

Population variability is lower in diverse rock pools when the obscuring effects of local processes are removed¹

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Abstract: Ecological theory predicts that species richness should impact population variability. In contrast, most empirical evidence suggests no or only a weak positive relationship between species richness and population variability. We investigated the hypothesis that the obscuring noise of local processes at small scales such as differences in environmental conditions and species composition may mask the effects of species richness on population variability. Using long-term data on invertebrate populations in rock pools, we considered species richness-population variability relationships using three analytic resolutions in which data for the two key variables, species richness and population variability, were averaged for each population at decreasing levels of resolution to successively remove more noise arising from local processes. Of these levels the resolution most useful in making predictions about the effect of species richness on population variability removed the most noise in population responses arising from local processes. Our results show that populations are less variable in species-rich environments, a finding that reiterates the importance of species richness not only for aggregate properties such as biomass stability, but also for individual species abundances. Comparing results at different resolutions also provides a methodology to identify relevant detail in richness-population variability relationships.

Keywords: diversity, environmental noise, resolution, rock pools, stability.

Résumé : En théorie, la richesse en espèces devrait avoir un effet sur la variabilité des populations. En réalité, les données empiriques suggèrent au contraire qu'il n'existe aucun lien, ou seulement une faible relation positive entre la richesse et la variabilité. Nous avons vérifié l'hypothèse selon laquelle le bruit des processus locaux à fine échelle, tels que des différences au niveau des conditions environnementales ou de la composition en espèces, masque les effets de la richesse sur la variabilité des populations. Pour ce faire, nous avons utilisé des données sur des populations d'invertébrés qui colonisent des mares présentes sur des rochers. Nous avons étudié les relations qui existent entre la richesse et la variabilité en utilisant trois méthodes de résolution analytique. Nous avons calculé les moyennes de variabilité et de richesse à différents niveaux décroissants de résolution pour enlever de façon successive un peu du bruit provenant des processus locaux. De ces niveaux de résolution, celui qui est le plus utile pour prédire les effets de la richesse sur la variabilité est celui qui enlève le plus de bruit provenant des processus locaux. Nos résultats montrent que les populations sont moins variables dans les environnements riches en espèces, ce qui réitère l'importance de la richesse en espèces, non seulement pour des propriétés comme la stabilité de la biomasse, mais aussi pour favoriser l'abondance des espèces individuelles. La comparaison de résultats à différents niveaux de résolution constitue également une méthodologie permettant d'identifier des détails pertinents ayant trait aux relations entre la richesse et la variabilité des populations.

Mots-clés : bruit environnemental, diversité, mares de rochers, résolution, stabilité.

Nomenclature : Merritt & Cummins, 1996; Therriault & Kolasa, 1999a; Thorp & Covich, 2001

Introduction

Species richness appears to affect variability in community abundance or biomass differently than population variability (May, 1973; Peterson, 1975; Tilman, 1996; Hughes & Roughgarden, 1998; McGrady-Steed & Morin, 2000; Romanuk & Kolasa, 2002; Gonzalez & Descamps-Julien, 2004). For communities, greater richness reduces temporal variability in aggregate community abundance (reviews McCann, 2000; Cottingham, Brown & Lemon, 2001; Loreau *et al.*, 2001) through biological and statistical processes, including overyielding (Tilman, 1999), complementarity (Hooper, 1998; Tilman, 1999; Norberg,

2000; Cardinale, Palmer & Collins, 2002), insurance effects and asynchronous population fluctuations (Petchey *et al.*, 1999; Yachi & Loreau, 1999), weak interaction effects (McCann, Hastings & Huxel, 1998), statistical averaging (Doak *et al.*, 1998), mean-variance relationships (Cottingham, Brown & Lennon, 2001), and sampling effects (Huston, 1997).

