

Environmental variability alters the relationship between richness and variability of community abundances in aquatic rock pool microcosms¹

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Abstract: The effect of species richness on the temporal variability of communities and populations continues to inspire investigations and debates; however, few empirical studies have addressed the crucial question of how the relationship between richness and variability changes along a gradient of environmental variability. We determined the relationship between species richness (S) and variability (coefficient of variation, CV) for both community and population abundances of aquatic invertebrates inhabiting 49 tropical coastal rock pools that differ in environmental variability. When all pools are considered, results support the hypothesis that variability in community abundance decreases with increases in species richness. In contrast, abundances of individual populations in more speciose communities vary no more than in species-poor communities. Richness-community variability relationships were detected in rock pools with low environmental variability (as measured by a multivariate index of environmental variability) and in rock pools with low variability in specific physico-chemical variables, *i.e.*, temperature, salinity, dissolved oxygen, and pH. The presence of richness-variability relationships in the less environmentally variable rock pools and not in the more variable rock pools suggests that environmental variability may play an important role in modulating richness-variability relationships.

Keywords: diversity-stability hypothesis, environmental variability, invertebrates, microcosms, rock pools, temporal variation.

Résumé : L'effet de la richesse des espèces sur la variabilité des communautés et des populations dans le temps continue d'inspirer les chercheurs. Ceci dit, peu d'études empiriques ont tenté de répondre à la question suivante : comment la relation entre la richesse et la variabilité des communautés et des populations change-t-elle le long d'un gradient de variabilité environnementale? Nous avons déterminé la relation existant entre la richesse en espèces (S) et la variabilité (coefficient de variation, CV) pour l'abondance des communautés et des populations d'invertébrés aquatiques pour 49 mares côtières tropicales sur substrat rocheux, ces dernières étant très différentes les unes des autres d'un point de vue environnemental. Lorsque toutes les mares sont prises en considération, les résultats confirment l'hypothèse que la variabilité de l'abondance des communautés diminue si la richesse en espèces augmente. En contrepartie, l'importance des populations dans les communautés plus riches en espèces ne varie pas davantage que dans les communautés plus pauvres. Des relations entre la richesse et la variabilité des communautés ont été observées dans des mares rocheuses avec faible variabilité environnementale (tel que mesuré par un indice multivarié de variabilité environnementale), ainsi que dans des mares avec peu de variabilité physico-chimique, *c'est-à-dire* au niveau de la température, de la salinité, de l'oxygène dissous et du pH. Comme il existe des relations entre la richesse et la variabilité dans les mares sur substrat rocheux où les conditions environnementales varient très peu alors que de telles relations sont absentes dans les mares aux conditions plus changeantes, il est possible que la variabilité environnementale joue un rôle important dans la modulation des relations entre richesse et variabilité.

Mots-clés : hypothèse de diversité-stabilité, variabilité environnementale, invertébrés, microcosmes, mares sur substrat rocheux, variation temporelle.

Introduction

Communities and populations fluctuate through time, and the causes and consequences of this variation hold a fundamental place in ecological thought. That species richness (S) *per se* may regulate variability has fascinated ecologists for almost half a century (MacArthur, 1955; Elton, 1958; Odum, 1959) and has emerged as a topic of considerable scientific and public interest (see McCann, 2000 and Cottingham, Brown & Lennon, 2001 for recent reviews; Mellinger & McNaughton, 1975; McNaughton, 1977, 1985; Berish & Ewel, 1988; Tilman & Downing, 1994; Tilman, 1996, 1999; Naeem & Li, 1997; McGrady-Steed & Morin, 2000; Collins, 2000; Lehman & Tilman, 2000). Recently, theoretical and empirical studies have suggested that environmental variability may influence the

relationship between richness and variability of species abundances through a variety of mechanisms (Doak *et al.*, 1998; Hughes & Roughgarden, 1998; Ives, Gross & Klug, 1999; Yachi & Loreau, 1999; Mulder *et al.*, 2001).

Environmental fluctuations are a primary structuring force in many aquatic communities and have been shown to affect community composition (Death, 1995; Therriault & Kolasa, 2001), mediate the effects of competition and predation (McAuliffe, 1984; Meffe, 1984), increase population variability, and lower community persistence and constancy (Ross, Matthews & Echelle, 1985; Wolda, Spitzer & Leps, 1992; Death & Winterbourn, 1994; Therriault & Kolasa, 2001). When species respond similarly to environmental fluctuations, the resulting positive covariances should weaken, but not entirely cancel, the degree to which community variability declines due to increased species richness (Doak *et al.*, 1998). This suggests that environmental fluctuations

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should modulate the effect of species richness on community and population variability.

