Research

Ecological realism and mechanisms by which diversity begets stability

Tamara N. Romanuk, Richard J. Vogt and Jurek Kolasa

T. N. Romanuk (tromanuk@gmail.com), Dept of Biology, Dalhousie Univ., Halifax, Nova Scotia, B3H 4J1, Canada. – R. J. Vogt, Dépt des Sciences Biologiques, Univ. du Québec à Montréal, CP 8888, Succ. Centre Ville, Montréal, QC, H3C 3P8, Canada. – J. Kolasa, Dept of Biology, McMaster Univ., 1280 Main Street, Hamilton, Ontario, L8S 4K1, Canada.

We investigated how ecological realism might impact the outcome of three experimental manipulations of species richness to determine whether the patterns and the mechanisms underlying richness–variability relationships differ as ecological communities are increasingly exposed to external forces that may drive richness–variability patterns in nature. To test for such an effect, we conducted experiments using rock pool meio-invertebrate communities housed in three experimental venues: controlled laboratory microcosms, artificially constructed rock pools in the field, and naturally occurring rock pools in the field. Our results showed that experimental venue can have a strong effect on the outcome of richness manipulation experiments. As ecological realism increased, the strength of the relationship between species richness and community variability declined from 32.9% in the laboratory microcosms to 16.8% in the artificial pools to no effect of species richness on community variability in the natural rock pools. The determinants of community variability also differed as ecological realism increased. In laboratory microcosms, community variability was driven solely by mechanisms related to increasing species richness. In artificial rock pools, community variability was driven by a combination of direct and indirect environmental factors as well as mechanisms related to increasing species richness. In the natural rock pools community variability was independent of species richness and was only related to environmental factors. In summary, we found that stabilizing mechanisms associated with species interactions were influential in establishing species richness–variability relations only in the less realistic experimental venues (the laboratory microcosms and the artificial rock pools in the field), and that these mechanisms diminished in importance as ecological realism and complexity of the experimental venue increased. Our results suggest that the effects of diversity might be more difficult to detect in natural systems due to the combined effects of biotic and abiotic forcing, which can mask our ability to detect richness effects.

Anthropogenic changes to natural systems may affect both diversity and stability independently of the effect of diversity on stability, emphasizing the importance of environmental drivers affecting both (Ives and Carpenter 2007). Recent studies have shown that the existence, strength, and even the direction of the relationship between species richness and temporal variability in population and community abundance can depend upon environmental factors including variability in temperature (Petchey et al. 1999, Gonzalez and Descamps-Julien 2004), temperature perturbation (Zhang and Zhang 2006a), or nutrient enrichment (Romanuk et al. 2006, Zhang and Zhang 2006b). The specific ranges of environmental conditions under which species richness has been shown to be stabilizing, however, appear to be highly idiosyncratic even when experiments are conducted using similar ecological communities (Ives and Carpenter 2007). For example, both Petchey et al. (2002) and Gonzalez and Descamps-Julien (2004) found no effect of increased variability in temperature on the relationship between species richness and temporal variability in abundance in

laboratory aquatic microcosms. Conversely, Romanuk and Kolasa (2002) found that temporal variability in aggregate community abundances declined with increasing species richness only in natural aquatic microcosms that were exposed to less variable environmental conditions. This disparity in results need not represent an inconsistency in interpreting the role of environmental drivers in understanding diversity–variability relationships. Instead, they may simply underscore the importance of how mechanisms underlying the relationship between a community's diversity and its temporal variability in abundance may change under different environmental circumstances. Indeed, as discussed by Srivastava and Velland (2005) the applicability of biodiversity–ecosystem functioning research to conservation rests on whether the results observed in experimental studies can be scaled-up to those relevant to conservation.

Experimental venue is an important but often overlooked aspect of experimental design (Carpenter 1996, Morin 1998, Drenner and Mazumder 1999, Skelly 2002). Understanding the limitations of conducting an experiment in artificial settings, such as laboratory microcosms, versus

in natural field settings is crucial when interpreting the outcome of ecological experiments, particularly when the conditions imposed in laboratory settings do not match those of their natural analogues (Morin 1998). The impact of species richness manipulations on changes in community biomass or ecosystem functioning over time deserves particular attention in this regard because patterns and mechanisms that are observed in highly controlled experiments may not correspond to patterns and mechanisms that operate in nature (Srivastava and Velland 2005). Previous work has suggested that the mechanisms by which species richness stabilizes communities may differ as experimental systems become more complex and as environmental control over population fluctuations increases (Ives and Carpenter 2007). For example, purported stabilizing mechanisms may begin to shift from those related to biotic interactions such as competition (Tilman 1999) to abiotic forcing as the experimental venue becomes more ecologically realistic. For example, in rock pools subject to a high frequency of desiccation events, diversity, species richness, evenness, and abundance change less over time relative to more permanent pools (Therriault and Kolasa 2002). Furthermore, these temporary pools have lower variability in community structure relative to more permanent pools (Therriault and Kolasa 2002). Paying closer attention to the shifts in underlying mechanisms as the ecological realism of the experimental venue changes might allow for a more thorough mechanistic understanding of diversity–variability relationships than solely verifying the presence or absence of such patterns.

In this study, we tested the idea that experimental venue will affect the outcome of three parallel experiments by disrupting presumed stabilizing effects of richness on population and community variability. We did so by manipulating the number of species in multi-trophic rock pool meio-invertebrate communities in laboratory microcosms and in the field in both artificially constructed and naturally occurring rock pools. These three experimental venues represent a gradient in ecological realism from laboratory microcosms, which were entirely controlled to limit spatial variability and exogenous forcing, to artificial rock pools, which were exposed to natural variation in environmental conditions but did not vary in size, shape and water volume (were kept full), through to the natural rock pools, which were exposed to natural spatial and temporal variation in environmental conditions including desiccation and differing pool morphometries. Our primary objective was to explore whether the relationship between species richness and temporal variability in both population and community abundance differs along this gradient in ecological realism and if the mechanisms underlying positive diversity–variability relations change as ecological realism increases.