For populations, the effect of richness on variability in abundance or biomass is unclear (McCann, 2000; Cottingham, Brown & Lemon, 2001). Empirical studies generally show non-existent or only very weak effects of richness on population variability (Tilman, 1996; Wardle *et al.*, 1999; McGrady-Steed & Morin, 2000; Romanuk & Kolasa, 2002). Exceptions include Valone and Hoffman (2003a), who found that plant species in more diverse

plots were less temporally variable than plant species in low-diversity plots. However, they only analyzed the relationship between temporal variability and diversity for individual species. The only experiment detecting a significant relationship between richness and population variability (i.e., all species analyzed together as we have done here) was Tilman (1996), who found that richness destabilized population abundances. However, only 2% of the variance in population variability was explained by richness. McGrady-Steed and Morin (2000) found no relationship between richness and protist population variability in laboratory microcosms, and Romanuk and Kolasa (2002) showed that population variability was unaffected by richness in natural rock pool communities, but Kolasa and Li (2003) found a stabilizing effect of richness on populations after they factored out the impact of species specialization, which is a separate source of population variability. Notably, Gonzalez and Descamps-Julien (2004) found that the stabilizing effect of richness in competitor assemblages may depend on environmental fluctuations. Theoretical predictions are also idiosyncratic, with models predicting that richness can increase (May, 1973; Lehman & Tilman, 2000), decrease (Ives, Gross & Klug, 1999; Ives, Klug & Gross, 2000; Li & Charnov, 2001; DeWoody et al., 2003), or have no effect on population variability (Tilman, 1999), depending on model construction.

The paucity of data detecting population responses to species richness suggests that there is no relationship, only a very weak relationship between species richness and population variability, or a methodological failure to detect a relationship. Population variability reflects interspecific and intraspecific interactions (Tilman, Lehman & Thompson, 1997) and variation in the physical environment, including resources (Loreau, 1998). Variation among individuals of each population may also contribute to the observed patterns. These "local" processes strongly vary among sites, resulting in extensive scatter (noise) in population variability values for any given species richness value (Tilman, 1996; McGrady-Steed & Morin, 2000; Romanuk & Kolasa, 2002; see also Tilman, Lehman & Thompson, 1997; Loreau, 1998).

Whether noise resulting from local differences in species compositions and local environmental differences could account for the apparent absence of impact of species richness on population variability reported by Romanuk and Kolasa (2002) warrants further investigation. To this end, we tested the relationship between species richness and population variability in a system of tropical rock pools inhabited by zooplankton and benthic invertebrates using three alternative resolutions of data. By aggregating data and thus lowering the resolution we removed increasing amounts of noise from the data. This method allowed us to determine the level of resolution most useful for making predictions about the effect of species richness on population variability. It is important to note that we are not suggesting that this method necessarily reflects a process arising when population variability is assessed at a metapopulation scale, although this may in fact be the case. The primary purpose in removing differences due to "local processes" is to assess

whether a significant relationship between species richness and population variability is masked by local differences in species composition and environmental conditions. Previous studies on the rock pool community have shown that differences in environmental conditions have strong effects on the resulting relationship between species richness and community variability (Romanuk & Kolasa, 2002).

Methods

STUDY SITE

We conducted our study in the supratidal zone near the Discovery Bay Marine Laboratory (18° 28' N, 77° 25' W) on the north coast of Jamaica (Schuh & Diesel, 1995; Kolasa et al., 1996; Kolasa, Hewitt & Drake, 1998; Therriault & Kolasa, 1999b; 2000; Romanuk & Kolasa, 2001; 2002; Therriault & Kolasa, 2002). The study site covered an area 50 m in diameter of mixed land and sea habitat. A few scattered mangrove trees (*Rhizophora* mangle) grew between the rocks and were a major source of detritus in some rock pools. Forty-nine pools were randomly chosen (Kolasa et al., 1996) and sampled in late December or early January in 1989, 1990, 1991, 1992, 1993, 1997, 1998, and in June 1997. Pools ranged from 14 to 248 cm in length (mean \pm SD = 56 \pm 35.0 cm), 10 to 188 cm in width (32.9 \pm 26.8 cm), and 1 to 37 cm in depth (12.8 \pm 8.3 cm). Elevation above sea level ranged from 1 to 235 cm (76.6 \pm 80.1 cm) at high tide, with the tide rarely exceeding 30 cm. Seven pools were tidal (although tidal flooding was not daily). The remaining 42 pools were maintained by rainwater and, very occasionally, wave splash or storm water.

