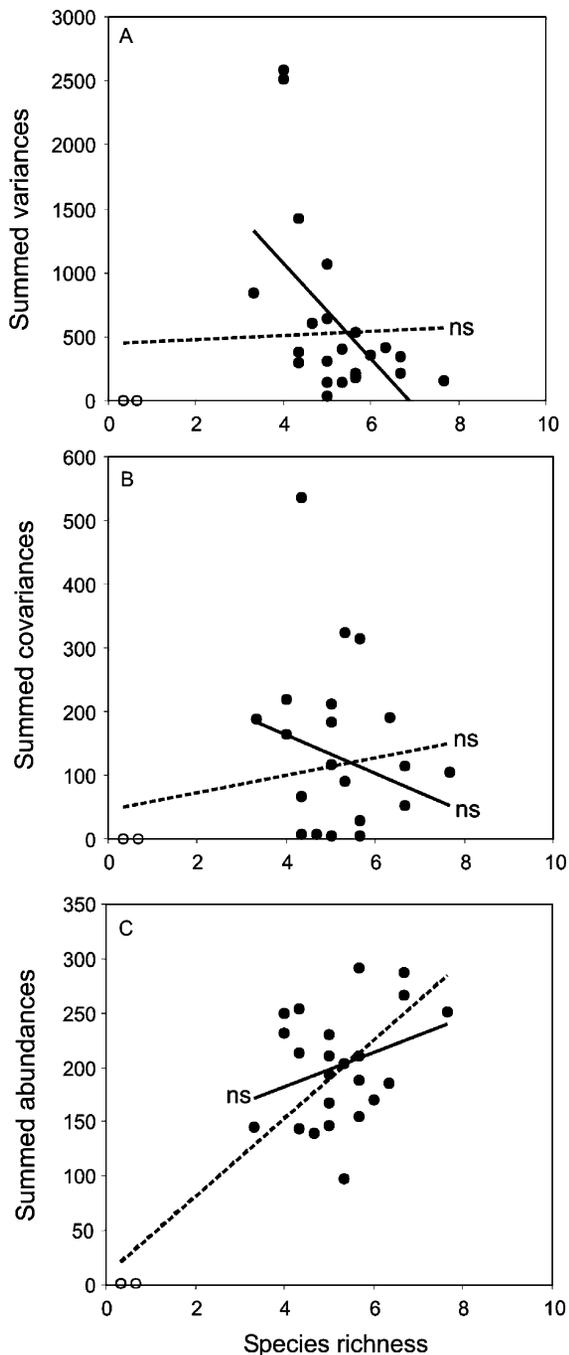


Fig. 4. Relationship between species richness and (A) summed variances, (B) summed covariances, and (C) abundance for DT = 0–100 (open circles, hatched lines) and for DT = 25–100 (black circles, solid lines).

differ between the population and community levels, it is possible that the underlying mechanisms differ, too. For example, Tilman (1996) attributed the stabilizing effect of S on community variability to increased negative covariances between species. In contrast, we find that in

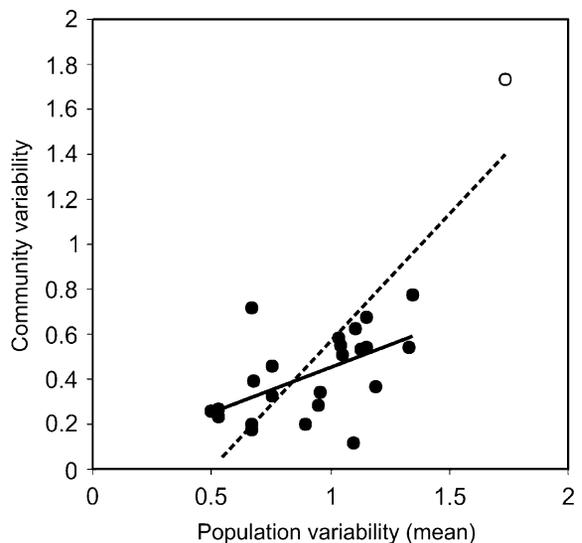


Fig. 5. Relationship between mean population variability and community variability for DT = 0–100 (open circles, hatched line) and DT = 25–100 (black circles, solid line).

multi-trophic microcosms increased species richness stabilizes both community and population abundances.

Second, the nature of communities and differences in types of interactions among species may determine which stabilizing mechanisms apply. Unlike in multi-trophic study systems, plants compete for the same resources (light, space, water, etc.) and are unlikely to exhibit strong resource facilitation, but will be dominated by competition. In highly competitive plant communities, population fluctuations are often asynchronous and would increase population variability as more species are added (Tilman 1996).

Third, in multi-trophic communities, effect of S on covariances is unknown but is unlikely to be linear. Similarly, effect of S on overyielding (\times parameter) may be obscured by energy loss during transfers between trophic levels and, indeed, by differences in body size among species.