To accomplish these goals, we directly compared the potential roles of various mechanisms by which diversity begets stability (Ives and Carpenter 2007) along a gradient of ecological realism. Since the initial observations by Odum (1953), Elton (1956), and MacArthur (1957), who observed that diverse communities are more stable than species-poor communities, the generality of this pattern has been empirically tested and verified in a wide-range of systems, but diversity–stability relationships have

been shown to be driven by multiple mechanisms (Ives and Carpenter 2007). In particular, we explored three classes of mechanisms by which species richness has been hypothesized to stabilize temporal variability in aggregate community abundance: overyielding (Tilman 1999), statistical averaging (Doak et al. 1998, Tilman et al. 1998), and competition or insurance effects (Tilman 1999, Yachi and Loreau 1999). Briefly, overyielding refers to an increase in mean community abundance with increasing species richness, which tends to stabilize community fluctuations (Tilman 1999). Higher population abundances also make it less likely that demographic or environmental stochasticity will result in species extinctions due to low numbers (Lande 1993). 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). As in economics, where diverse portfolios are less susceptible to fluctuations, the sum of several randomly varying entities will be less variable than the average entity as long as species fluctuations are out of phase with one another, an effect that becomes more pronounced with increasing numbers of species. To find evidence for such an effect, 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 effects help to maintain community-level stability when populations respond differentially to fluctuations in the environment as particularly tolerant species compensate in numbers for reduction in abundances of more sensitive species. In this way, insurance effects can be stabilizing when populations fluctuate asynchronously (Tilman 1999, Ives et al. 2000).

We further explored whether there was a stabilizing effect of species richness on component populations as previous research, particularly in aquatic systems, has highlighted the possibility that a stabilizing effect of species richness on aggregate community properties may be an epiphenomenon of processes operating at the population level (Petchey et al. 2002, Romanuk 2002, Romanuk and Kolasa 2004, Vogt et al. 2006, Romanuk et al. 2006). In the artificial and natural rock pools, we additionally considered the role of environmental drivers on both species richness, community variability, population variability, and summed abundances, variances, and covariances.

Methods

The study site

Rock pools communities consisting of aquatic meio- and micro-invertebrates were located on a fossilized reef near the Discovery Bay Marine Laboratory on the northern coast of Jamaica (18°28′N, 77°25′W). This site has been described in Therriault and Kolasa (1999, 2002), Romanuk and Kolasa (2002, 2004, 2005) and Kolasa and Li (2003). Two hundred and thirty erosional solution pools with a maximum volume greater than 250 ml are present on the fossil reef across an area of 50 m. On average, the pools are located within 1 m of the nearest neighbor and none are separated by

more than 5 m from the nearest pool. Their elevation above sea level ranges from 1–235 cm (mean = 76.6 ± 80.1 SD) at high tide, with the tide rarely exceeding 30 cm.

Species assemble in the rock pools along a salinity gradient, which is largely determined by elevation and exposure to the sea (Therriault and Kolasa 1999). While species composition changes along the salinity gradient, many species are euryhaline and are able to colonize and persist in freshwater, brackish, marine and hypersaline pools. Only freshwater pools (salinity 0 ppt) were used in these experiments. The pool communities also contain an abundant assemblage of microorganisms maintained by a range of autochtonous to allochtonous energy inputs (mangrove leaves, dead macroinvertebrates, green and brown algae). Resources, in the form of various microorganisms and detritus, are very abundant in the pools.

In a 10 year observational study of the rock pool communities (Romanuk and Kolasa 2002) the dominant species identified were a harpacticoid copepod, *Nitocra spinipes* (present in 70% of samples), a cyclopoid copepod, *Orthocyclops modestus* (70%), an ostracod *Candona* sp. (34%), an unidentified nematode species (31%), and a *Culex* mosquito (31%). Other common species include a daphnid, *Ceriodaphnia* sp., and several fresh and brackish water ostracods. The majority of species are small benthic animals ranging from 60–500 μm but some are plankton-like (*O. modestus, Ceriodaphnia rigaudi*) and swim in the water column. The full list of the taxa (69 species) identified to date includes: Turbellaria (7), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (20), Copepoda (6), Cladocera (4), Decapoda (crab) larvae (1), Decapoda (shrimps) (3), Amphipoda (1), Isopoda (1) and Insecta (18). Only the larval stages of insects, except for an occasional beetle and corixid bug, are observed in rock pools.

The experimental system

We conducted three parallel experiments using communities of zooplankton and benthic invertebrates collected from natural rock pool communities. The initial experimental communities included 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 rigaudi*), and one species of nematode worm. We did not control for species smaller than 63 μm, so rotifers, protists, phytoplankton, microbes, as well as juvenile stages of certain species such as copepod nauplii were present to varying degrees in the experimental multi-trophic community, but were neither enumerated nor directly considered in the analysis.

Experimental venue

The three experiments presented a gradient of ecological realism. The first experiment was conducted in laboratory microcosms where the communities were housed in 500 ml plastic beakers, had constant water volume, and were kept under controlled laboratory conditions. As such, all laboratory communities experienced similar physicochemical and morphometric conditions (except for any possible variability imposed by the species richness manipulation). The second set of experimental communities was established in artificial rock pools constructed from concrete and located in the field. They were situated 1–6 m from the ocean, and were partially protected from salt spray due to natural features of the landscape. Artificial rock pool communities were standardized for volume (2 l), shape, and were always kept full of water. The artificial rock pool communities thus experienced an intermediate level of spatial and temporal variability in physiochemical and morphometric conditions relative to the laboratory microcosms and natural rock pools, and represented an intermediate position along the gradient of ecological realism. The third set of experimental communities was established in naturally formed rock pools that were adjacent to the artificial rock pools (between 100–130 m away), but were situated within 0.1–4 m of the ocean. The natural rock pool communities ranged in volume from 500 to 20 000 ml and in depth from 5 to 30 cm, were subject to variable salinity due to ocean spray, and were allowed to desiccate. As such, the natural rock pool communities experienced the least degree of control over environmental factors and represented the most realistic condition. Both the natural rock pools and the artificial rock pools were subject to colonization from species not included in the original experimental communities (Table 1, Supplementary Material Appendix 1) and to natural allochthonous organic matter inputs from leaf litter.