ECOLOGY AND BIOTA OF TROPICAL ROCK POOLS

The pool communities consisted of aquatic meio- and micro-invertebrates. The dominant species were a harpacticoid copepod, *Nitocra spinipes* (present in 70% of samples); a cyclopoid copepod, *Orthocyclops modestus* (70%); an ostracod *Candona* sp. (34%); a nematode species (31%); and a *Culex mosquito* (31%). Other common species included a cladoceran, *Ceriodaphnia* sp., and several fresh and brackish water ostracods. Most species were benthic animals ranging from 0.6 to 5 mm, but some were plankton-like (i.e., *O. modestus*). The full list of taxa included Turbellaria (7), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (20), Copepoda (6), Cladocera (4), Decapoda larvae and various shrimps (4), Amphipoda (1), Isopoda (1), and Insecta (18). Apart from the 69 species that were included in our primary data set, some transient visitors were found, including gastropods (Littorinidae and Neritidae), hermit crabs, and the brachy-uran crabs *Pachygrapsus* sp. (Schuh & Diesel, 1995).

There are no pronounced species-area effects on abundance or species richness between pools of different sizes. Pool volume was unrelated to both mean richness ($r^2 = 0.001$, $P = 0.819$, $n = 365$) and mean community density ($r^2 = 0.037$, $P = 0.194$, $n = 365$). Seasonal differences, assessed as the difference in richness and abundance between June ($n = 2$) and January ($n = 6$) sampling dates, were low due to the relatively constant annual tem-

perature and accounted for < 2% of the variability in density and none of the variability in species richness (T. N. Romanuk & J. Kolasa, unpubl. data).

The rock pool communities experience high rates of colonization and desiccation. A range of 0.4-17.6 copepods · mL⁻¹ was counted in the detritus layer of the rock pools 24 h after rain, although their source was not determined (Schuh & Diesel, 1995). The system-wide mean ± SD species richness was 5.73 ± 2.69 per pool, with an abundance of 1,606 ± 2,964 ranging from zero to > 50,000 individuals · L⁻¹. In colonization experiments involving 20 natural pools with no initial in situ sources of individuals, comparable mean species richness was attained in 6 months or less (J. Kolasa, unpubl. data). Furthermore, 27 artificial pools exposed to natural colonization accumulated 13 species after only 17 d (J. Kolasa, unpubl. data). These results indicate that dispersal completely reconstituted the fauna between the 12-month sampling intervals.

SAMPLING

Each pool sample consisted of 500 mL of water and sediments. Water was thoroughly stirred with a stick to dislodge organisms from pool sides and bottom to ensure a homogenous sample. Next, a variety of locations (water surface, pool bottom, water column) were rapidly sampled using a 100-mL dip container (*i.e.*, plastic cup). This method effectively samples all the organisms larger than 63µm in the pools. It is important to note that the zooplankton and benthic invertebrates do not cling to the sides of the pools, stirring the pools before sampling ensures that all organisms are in the water column at the time of sampling. Samples were immediately preserved in the field with 50% ethanol. This collection technique did not retain protozoans or smaller micrometazoans (*i.e.*, copepod nauplii). Overall, 392 samples were collected from 49 pools, with 365 containing organisms. The same 49 pools were sampled once a year for 8 y. Sixty-nine species were identified and counted, totalling > 300,000 individuals from all samples.

DATA ANALYSIS

We applied three complementary analyses, two of which gradually reduced noise arising from local processes. The "high noise" analysis preserved the variance arising from local processes and is analogous to the calculation of species or population variability presented in Tilman (1996), McGrady-Steed and Morin (2000), and Romanuk and Kolasa (2002). The "intermediate noise" analysis reduced variance in richness for each species or metapopulation while preserving the range of population variability responses at each richness value. The "low noise" analysis reduced both richness and species or metapopulation variance. It is important to note that despite conventional usage in the diversity-stability literature (Tilman, 1996; McGrady-Steed & Morin, 2000; Romanuk & Kolasa, 2002), the "high noise" (and the "intermediate noise") analyses **violate** the assumption of independence, as multiple points correspond to the same species and the same pool.