The question remains as to the ecological mechanisms responsible for reduced variability of populations in more diverse communities. Resource-use complementarity has been suggested as a primary mechanism explaining why ecosystem functions may be less variable as diversity increases (Petchey 2003, Petchey et al. 2004b). Since we have found that CV_{com} and CV_{pop} are related in the experimental microcosm system, and that CV_{pop} underlie this relationship, we can reasonably speculate that resource-use complementarity could be one of the specific conditions contributing to the reduction of CV_{pop} . This idea however will require further conceptual development followed by testing.

In conclusion, our results show that species richness reduces temporal variability of community, population, and individual species abundances in microcosm com-

munities assembled of rock pool invertebrates. We found a conclusive link between population and community variability suggesting that the negative relationship between species richness and community variability arose through the stabilizing effect of species richness on the component populations. Populations were stabilized by species richness in part due to mean–variance scaling and possibly through other mechanisms, some of which might involve interactions (partitioning, facilitation, augmentation) revolving around communal resource use.

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References

- Beisner, B. E. and Romanuk, T.N. 2005. Insights from studies of relationships between diversity, productivity and invasibility: assessing community resistance and change. – In: de Ruiter, P. C., Wolters, V. and Moore, J. C. (eds), *Food webs: ecological networks in the new Millennium*. Elsevier/Academic Press, In Press.
- Cottingham, K. L., Brown, B. L. and Lennon, J. T. 2001. Biodiversity may regulate the temporal variability of ecological systems. – *Ecol. Lett.* 4: 72–85.
- De-Woody, Y. D., Swihart, R. K., Craig, B. A. et al. 2003. Diversity and stability in communities structured by asymmetric resource allocation. – *Am. Nat.* 161: 514–527.
- Díaz, S. and Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. – *Trends Ecol. Evol.* 16: 646–655.
- Doak, D. F., Bigger, D., Harding, E. K. et al. 1998. The statistical inevitability of stability–diversity relationships in community ecology. – *Am. Nat.* 151: 264–276.
- Downing, A. L. and Leibold, M. A. 2002. Ecosystem consequences of species richness and composition in pond food. – *Nature* 416: 837–841.
- Franklin, R. B., Garland, J. L., Bolster, C. H. et al. 2001. Impact of dilution on microbial community structure and functional potential: comparison of numerical simulations and batch culture experiments. – *Appl. Environ. Microbiol.* 67: 702–712.
- Garland, J. L. and Lehman, R. M. 1999. Dilution/extinction of community phenotypic characters to estimate relative structural diversity in mixed communities. – *FEMS Microbiol. Ecol.* 30: 333–343.
- Galkovskaya, G. A. 1996. Population interactions and stability of planktonic communities. – *Hydrobiol. J.* 32: 10–16.
- Giller, P. S., Hillebrand, H., Berninger, U. G. et al. 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. – *Oikos* 104: 423–436.
- Gillooly, J. F. 2000. Effect of body size and temperature on generation time in zooplankton. – *J. Plankton Res.* 22: 241–251.
- Goldberg, D.E., Turkington, R., Olsvig-Whittaker, L. et al. 2001. Positive and negative abundance-dependence in an annual plant community: variation among life history stages, growth forms, and physical environments. – *Ecol. Monogr.* 71: 423–446.
- Gonzales, A. and Descamps-Julien, B. 2004. Population and community variability in randomly fluctuating environments. – *Oikos* 106: 105–116.
- Hector, A., Bazeley-White, E., Loreau, M. et al. 2002. Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. – *Ecol. Lett.* 5: 502–511.
- Hooper, D. U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. – *Ecology* 79: 704–719.
- Hughes, J. B. and Roughgarden, J. 2000. Species diversity and biomass stability. – *Am. Nat.* 155: 618–627.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. – *Oecologia* 110: 449–460.
- Ives, A. R., Gross, K. and Klug, J. L. 1999. Stability and variability in competitive communities. – *Science* 286: 542–544.
- Ives, A. R., Gross, K. and Klug, J. L. 2000. Stability and species richness in complex communities. – *Ecol. Lett.* 3: 399–411.
- Kisand, V. and Wickner, J. 2003. Combining culture-dependent and -independent methodologies for estimation of richness of estuarine bacterioplankton consuming riverine dissolved organic matter. – *Appl. Environ. Microbiol.* 69: 3607–3616.
- Kolasa, J. and Li, B. L. 2003. Removing the confounding effect of habitat specialization reveals the stabilizing contribution of diversity to species variability. – *Proc. R. Soc. B* 270: 198–201.
- Kolasa, J. and Romanuk, T. N. 2005. Assembly of unequals in the unequal world of a rock pool metacommunity. – In: Holyoak, M., Leibold, M. A. and Holt, R. D. (eds), *Metacommunities: spatial dynamics and ecological communities*. Univ. of Chicago Press, In Press.
- Kondoh, M. 2003. Foraging adaptation and the relationship between food-web complexity and stability. – *Science* 299: 1388–1391.
- Lehman, C. H. and Tilman, D. 2000. Biodiversity, stability, and productivity in competitive communities. – *Am. Nat.* 156: 534–552.
- Li, B. L. and Charnov, E. L. 2001. Diversity–stability revisited: scaling rules for biological communities near equilibrium. – *Ecol. Modell.* 140: 247–254.
- Loreau, M. 1998. Biodiversity and ecosystem functioning: a mechanistic model. – *Proc. Natl Acad. Sci. USA* 95: 5632–5636.
- May, R. H. 1973. *Stability and complexity in model ecosystems*. – Princeton Univ. Press.
- MacArthur, R. H. 1955. Fluctuation of animal populations and a measure of community stability. – *Ecology* 36: 533–536.
- McGrady-Steed, J. and Morin, P. J. 2000. Biodiversity, abundance compensation, and the dynamics of populations and functional groups. – *Ecology* 81: 361–373.
- Naeem, S. 2002. Biodiversity equals instability? – *Nature* 416: 23–24.
- Naeem, S. and Li, S. 1997. Biodiversity enhances ecosystem reliability. – *Nature* 390: 507–509.
- Naeem, S., Thompson, L. J., Lawler, S. P. et al. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. – *Philos. Trans. R. Soc. B* 347: 249–262.
- Petchey, O. L. 2000. Prey diversity, prey composition, and predator population stability in experimental microcosms. – *J. Anim. Ecol.* 69: 874–882.
- Petchey, O. L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. – *Oikos* 101: 323–330.
- Petchey, O. L., Casey, T., Jiang, L. et al. 2002. Species richness, environmental fluctuations, and temporal change in total community biomass. – *Oikos* 99: 231–240.
- Petchey, O. L., Downing, A. L., Mittelbach, G. et al. 2004a. Species loss and the structure and functioning of multi-trophic aquatic systems. – *Oikos* 104: 467–478.
- Petchey, O. L., Hector, A. and Gaston, J. 2004b. How do different measures of functional diversity perform? – *Ecology* 85: 847–857.