Experimental design and sampling

All three experiments consisted of 30 communities that varied along a species richness gradient imposed using a dilution series, a practice shown to be effective in establishing gradients in species richness in rock pool communities (Romanuk and Kolasa 2005, Vogt et al. 2006, Romanuk et al. 2006). In a dilution series, species-poor communities comprise subsets of species-rich communities (Giller et al. 2004) with the species richness gradient persisting as density becomes equivalent between communities after re-growth (Franklin et al. 2001). Dilution series have been shown to successfully manipulate the diversity of various cultures including bacteria (Franklin et al. 2001) and rock pool meiofauna (Romanuk and Kolasa 2005, Romanuk et al. 2006, Vogt et al. 2006). Dilution series mimic one particular type of species loss, where rarer species are excluded as the mixture is increasingly diluted.

To assemble the experimental communities, water was collected from the natural rock pools used in the experiment and from five additional freshwater rock pools (salinity 0 ppt). The species pool used to assemble the experimental communities was the same for all three experiments. Rock pool water was filtered through a 63 μm mesh net and was combined in varying proportions to create the species richness gradient. Before assembling the communities for the natural and artificial rock pools the prospective pools were drained, dried out, and treated with salt water to remove any remaining freshwater species.

The three experiments ran for eight weeks between November 2000 and January 2001. Biotic samples were taken at the end of weeks two, five, and seven for the laboratory microcosms and the artificial rock pools, and at

the end of weeks two, five and eight for the natural rock pools (hereafter, weeks are referred to as two, five and seven). Before sampling, each microcosm was gently stirred to homogenize its contents to ensure that a representative sample of the community was taken. Samples were filtered through a 63 µm mesh, preserved in 50% ethanol and processed using a dissecting microscope. We excluded eight replicates from our analysis. The eight excluded replicates all had average species richness of less than one. The inclusion of these replicates of extremely low abundances disproportionately inflated CV for these communities (Vogt et al. 2006). The final number of replicates used for analysis was n = 24 for the laboratory microcosms, n = 28 for the artificial rock pools, and n = 30 for the natural rock pools.

Environmental variables

For the artificial and natural rock pools we measured temperature, salinity, pH, and depth each week when the biotic samples were taken. For the natural pools we also measured lip depth (depth from the limestone shelf) as well as pool volume (ml).

Data analysis

Mean species richness and mean abundances were calculated as the mean number of species or individuals, respectively, in each microcosm or rock pool over the three sampling dates. Variability in abundance was calculated as coefficients of variation (CV; standard deviation/mean), which standardize for differences in abundance (Cottingham et al. 2001). Community variability was calculated as the CV of summed abundances of all species in each replicate. Mean population variability was calculated as the mean of all species CV's in a microcosm:

$$CV_{mean} = \frac{1}{S} \sum_{i=1}^{S} \frac{\sigma_i}{\mu_i}$$

where CV_{mean} is the mean population variability of all species present in a microcosm or a rock pool, S is the number of species therein, σ_i is the standard deviation of population size of species i during the course of the three censuses, and μ_i is the mean population size of species i over the same censuses. This method yields a single measure of population variability per replicate and can be used to relate community and population variability directly (Romanuk 2002, Steiner et al. 2005, Vogt et al. 2006). Summed variances, summed covariances, summed abundances, mean-variance scaling relationships, and evenness, J', were calculated according to the procedures outlined in Doak et al. (1998) and Tilman (1999). For the artificial and natural rock pools we further used mean and standard deviations of temperature, salinity, pH, and depth as explanatory variables in our models and for the natural rock pools we additionally included maximum potential depth (depth from the deepest point to the limestone shelf) and initial pool volume (ml).

Our analysis was conducted in three steps: 1) we used general linear models (GLM) to test for interactions between experimental venue and mean species richness on community and population variability. To fit the GLMs we first used a 'homogeneity of slopes model' to test for significant differences in slopes based on environmental venue. Where significant differences in slopes were found a 'separate slopes' model was used in further analysis; where no significant differences in slopes were found, ANCOVA was used in further analysis. A separate slopes model was used in the former case as a traditional analysis of covariance (ANCOVA) is inappropriate when the categorical and continuous predictors interact in influencing responses on the outcome (Statsoft 2004). Mean abundances, summed abundances, and summed variances were log transformed to meet model assumptions of normality. All analyses were conducted in Statistica ver. 6.0 (Statsoft 2004).

Results

Mean species richness (S) over time was significantly higher in the laboratory microcosms and natural rock pools (mean S = 5.2, Tukey HSD p < 0.001) than in the artificial rock pools (mean S = 3.37; Fig. 1a). Mean community abundance (N) was significantly higher in the natural rock pools (mean N = 257.34, Tukey HSD p < 0.001) than in the artificial rock pools (mean N = 90.22, Tukey HSD p < 0.001) and
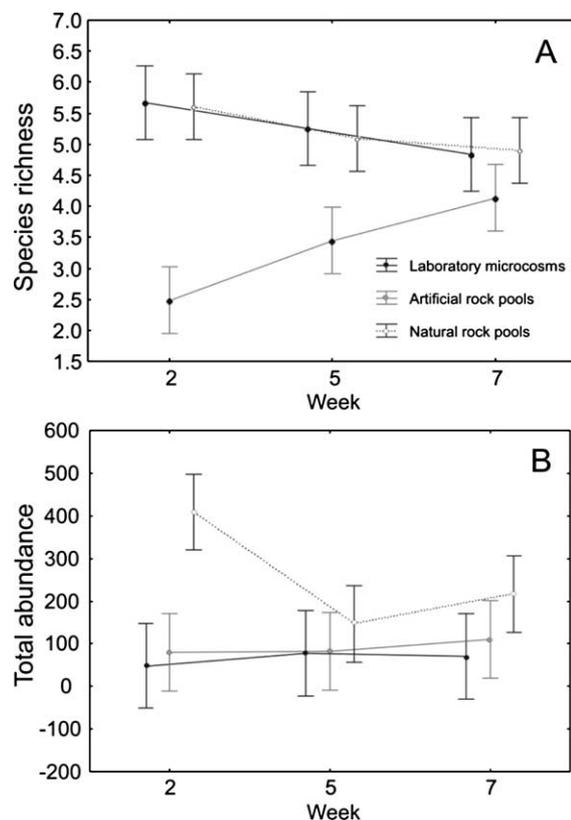

Figure 1. Temporal changes in (a) mean species richness, and (b) mean community abundance over the three sampling dates: laboratory microcosms (black lines), artificial rock pools (grey lines), natural rock pools (hatched lines). Shown are the 95% CI. Note that for natural pools week 7 samples were actually taken in week 8.

laboratory microcosms (mean $N = 65.7$; Fig. 1b). Mean abundance in the artificial and laboratory microcosms did not differ significantly (Tukey HSD $p = 0.818$). For details on how community composition changed over time see Table 1 in the Supplementary Material Appendix 1.