Two values of species richness were used to relate species richness to population variability. For individual pools, species richness was calculated as the mean number of species over all census dates (local richness S_{local}). For example, the harpacticoid copepod *Nitocra spinipes* occurred in 46 out of 49 rock pools. Species richness was then averaged for each rock pool over the eight census dates to obtain 46 S_{local} values of S for *N. spinipes*. S_{local} values were obtained for each species included in the analysis ($n = 28$). In contrast, regional richness was calculated as the mean number of species found in each pool on all dates where a species of interest occurred (regional richness, S_{region}). For example, *N. spinipes* occurred in 223 of 365 samples, cumulatively over the eight dates. Species richness was then averaged for the 223 instances to obtain the regional richness, S_{region} for *N. spinipes*. S_{region} values were obtained for each species included in the analysis ($n = 28$).

Population variability of a species was calculated as the coefficient of variation (CV, standard deviation/mean) of a population density in each pool (CV_{local}), or of a population density summed over all pools (CV_{region}). Smaller values of CV indicate a population whose density varies less among sampling dates. Local population variability was determined as the coefficient of variation in population abundance of species in each pool over the eight sampling dates. Regional population variability was determined as the coefficient of variation in population abundances summed over all pools over the eight sampling dates. Preliminary data exploration suggested that all three analyses conformed to a 1st order linear model allowing regression analysis where i) high noise $S_{local} = aCV_{local} + b$, ii) intermediate noise, $S_{region} = aCV_{local} + b$, and iii) low noise, $S_{region} = aCV_{region} + b$. To examine whether the relationship between species richness and population variability differed between abundant and rare species we first ranked species by their abundance and then modeled the relationship between species richness and population variability by adding each species into the data set according to their rank. A species was excluded from the analysis if it was present on less than two sampling dates, *i.e.*, coefficient of variation could not be obtained.

Results

The regression analysis yielding the best resolution removed the most noise arising from local processes. S_{region} was negatively related to CV_{region} with 16% of the variance explained ($P = 0.032$, $n = 28$; Figure 1, line e). Although S_{region} was also negatively related to CV_{local} , it explained only 5% of the variance ($P = 0.00001$, $n = 390$, Figure 2a). In contrast, no relationship was detected between S_{local} and CV_{local} ($P = 0.715$, $n = 390$, Figure 2b). Because abundant species can vary less in relative terms (Waltho & Kolasa, 1994), we considered that such species might respond differently to S_{region} than rare species. When populations were added into the regression in groups of high to low density, variability of populations with the highest density (1-5) was strongly negatively related to S_{region} ($r^2 = 0.953$, $P = 0.004$, $n = 5$; Figure 1, line a). As groups of populations with lower density were

added into the regression (Figure 1, lines b-e), the explained variance decreased from 58% (rank 1-10) to 16% (rank 1-28). Interestingly, when populations were added into the analysis individually, species additions beyond the 11 top-ranking populations became asymptotic (*i.e.*, they had no further effect on the global relationship, Figure 3).

Regional richness declined with rock pool occupancy (the number of pools a species was observed in over all sampling dates; $r^2 = 0.262$, $P = 0.005$; Figure 4a) and

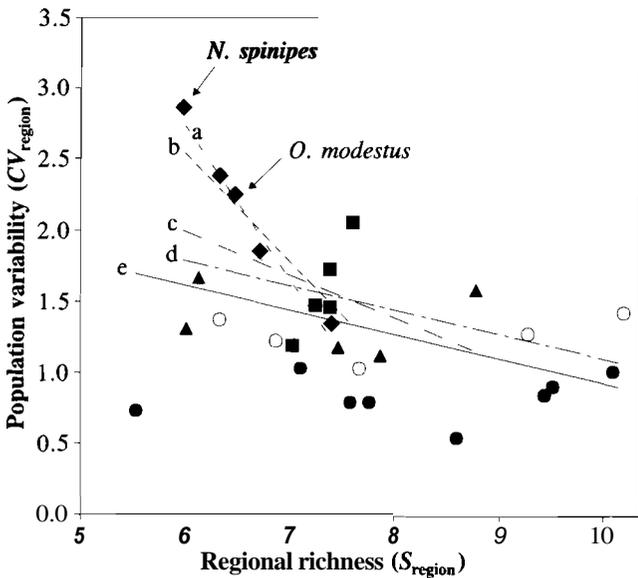


FIGURE 1. Low noise model. Population variability (CV_{region}) is negatively correlated with average richness, S_{region} . Each dot represents all the populations of one species. Regression lines are for populations according to rank order in density: a) 1-5 ($r^2 = 0.953$, $P = 0.004$, $n = 5$), b) 1-10 ($r^2 = 0.58$, $P = 0.01$, $n = 10$), c) 1-15 ($r^2 = 0.219$, $P = 0.078$, $n = 15$), d) 1-20 ($r^2 = 0.157$, $P = 0.083$, $n = 20$), e) 1-28 ($r^2 = 0.164$, $P = 0.032$, $n = 28$).