- Pfisterer, A. B. and Schmid, B. 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. – *Nature* 416: 84–86.
- Romanuk, T. N. 2002. The relationship between diversity and stability in tropical rock pools. PhD thesis, McMaster Univ., Hamilton.
- Romanuk, T. N. and Kolasa, J. 2001. Simplifying the complexity of diversity dynamics. – *Écoscience* 8: 259–263.
- Romanuk, T. N. and Kolasa, J. 2002. Environmental variability alters the relationship between species richness and community variability in natural rock pool microcosms. – *Écoscience* 9: 55–62.
- Romanuk, T. N. and Kolasa, J. 2004. Population variability is lower in diverse rock pools when the obscuring effects of local processes are removed. – *Écoscience* 11: 455–462.
- Romanuk, T.N. and Kolasa, J. 2005. Resource limitation, biodiversity, and competitive effects interact to determine the invasibility of rock pool microcosms. – *Biol. Invas.* 7: 711–722.
- Srivastava, D. S., Kolasa, J., Bengtsson, J. et al. 2004. Are natural microcosms useful model systems for ecology? – *Trends Ecol. Evol.* 19: 279–384.
- Steiner, C. F. 2005. Temporal stability of pond zooplankton assemblages. – *Freshwater Biol.* 50: 105–112.
- Steiner, C. F., Long, Z. T., Krumins, J. et al. 2005. Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. – *Ecol. Lett.* 8: 819–828.
- Taylor, D. L. and Bruns, T. D. 1999. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: minimal overlap between the mature forest and resistant propagule communities. – *Mol. Ecol.* 8: 1837–1850.
- Therriault, T. and Kolasa, J. 1999. Physical determinants of richness, diversity, evenness and abundance in natural aquatic microcosms. – *Hydrobiologia* 412: 123–130.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. – *Ecology* 77: 350–363.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. – *Ecology* 80: 1455–1474.
- Tilman, D., Lehman, C. L. and Bristow, C. E. 1998. Diversity–stability relationships: statistical inevitability or ecological consequence. – *Am. Nat.* 151: 277–282.
- Tilman, D., Reich, P. B., Knops, J. et al. 2001. Diversity and productivity in long-term grassland experiment. – *Science* 294: 843–845.
- Valone, T. J. and Hoffman, C. D. 2003. Population stability is higher in more diverse annual plant communities. – *Ecol. Lett.* 6: 90–95.
- Worm, B. and Duffy, J.E. 2003. Biodiversity, productivity, and stability in real food webs. – *Trends Ecol. Evol.* 18: 628–632.
- Yachi, S. and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. – *Proc. Natl Acad. Sci. USA* 96: 1463–1468.

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