Community and mean population variability decreased with increasing species richness in the laboratory microcosms (Fig. 2a–b) and in the artificial rock pools but not in the natural rock pools. In the laboratory microcosms species richness explained 32.9% ($p = 0.004$) of the variance in community variability and 40.1% ($p < 0.001$) of the variance in population variability. In the artificial rock pools species richness explained 16.8% ($p = 0.036$) of the variance in community variability and 17.9% ($p = 0.025$) of the variance in mean population variability. In the natural rock pools there was no effect of species richness on either community variability ($p = 0.696$) or mean population variability ($p = 0.335$). There was no interaction between experimental venue and species richness on community variability ($p = 0.231$) and no effect of environmental venue on community variability ($p = 0.552$). In contrast, there was a significant interaction between experimental venue and species richness on mean population variability ($F_{3,76} = 7.089$, $p < 0.001$).

Mean population variability and community variability were positively related in all three experimental venues (laboratory microcosms $r^2 = 0.307$, $p = 0.005$; artificial rock pools $r^2 = 0.294$, $p = 0.003$; natural rock pools $r^2 = 0.343$, $p < 0.001$; Fig. 4). There was no significant interaction between environmental venue and mean population variability on community variability ($F_{2,76} = 2.51$, $p = 0.088$).

Summed abundances, variances, and covariances

Summed abundances were unrelated to species richness in the laboratory microcosms ($p = 0.249$) and the natural rock pools ($p = 0.794$; Fig. 3a). In the artificial rock pools summed abundances increased with increasing species richness ($r^2 = 0.149$, $p = 0.042$). There was a significant interaction between experimental venue and species richness on summed abundances ($F_{3,76} = 2.82$, $p = 0.044$). Summed abundances were also lower in the laboratory microcosms than in the artificial or natural rock pools ($F_{2,76} = 5.84$, $p = 0.004$).

Summed variances decreased with increasing richness in the laboratory microcosms ($r^2 = 0.245$, $p = 0.014$; Fig. 3b). In the artificial microcosms, summed variances tended to increase as richness increased, but this increase was insignificant ($r^2 = 0.112$, $p = 0.08$). In the natural rock pools, summed variances were unrelated to species richness ($p = 0.832$). There was a marginally insignificant interaction between environmental venue and species richness on summed variances ($F_{3,76} = 2.31$, $p = 0.083$) and summed variances increased from the laboratory microcosms
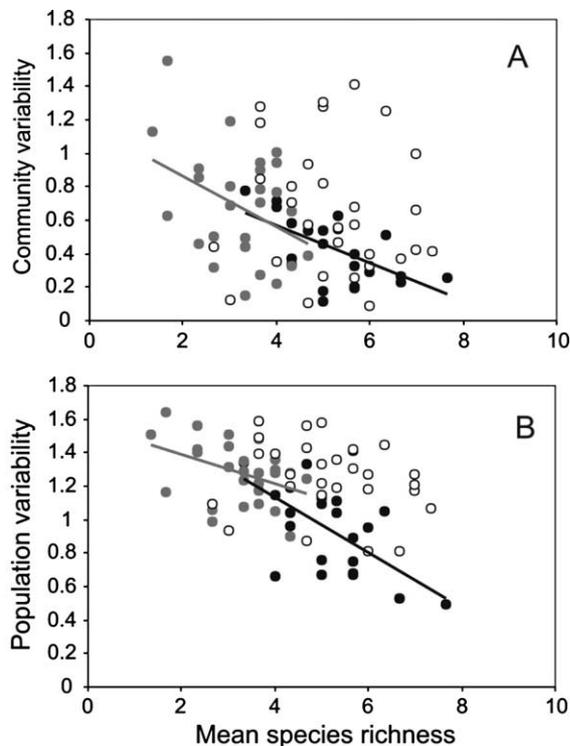

Figure 2. Effect of species richness on (a) community variability and (b) mean population variability for laboratory microcosms (black circles), artificial rock pools (grey circles) and natural pools (open circles).
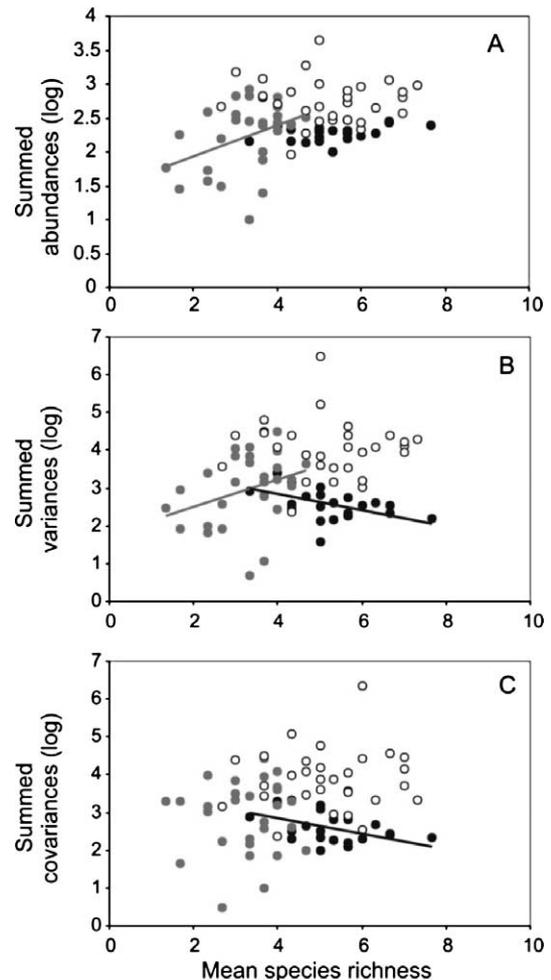