regional population variability increased with rock pool occupancy ($r^2 = 0.759$, $P > 0.0001$; Figure 4b). These relationships remained strong when the two species with occupancy > 200 were removed from the analysis (S_{region} $r^2 = 0.214$, $P = 0.01$; CV_{region} $r^2 = 0.671$, $P > 0.0001$). Taken together, these patterns suggest that statistical averaging is not responsible for the decrease in regional population variability with increasing regional richness.

Discussion

Our results show that changing the resolution at which species richness-population variability relationships are analyzed allows detection of the effects of species richness on population variability that were otherwise obscured. There was no relationship between S_{local} and CV_{local} (the high noise analysis). In contrast, S_{region} was significantly correlated with both CV_{local} and CV_{region} . The scale that removed the most variance arising from local processes, CV_{region} (the low noise analysis), resulted in the most sensitive test, and allowed discrimination of ecological patterns that otherwise were statistically invisible (high noise analysis; Figure 2b) or underestimated (intermediate noise analysis; Figure 2a). Thus, as the diversity of local influences was removed from the calculations of both richness and population variability, the explained variance between species richness and population variability meaningfully increased.

Valone and Hoffman (2003a) found a similar pattern when they analyzed the relationship between temporal variability of individual species and plant diversity. In their study, the majority of individual species were less temporally variable in more diverse plots. Furthermore, no species showed a trend of a decline in variability with increasing plant diversity (Valone & Hoffman, 2003a). While they did not analyze the relationship for all species combined as we have done here, their results are sugges-

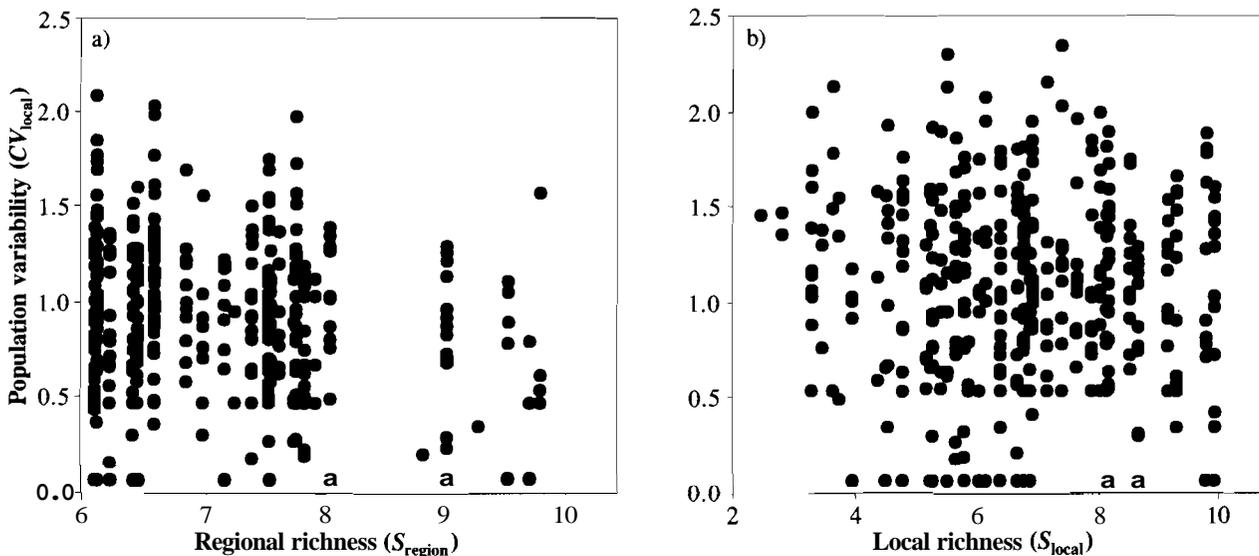


FIGURE 2. Temporal variability of populations in each rock pool as a function of species richness. a) Intermediate noise model. Population variability (CV_{local}) of each population in each rock pool as a function of average richness, S_{region} . All the populations of one species have by definition the same S_{region} ; thus, each vertical set of points represents a range of values observed within a population of a single species (except when two species happen to have the same S_{region}). b) High noise model. Population variability (CV_{local}) of each population in each rock pool as a function of local richness, S_{local} .