Figure 3. Effect of mean species richness on (a) summed abundances (log), (b) summed variances (log) and (c) summed covariances (log) in laboratory microcosms (black circles), artificial rock pools (grey circles), and natural pools (open circles).
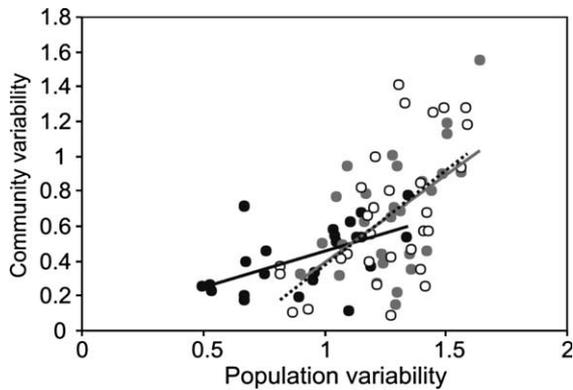
Figure 4. Relationship between mean population variability and community variability for laboratory microcosms (black circles), artificial rock pools (grey circles), and natural pools (open circles).

through to the artificial and natural rock pools ($F_{2,76} = 4.736$, $p = 0.012$). The slope of the mean-variance scaling relationship was greater than 1 in all three experimental venues and did not differ significantly across environmental venues (laboratory microcosms, slope = 1.339; artificial pools, slope = 1.877; natural rock pools, slope = 1.6; data not shown). There was no relationship between species richness and evenness, J', in any of the three experiments and no interaction between experimental venue and species richness on J' ($F_{2,76} = 0.721$, $p = 0.489$; data not shown).

Summed covariances decreased with increasing species richness in the laboratory microcosms ($r^2 = 0.225$, $p = 0.019$) but were unrelated species richness in the artificial ($p = 0.86$) and natural rock pools ($p = 0.7$; Fig. 3c) suggesting that in the laboratory microcosms population abundances were affected by fluctuations in the abundance of other species whereas in the artificial and natural rock pools population abundances were less affected by biotic forcing. There was no interaction between experimental venue and summed covariances ($p = 0.647$), but summed covariances were higher in the natural rock pools than in the laboratory microcosms and artificial rock pools (Tukey HSD p < 0.001).

Environmental variables

Artificial rock pools
In the artificial rock pools mean species richness and mean population variability were not correlated with any of the measured environmental factors. Community variability was weakly related to environmental factors with a trend towards increasing community variability with increased SD of both salinity and temperature and decreased community variability with increasing SD of depth (adjusted $R^2 = 0.11$, $p = 0.12$). Summed abundances and summed variances were strongly correlated with environmental factors, increasing with increasing temperature and decreasing with increases in SD of temperature and SD of depth (summed abundances adjusted $R^2 = 0.334$, $p = 0.005$; summed variances adjusted $R^2 = 0.315$, $p = 0.007$). There was a trend towards summed covariances decreasing with increasing depth and temperature and increasing with increasing SD of temperature (adjusted $R^2 = 0.154$, $p = 0.073$).

Natural pools
In the natural rock pools mean species richness was marginally lower in rock pools with higher SD of temperature (adjusted $R^2 = 0.09$, $p = 0.06$). Community variability was marginally higher in pools with greater SD of depth and lower in shallower pools and pools with higher temperature (adjusted $R^2 = 0.147$, $p = 0.068$). In contrast, population variability was unaffected by environmental factors ($p = 0.861$). Likewise, summed abundances ($p = 0.286$), summed variances ($p = 0.289$), and summed covariances ($p = 0.224$) were not correlated with environmental factors. Rock pool morphometry (i.e. lip depth and volume) had no effect on species richness, population variability or community variability in the natural rock pools ($p > 0.05$ for all).

Discussion

Global declines in biodiversity have focused the attention of the ecological community on the consequences of species loss to the continued functioning of ecological systems (May 1999, McCann 2000, Srivastava and Velland 2005). The search for generalities in patterns of diversity–variability relationships has shown that, in general, diverse communities are more stable than comparably depauperate ones (Cottingham et al. 2001). In natural systems, however, the environment may affect both diversity and stability independently of the effect of diversity on stability, emphasizing the importance of environmental drivers affecting both (Ives and Carpenter 2007). Comparing the patterns and underlying mechanisms by which species richness stabilizes communities across laboratory and field experiments is one way to facilitate our understanding of how diversity may stabilize communities in nature. Field experiments may mask the effects of biotic variables that would be observed in laboratory experiments that control for exogenous forcing. Our goal in conducting these three experiments was to directly test how species richness manipulations might affect community and population stability along a gradient of ecological realism in an attempt to disentangle the potential role of environmental versus biotic drivers in diversity–variability relationships. This approach was meant to provide insight into how both the patterns and the underlying mechanisms by which species richness stabilizes community and population abundances might differ between controlled experimental conditions and more natural communities.

A large body of biodiversity–ecosystem functioning research has been focused on exploring the mechanisms that might underlie positive diversity–variability relationships (Petchey et al. 2002, Valone and Hoffman 2003, Caldeira et al. 2005, Vogt et al. 2006). Recent meta-analyses using long-term datasets, however, such as the recent review by Valone and Barber (2008) on the potential operation of the insurance effect in bird populations have called the applicability of these kinds of mechanisms to natural communities into question.

Valone and Barber (2008) showed that covariances between species-pairs in a wide range of taxa were much more often positive than negative, potentially resulting from shared responses of coexisting species to fluctuations in a

common resource base, possibly driven by climatic factors. Since a negative relation between diversity and summed covariances is necessary to invoke the insurance effect, their results suggest that the insurance effect might not be as pervasive in natural communities as might be expected from theory or may be masked by environmentally driven fluctuations in species abundances.