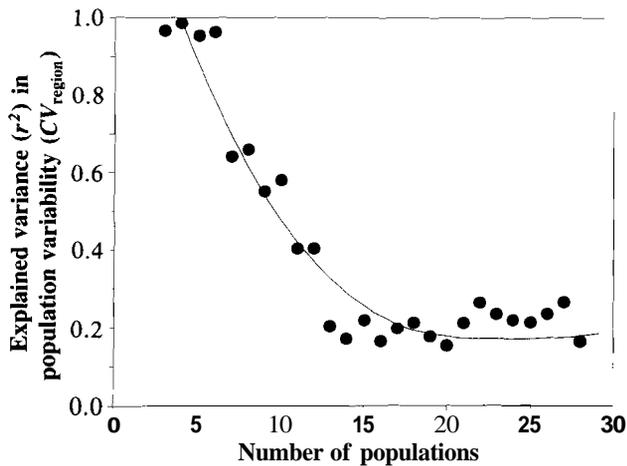


FIGURE 3. Contributions of each population into the model for population variability (CV_{region}) according to rank in density. Explained variance (r^2) at each step, with populations added into the model from the highest to the lowest rank.

tive that changing the resolution of analysis may uncover significant relationships that may have gone undetected. Furthermore, Valone and Hoffman (2003b) showed that community variability also declined, albeit weakly, with increasing diversity, suggesting that the patterns seen at the species level (Valone & Hoffman, 2003a) may be similar to patterns seen at the community level (Valone & Hoffman, 2003b).

The obscuring effects of local processes or sampling error may be especially pronounced in populations with high variability such as in these rock pools, where population CVs exceed 50% of the mean (range = 0.51 to 2.89, mean \pm SD = 1.35 ± 0.545). In these cases, local processes such as environmental noise and community composition are likely to obscure many ecological patterns arising from species interactions. Furthermore, 31 of the 49 pools in the rock pool metacommunity are "temporary", which we define as pools that have been found dry at least once over a 10-y period. The other 18 pools are "permanent" and have never been found dry. Desiccation is a major structuring force in the rock pool metacommunity and has been shown to affect the species richness, diversity, abundance, and community composition of the pools, as well as abiotic conditions (Therriault & Kolasa, 2002). In systems where there is a wide range of physical stability patterns and these patterns have strong effects on the biotic communities, it is likely that strong effects of environmental control might mask a weaker, yet still important, biotic control (Romanuk & Kolasa, 2002).

The rationale for using different levels of aggregation is primarily to remove the noise generated by differing local environmental conditions and community compositions. Thus, while there may be an ecological rationale for looking at average values (Mikkelsen, 1999), our primary purpose here was to address whether a process relevant to diversity-stability research is obscured by local variability in environmental conditions and community composition. Our main result - that species that inhabit pools with higher on average richness are more stable

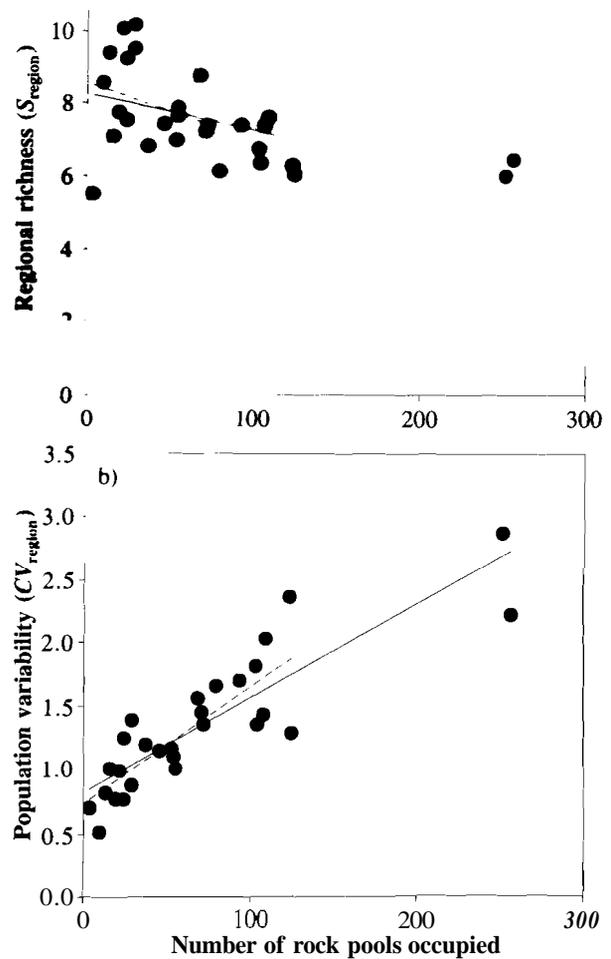


FIGURE 4. a) Average richness, S_{region} , and b) average population variability, CV_{region} , as a function of rock pool occupancy. Pool occupancy significantly correlates with both S_{region} and CV_{region} (average over 8 sampling dates).

than species that are found in less diverse pools - is intriguing. Three aspects of the rock pool system ecology are worth considering here: 1) the effect of environmental variability on species richness, 2) the effects of increasing species richness on resource use, and 3) the potential roles of metapopulation dynamics on species richness-variability patterns.

In rock pool communities, pools with highly variable physicochemical conditions have fewer species (Therriault, 2002). Thus, one explanation for a negative correlation between species richness and population variability is that environmental variability both decreases the number of species that can inhabit a pool and increases the variability of constituent populations. For example, the copepods *N. spinipes* and *O. modestus* inhabited more rock pools than any other species, had highly variable dynamics on a regional scale, and tended to occur in pools with lower than average richness. These copepods are tolerant of a wide range of environmental conditions and thus can inhabit rock pools that other species can not successfully colonize due to harsh environmental conditions. While these copepods appear to drive at least part

of the overall relationship between regional richness and metapopulation variability in the rock pools, on a local scale their variability is either unaffected (*O. modestus*, $P = 0.354$) or only weakly affected by local species richness (*N. spinipes*, $r^2 = 0.115$, $P = 0.017$).

Based on modeling work (Petchey *et al.*, 1999; Yachi & Loreau, 1999), it is probable that proportionally more community members will fail to function as environmental fluctuations increase in habitats with lower species richness. If species interactions play a role in population stability, decreases in species richness may lead to more variable populations. The possibility that species interactions are stabilizing in rock pools, and that having greater species richness may decrease population variability, centres around the potential role of niche differentiation as a stabilizing mechanism (Norberg, 2000) and the ways in which completeness of resource use could lead to more stable populations. Rock pool ecosystems are predominantly detritus based. In rock pools with a high proportion of unused resources the densities of populations may fluctuate more than in pools in which resource use is more complete. As the available resources in a community decrease, fluctuations in population densities may be reduced. In these situations, having a larger number of species in a pool may act to stabilize populations by facilitating access to available resources, which would in turn lead to more complete resource use. For example, the species richness of ostracods in any one rock pool can be as high as eight species. Ostracods are all detritivores and have a small range of body sizes, which suggests that ostracods likely partition their resources according to particle size. If greater species richness facilitates access to previously unavailable resources, this may act to stabilize population abundances by increasing available resources and to stabilize community abundances through more complete resource use in diverse communities.