In the laboratory microcosms the positive diversity–variability relationship was driven by decreases in summed covariances and summed variances as species richness increased. The artificial rock pools, on the other hand, showed a trend towards an increase in summed variances with increasing richness in addition to an increase in summed abundances with species richness. Thus, the artificial rock pools present evidence that species richness can contribute to both increases and decreases in temporal variability. Community variability in the artificial pools was also directly affected by environmental conditions. In the natural rock pools, on the other hand, temporal variability in community abundance was unrelated to species richness and was directly affected by environmental conditions. Clearly, as the level of ecological realism increased, the role of environmental factors became more influential in regulating temporal variability in community abundance.

Two questions arising from our results are of particular interest. First, why was a positive diversity–variability pattern observed in the laboratory microcosms and artificial rock pools but not in the natural rock pools? Second, how did the mechanisms underlying these patterns change along the imposed gradient of ecological realism? To begin to answer these questions, it is important to summarize how the three experiments differed along the aforementioned gradient of ecological realism. As detailed above, the three experiments differed substantially in physicochemical conditions, the morphometry of the pools and location. While the laboratory microcosms experienced relatively constant conditions, both the artificial and natural rock pools experienced natural patterns of variability in physicochemical conditions, received allochthonous inputs from the landscape, and were open to colonization. What differentiated the latter two experiments was: the range in pool size among the natural pools which varied from 500 to 20 000 ml while the artificial pools were the same size and shape, the natural pools were allowed to desiccate while the artificial pools were regularly refilled, and the natural pools experienced a greater range in elevation, while the artificial pools were all located on the same rock platform. Colonization and extinction events in the artificial and natural pools resulted in a less defined diversity gradient and a decrease in species richness over time, which was not the case in the laboratory microcosms where species richness increased due to the development of nauplii into adults. Initial species composition was relatively similar in all three experiments as the species used in the dilution series were collected from the same set of natural rock pools. As time progressed, however, the communities in the artificial and natural rock pools began to diverge from their initial compositions, due to colonization and extinction, whereas the species compositions in the laboratory microcosms remained relatively constant.

There are many potential interpretations for the weakening of the relationship between diversity and variability

along the gradient of ecological realism. Strikingly, the decline in the strength of the effect of species richness on both community and population variability with the increase in ecological realism was gradual, decreasing from ∼35% explained variance in the laboratory microcosms to ∼17% in the artificial pools to no effect of species richness on biotic variability in the natural pools. There are at least three plausible reasons why the diversity–variability relation appeared to weaken as ecological realism increased. First, the gradient in ecological realism encompassed an increase in spatial and temporal variability in physicochemical conditions, potentially preventing the detection of a stabilizing effect of species richness simply due to increased "noise" in the data (Romanuk and Kolasa 2004, Kolasa and Li 2003). In support of this possibility, the spatial variance (among replicate microcosms and pools) in both population and community variability was greater in the artificial and natural rock pools than in the laboratory microcosms (Fig. 2a–b). Second, community composition diverged from initial composition in the artificial and natural pools, but not in the laboratory microcosms, where species identities remained relatively similar to initial composition (Table 1, Supplementary Material Appendix 1). This increase in divergence and variability in community composition in the artificial and natural pools likely also have increased the 'noise' in the data. Third, the temporal extent of the experiment in the natural rock pools may not have been long enough to allow strong inter-specific interactions to stabilize community abundances (Cardinale et al. 2007). A previous long-term (10 year) observational study on the relationship between species richness and community variability in natural un-manipulated rock pools showed that community variability in abundance declined with increasing species richness but only in pools that experienced lower variability in abiotic conditions (Romanuk and Kolasa 2002). Thus, it is possible that the temporal extent of the experiments in the natural rock pools (eight weeks for the natural pools and seven weeks for the laboratory and artificial pools), may have been too short to detect a stabilizing role of species richness, whereas in the laboratory microcosms and artificial pools reductions in exogenous forcing and spatial variability in habitat factors may have facilitated a more rapid return to equilibrium-like dynamics. While the strength of diversity–stability relations have not yet been analyzed according to the duration of the experiment, Cardinale et al. (2007) has shown that the net effect of plant richness on plant biomass is higher in experiments that last for longer durations due to an increase in the magnitude of species complementarity effects with time and Stachowicz et al. (2008) has shown that seaweed species richness increases biomass accumulation more strongly in long term (3-year) experiments than in short term (2-month) experiments.

An answer to the second question must include a justification for why the mechanisms underlying the stabilizing effect of richness might also differ along the gradient of ecological realism. As ecological realism increases so too does the potential role of environmental forcing (Morin 1998). Environmental conditions can affect species richness and both community and population variability directly (Ives and Carpenter 2007) and can also modulate the strength of richness effects on variability by

affecting the components of stability (the summed abundances, summed variances and summed covariances) and their interaction with species richness. For example, in the laboratory experiment, species richness was determined solely by the experimental manipulation of species richness. Likewise, since all of the microcosms were exposed to identical environmental conditions, any differences in population and community variability would have been due to endogenous effects as opposed to external forcing. Differences in summed abundance, summed variance and summed covariance, and their relations with species richness, were thus necessarily restricted to the changes imposed by the dilution series and the realized population dynamics. In the artificial and natural rock pools, however, all of these factors had the potential to be affected by potentially non-uniform environmental conditions. Both species richness and biotic variability could have been affected directly by environmental conditions. Likewise, environmental conditions could have affected the components of stability (summed abundances, summed variances and summed covariances) directly or indirectly through their interaction with species richness. Therefore, as ecological realism increased, the outcome of the experiment became dependent on an increasingly complex set of factors. As ecological realism increased from the laboratory microcosms through to the artificial and natural pools, species richness became more spatially variable among replicates, population and community variability increased, and the summed abundances, summed variances and summed covariances also increased in magnitude.