The third reason that populations may be more stable in rock pools with higher richness is that rock pool communities are linked through dispersal and can thus be thought of as a metacommunity, with individual species in the system constituting metapopulations. This aspect of the rock pool system has various effects on both population and community dynamics (Kolasa & Romanuk, in press), and it may point to a unique effect of species richness on metapopulation variability. Recall that 1) species that inhabit pools with on average greater species richness are less variable than species that inhabit pools with on average lower species richness, 2) abundant species on average inhabit pools with lower species richness than rare species, and 3) abundant species densities vary more than those of rare species. Taken together, these results suggest that abundant and rare species respond to species richness differently, indicating that there may be scale discontinuities for how species respond to species richness based on their abundance (Kolasa & Romanuk, in press). When we entered the most abundant species into the model first, a strong relationship between population variability and species richness emerged that subsequently weakened with progressive inclusion of less abundant species. Thus, the variability of abundant species was strongly dependent on species richness. However, abun-

dant species also had higher population variability than rare species and always inhabited pools with lower richness. In contrast, species richness had a weaker effect on the population variability of rare species, as theoretically postulated by Kolasa and Li (2003). Rare species also had lower population variability and were strongly associated with species-rich pools. Thus, this observation confirms that abundant and rare species respond differently to species richness in the rock pool metacommunity.

STATISTICAL AVERAGING

Population variability significantly declined in richer environments, supporting the hypothesis that populations are stabilized by richness. We need to consider, however, whether this pattern of decreasing variability in richer environments is biologically generated (Cottingham, Brown & Lennon, 2001) or a result of statistical averaging (Doak *et al.*, 1998), *i.e.*, the tendency for the sum of several randomly and independently varying items to be less variable than the average item. Such a statistical averaging, or portfolio, effect has been proposed as an explanation for decreased variability in richer communities, independent of direct compensation between species (Doak *et al.*, 1998).

Can averaging effects be invoked to explain the reductions in population variability in richer environments that we have detected? Such effects could be invoked if more pools were averaged together for populations that inhabited pools with higher species richness levels. However, occupancy is negatively correlated with pool species richness ($r^2 = 0.262$, $P < 0.005$, $n = 28$; Figure 4). Thus, unlike richness-community variability relationships where reductions in variability can be explained in part by the results of statistical averaging (Doak *et al.*, 1998), our analyses suggest that in these rock pools, the observed reduction of population variability with increasing richness probably reflects biological factors. Although successive collapse of variance might be expected to improve resolution, this is overpowered by large reductions in n (from 390 to 28 data points), which should have an opposite contribution in regression analysis. The fact that a clear pattern (Figure 1) was obtained by the method of removal of variation (where no pattern was visible otherwise; Figure 2b) suggests a biological reality regardless of the statistical method for achieving resolution.

In conclusion, there are three key differences between this and previous studies. Firstly, this study involves a consumer community spanning several trophic levels. Previous studies have focused primarily on terrestrial plant communities (McNaughton, 1985; Tilman, 1996; Naeem & Li, 1997; Wardle *et al.*, 1999), with the exception of Amarasekare (2003), who analyzed a multitrophic community of host-parasitoid insects. The possible implications of multiple trophic levels should not be discounted (Cottingham, Brown & Lennon, 2001), although Ives, Gross, and Klug (1999) suggest that there should be no qualitative difference in richness-variability relationships for multi-trophic communities. Second, species richness was not artificially manipulated (Romanuk & Kolasa, 2002). Instead, we used a natural richness gradient to test whether there was a correlation between species richness

and population variability. Such unmanipulated communities have much greater variation than experimental systems, which could preclude detecting any clear richness-variability relationships. Remarkably, the results obtained utilizing the procedures developed here appear to be quite unambiguous compared to those reported in any previous studies (Tilman, 1996; McGrady-Steed & Morin, 2000; Romanuk & Kolasa, 2002; Kolasa & Li, 2003).

Lastly, we found that species richness was negatively correlated with population variability. A previous analysis of the relationship between species richness and community variability in rock pools showed that species richness was negatively correlated with community variability (Romanuk & Kolasa, 2002). This concordance between the effects of species richness on variability at both the population and community level has been predicted theoretically (Ives, Gross & Klug, 1999; Li & Charnov, 2001) with no necessary direct effects of species number at the aggregate community level. Instead, biodiversity may decrease community variability by increasing the diversity of species responses to environmental fluctuations (Ives, Gross & Klug, 1999, but see Gonzalez & Descamps-Julien, 2004 for alternative interpretation). In this way, a decrease in population variability with increasing richness may translate into lower variability of communities. Our results support this hypothesis. If we consider the community as a hierarchical system where lower levels in the hierarchy affect the properties of higher levels, the stabilizing effects of richness on populations of component species could yield more stable communities in richer environments.

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