As mentioned above, the positive diversity–variability relation in the laboratory microcosms appears to have resulted from the operation of two mechanisms: declines in both summed variances and summed covariances with increasing species richness. Both of these mechanisms likely contributed to the net effect of a decline in community variability with increasing species richness. Changes in the summed variances and summed covariances with increasing species richness have been observed in a number of experimental manipulations of species richness; the generality of the importance and implications of these changes, however, is far from clear. For example, Tilman et al. (2006) found that decadal stability in plant biomass increased with increasing species richness, but only identified a decline in the summed variances and an increase in the summed abundances with increasing species richness as potential mechanisms. Caldeira et al. (2005) found an increase in both the summed covariances and summed variances as richness increased in old field communities. Valone and Hoffman (2003) found no relation between species richness and either the summed variances or covariances in annual plant communities despite observing a negative relation between species richness and community variability. Petchey et al. (2002) found that summed covariances became more negative with increasing species richness in constant environments in protist microcosms, suggesting that competitive interactions became stronger as species richness increased, potentially stabilizing community abundances; this stabilizing effect of a decline in summed covariances, however, occurred concurrently with an increase in the summed variances as species richness increased. All of these patterns were observed in studies that reported at least a weak stabilizing effect of species richness on temporal variability in aggregate biomass or abundance. Collectively, these results argue for the complexity of mechanisms underlying diversity–variability relations when considering changes in summed covariances and variances with changes in species richness.

As ecological realism increased from the laboratory microcosms through to the natural rock pools, summed covariances became more positive, and the role of the covariance effect, which requires summed covariances to become more negative as diversity increases, weakened. In the artificial pools, summed covariances were independent of species richness and the summed variances and summed abundances increased with species richness. Increases in the summed variances with species richness can contribute to increased temporal variability (Caldiera et al. 2005), but can also lead to a stabilising effect if the slope of the log variance-log mean abundance relationship is greater than 1 (Doak et al. 1998, Tilman et al. 1998) as we found here. Petchey et al. (2002) observed a similar result in their experimental manipulation of species richness in protist microcosms, an increase in summed variances with increasing species richness concurrently with mean–variance scaling relations >1. Therefore, while the net diversity effect in the artificial pools was still positive, increases in species richness contributed to both increased and decreased temporal variability, which could have accounted for the weaker overall relation between species richness and community variability in the artificial pool experiment relative to that noted in the laboratory pool experiment. Environmental factors, both direct and indirect, were also observed to be important in the artificial pools with community variability, summed abundances, summed variances and summed covariances all co-varying with one or more environmental factors.

Finally, in the natural rock pools, we detected no relationship between species richness and community variability and no effect of species richness on summed variances, summed covariances or summed abundances (as would be expected given the lack of any effect of richness on community variability). Of the three experimental venues, we observed a direct effect of environmental conditions on species richness only in the natural rock pools where species richness decreased with increasing variability in depth, a trend that has been noted previously in this system (Therriault and Kolasa 2002). Community variability was also directly affected by environmental conditions. Community variability was higher in pools with greater SD of depth (a measure of pool permanence), and was lower in shallower pools and pools with higher temperature. Thus, in the natural pools, environmental conditions affected both species richness and community variability directly.

The relationship between population and community variability

Results from early empirical and theoretical studies suggested that the stabilizing effect of species richness on community abundances is contingent on increased variability of populations (May 1972, Tilman 1996). However, recent empirical studies in rock pool communities (Romanuk 2002, Kolasa

and Li 2003, Romanuk and Kolasa 2002, Kolasa 2005, Vogt et al. 2006, Romanuk et al. 2006), pond zooplankton (Steiner et al. 2005) and grasslands (Valone and Hoffman 2003) have shown that species richness can stabilize both population and community abundances. This pattern has also been predicted theoretically (Ives et al. 1999, 2000, DeWoody et al. 2003, Li and Charnov 2001). The importance of this pattern in biodiversity–ecosystem functioning research has received only minor attention, which is somewhat surprising as the majority of empirical studies have reported either a stabilizing effect of species richness on population variability (Romanuk 2002, Petchey et al. 2002, Valone and Hoffman 2003, Romanuk and Kolasa 2004, Steiner et al. 2005,) or no effect of species richness on population variability (McGrady-Steed and Morin 2000, Steiner 2005). Indeed, the only studies that have shown negative effects of species richness on population variability are Tilman (1996), Gonzalez and Decamps-Julian (2004) and Caldeira et al. (2005). We found similar patterns for the effect of species richness on temporal variability in mean population abundance as we did for community variability: populations were stabilized by increasing richness in the laboratory microcosms and artificial rock pools but not in the natural rock pools. Furthermore, population and community variability were positively correlated in all three experimental venues. These patterns suggest that the stabilizing effect of species richness on community variability may simply be an epiphenomenon resulting from the stabilizing effect of species richness on populations. In contrast to the stabilizing effect of species richness on population abundances in the laboratory microcosms and artificial rock pools, in the natural rock pools there was no relationship between species richness and population variability. Whether or not species richness stabilized variability in mean population abundances, however, more variable communities also had more variable populations.

Conclusion

The results presented here are of significant importance because they identify circumstances under which the generality of diversity–variability relationships can be restricted. Previous observational work in tropical rock pool communities (Romanuk and Kolasa 2002), combined with the results from this study, suggest that as ecological realism increases, the potential for identifying a stabilizing role of species richness on temporal variability in population and community abundances declines. The role of biotic interactions also weakens along the gradient of ecological realism as the relations between species richness and the components of stability (summed abundances, variances and covariances) become less numerous in the artificial pools, and disappear completely in the natural pools. Summed covariances were positive and higher in the artificial and natural pools than in the laboratory microcosms suggesting that synchrony in response to environmental fluctuations increased with influence of environmental forcing (Yachi and Loreau 1999), potentially dampening the expected stabilizing effect of species richness on variability in community abundances.

Our results do not suggest that biodiversity is unimportant or less important to the stability and functioning of natural versus artificial or laboratory communities. In nature, biodiversity contributes to the functioning of ecosystems (Duffy 2009) and may contribute more strongly to ecosystem functions, particularly to changes in biomass, as the duration of experiments increase (Cardinale et al. 2007). Effects of diversity, however, might be more difficult to detect in natural systems due to the combined effects of biotic and abiotic forcing, which can mask our ability to detect richness effects. The results presented here show that the patterns underlying stabilizing effects of diversity differ based on the ecological realism of the experimental venue. Our results differ from recent studies looking at the role of ecological realism on richness effects on productivity. For example, Stachowicz et al. (2008) found that seaweed biomass accumulation increased with species richness only in a field experiment and not in the related mesocosm study. However, similar to our interpretation, Stachowicz et al. (2008) argue that the mesocosm experiments may detect only a subset of possible mechanisms that operate in the field over the longer term. An increased emphasis on conducting both biodiversity–ecosystem functioning and biodiversity–stability experiments across gradients in ecological realism, for different durations and incorporating effects of environmental drivers, is needed to determine the generality of these patterns in biodiversity–ecosystem function and biodiversity–stability research.

References

Caldeira, M. C. et al. 2005. Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. – Oikos 110: 115–123.

Cardinale, B. J. et al. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. – Proc. Natl Acad. Sci. 104: 18123–18128.

Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. – Ecology 77: 677–680.

Cottingham, K. L. et al. 2001. Biodiversity may regulate the temporal variability of ecological systems. – Ecol. Lett. 4: 72–85.

DeWoody, Y. D. et al. 2003. Diversity and stability in communities structured by asymmetric resource allocation. – Am. Nat. 162: 514–527.

Doak, D. F. et al. 1998. The statistical inevitability of diversity-stability relationships in community ecology. – Am. Nat. 151: 264–276.

Drenner, R. W. and Mazumder, A. 1999. Microcosm experiments have limited relevance for community and ecosystem ecology: comment. – Ecology 80: 1081–1085.

Duffy, J. E. 2009. Why biodiversity is important to the functioning of real-world ecosystems. – Front. Ecol. Environ., in press.

Elton, C. 1956. The ecology of invasions by animals and plants. – Univ. of Chicago Press.

Franklin, R. B. 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.

Giller, P. S. et al. 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. – Oikos 104: 423–436.

Gonzalez, A. and Descamps-Julien, B. 2004. Population and community variability in randomly fluctuating environments. – Oikos 166: 105–116.

Ives, A. R. and Carpenter, S. R. 2007. Stability and diversity of ecosystems. – Science 317: 58–62.

Ives, A. R. et al. 1999. Stability and variability in competitive communities. – Science 286: 542–544.

Ives, A. R. et al. 2000. Stability and species richness in complex communities. – Ecol. Lett. 3: 399–411.

Kolasa, J. 2005. Complexity, system integration and susceptibility to change: biodiversity connection. – Ecol. Complexity 2: 431–442.

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. Lond. B 270: S198–201.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. – Am. Nat. 142: 911–927.

Li, B. L. and Charnov, E. L. 2001. Diversity-stability relationships revisited: scaling rules for biological communities near equilibrium. – Ecol. Modell. 140: 247–254.

May, R. M. 1972. Stability and complexity in model ecosystems. – Princeton Univ. Press.

May, R. M. 1999. Unanswered questions in ecology. – Philos. Trans. R. Soc. Lond. B 354: 1951–1959.

MacArthur, R. 1957. On the relative abundance of bird species. – Proc. Natl Acad. Sci. 43: 293–295.

McCann, K. 2000. The diversity–stability debate. – Nature 405: 228–233.

McGrady-Steed, J. and Morin, P. J. 2000. Biodiversity, density compensation and the dynamics of populations and functional groups. – Ecology 81: 361–373.

Morin, P. J. 1998. Realism, precision, and generality in experimental tests of ecological theory. – In: Resetarits, W. J. and Bernardo, J. (eds), Issues and perspectives in experimental ecology. Oxford Univ. Press, pp. 50–70.

Odum, E. P. 1953. Fundamentals of ecology. – W. B. Saunders Co.

Petchey, O. L. et al. 1999. Environmental warming alters food-web structure and ecosystem function. – Nature 402: 69–72.

Petchey, O. L. et al. 2002. Species richness, environmental fluctuations and temporal change in total community biomass. – Oikos 99: 231–240.

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. 2002. Environmenal variability alters the relationship between species richness and variability of community abundance in aquatic rock pool microcosms. – Ecoscience 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. – Ecoscience 11: 455–462.

Romanuk, T. N. and Kolasa, J. 2005. Resource limitation, biodiversity and competitive effects interact to determine the invisibility of rock pool microcosms. – Biol. Invas. 7: 711–722.

Romanuk, T. N. et al. 2006. Nutrient enrichment weakens the stabilizing effect of species richness. – Oikos 114: 291–302.

Skelly, D. K. 2002. Experimental venue and estimation of interaction strength. – Ecology 83: 2097–2101.

Srivastava, D. and Velland, M. 2005. Biodiversity-ecosystem function research: is it relevant to conservation. – Annu. Rev. Ecol. Evol. Syst. 36: 267–294.

Stachowicz, J. J. et al. 2008. Complementarity in marine biodiversity manipulations: reconciling divergent evidence from field and mesocosm experiments. – Proc. Natl Acad. Sci. 105: 18842–18847.

Steiner, C. F. 2005. Temporal stability of pond zooplankton assemblages. – Freshwater Biol. 50: 105–112.

Steiner, C. F. et al. 2005. Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. – Ecol. Lett. 8: 819–828.

Therriault, T. W. and Kolasa, J. 1999. Physical determinants of richness, diversity, evenness and abundance in natural aquatic microcosms. – Hydrobiologia 412: 123–130.

Therriault, T. W. and Kolasa, J. 2002. Desiccation frequency reduces species diversity and predictability of community structure in coastal rock pools. – Isr. J. Zool. 47: 477–489.

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. et al. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence. – Am. Nat. 151: 277–282.

Tilman, D. et al. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. – Nature 441: 629–632.

Valone, T. J. and Hoffman, C. D. 2003. A mechanistic examination of diversity-stability relationships in annual plant communities. – Oikos 103: 519–527.

Valone, T. J. and Barber, N. A. 2008. An empirical evaluation of the insurance hypothesis in diversity–stability models. – Ecology 89: 522–531.

Vogt, R. J. et al. 2006. Species richness–variability relationships in multi-trophic aquatic microcosms. – Oikos 113: 55–66.

Yachi, S. and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. – Proc. Natl Acad. Sci. 96: 1463–1468.

Zhang, Q. and Zhang, D. 2006a. Resource availability and biodiversity effects on the productivity, temporal variability, and resistance of experimental algal communities. – Oikos 114: 385–396.

Zhang, Q. and Zhang, D. 2006b. Species richness destabilizes ecosystem functioning in experimental aquatic microcosms. – Oikos 112: 218–226.

Supplementary material (available online as Appendix O17273 at <www.oikos.lu.se/appendix>) Table 1.