It appears that environmental variability can alter the relationship between richness and variability in three ways. First, environmental variability can force variability of population abundances and thus community variability through increased synchrony in temporal fluctuations of component populations. For example, Peterson (1975) found that temporal variability of species abundances was greater at sites that experienced frequent heavy rains than at sites that experienced less severe rainstorms; however, the proportionate community composition varied equally over time in both sites due to increasing synchrony of populations in the more variable sites. Second, environmental variability can determine species richness, which in turn may regulate or covary with community variability (Sankaran & McNaughton, 1999). Kushlan (1976) found that a prolonged period of stable water conditions in Everglades marshes increased fish species richness but favored alterations in the composition of the community, shifting it from a community previously regulated by fluctuating abiotic conditions to one regulated by predation. Conversely, communities in harsh environments (high environmental variability) often have lower species richness (Connell, 1978), increasing the probability that proportionately higher numbers of community members will fail to function as the environment fluctuates (Petchey *et al.*, 1999; Yachi & Loreau, 1999). Third, environmental variability is thought to influence richness-variability relationships by altering the variance-covariance structure of populations (Tilman, 1999). When species respond differently to environmental conditions, the resulting negative covariances should buffer aggregate properties against change (Ives, Gross & Klug, 1999; Yachi & Loreau, 1999).

Aquatic invertebrate communities inhabiting rock pool microcosms are particularly suitable for analyzing richness-variability relationships. On the north coast of Jamaica, coastal rock pools are a common feature on uplifted fossil reefs. The rock pools span a gradient from freshwater to hypersaline conditions and contain communities of micro- and meio-invertebrates (mostly crustaceans, insects, and worms). Many species are euryhaline, *i.e.*, *Nitocra spinipes* (Boeck), and able to tolerate a wide range of salinity. Rock pool communities are also highly variable in space (Therriault & Kolasa, 1999) and time (Schuh & Diesell, 1995; Therriault & Kolasa, 2000; Romanuk & Kolasa, 2001), with a complex disturbance regime consisting of frequent high intensity desiccation events that interact with diurnal and annual abiotic variability to affect spatial and temporal dynamics (Therriault & Kolasa, 2001; Romanuk & Kolasa, 2001). Further, these small aquatic communities represent a natural analogue to many experimental systems (Tilman, 1996; Naeem & Li, 1997; McGrady-Steed & Morin, 2000).

We used long-term data from a series of 49 rock pools to test the general hypothesis that community abundance is less variable in rock pools with greater species richness (MacArthur, 1955; Elton, 1958; Odum, 1959; McNaughton, 1977; Tilman, 1996) while variability in the population abundances of individual species increases with richness (May, 1973; Gardner & Ashby, 1970; DeAngelis, 1975; Gilpin, 1975; Pimm, 1979). We further hypothesized that

environmental variability (Therriault & Kolasa, 2000) would alter the relationship between richness and community variability (Yachi & Loreau, 1999). We expected that increasing environmental variability would increase the positive covariances between species and decouple potential dampening interactions among species themselves (*i.e.*, species would respond more similarly to environmental fluctuations as those fluctuations increase in magnitude and less to each other). Such processes would result in a weaker richness-variability relationship (*i.e.*, showing no or low correlation) in the more variable rock pools and a stronger relationship (*i.e.*, show higher negative correlation) in less variable rock pools. Finally, if some populations are able to compensate for the decreasing abundance of disturbance prone populations, the relationship between richness and population variability should be stronger in the less variable rock pools.

Methods

STUDY SITE

Two hundred and thirty dissolution rock pools with a maximum volume greater than 250 ml are present on the fossil reef within a radius of 25 m of mixed land and sea environment at the Discovery Bay Marine Laboratory on the northern coast of Jamaica, West Indies (Kolasa *et al.*, 1996; Kolasa, Hewitt & Drake, 1998). A few mangrove trees (*Rhizophora mangle*) grow between the rocks and, along with *Croton*, *Jacquinia*, and *Strumfia* bushes, are a major source of detritus in some rock pools. Forty-nine rock pools were randomly chosen (Kolasa *et al.*, 1996) and monitored yearly in late December or early January for 8 years. The rock pools are small in size, ranging from 13 to 235 cm in width and length, and vary from 1 to 37 cm in depth (mean depth = 12.8 ± 8.3 SD). Volumes are highly diversified and range up to 115 liters with a mean of 12 ± 21 SD. On average the rock pools are located within 1 m of the nearest neighbor, and none are separated by more than 5 m from the nearest rock pool. Their elevation above sea level ranges from 1 to 235 cm (mean = 76.6 ± 80.1 SD) at high tide, with the tide rarely exceeding 30 cm. Four rock pools are tidal (although tidal flooding is not daily), but most are maintained by atmospheric precipitation and, very occasionally, wave splash water.

BIOTIC COMPOSITION

Each faunal sample consisted of 500 ml of water and sediments from a pool slightly stirred to dislodge organisms from its sides and bottom and to homogenize their distribution. Organisms were caught in a 63 μ m net with a collecting container and immediately preserved in 50%-70% ethanol. Overall, 392 samples have been analyzed from 49 rock pools over 8 dates. Additional information on pool dimensions, physical variables, overall variability, and their impact on species richness and composition have been reported previously (Therriault & Kolasa, 1999; Romanuk & Kolasa, 2001). The dominant species are a harpacticoid copepod, *Nitocra spinipes* Boeck (present in 70% of samples), a cyclopoid copepod, *Orthocyclops modestus* Herrick (70%), an ostracod *Candona* sp. (34%), a nematode species (31%), and a *Culex* mosquito (31%). Other common species

include a daphnid, *Ceriodaphnia* sp., and ostracods representing several fresh and brackish water families and genera. The majority of species are small benthic animals ranging from approximately 0.5 to 5 mm, but some are plankton-like (*O. modestus*, *C. rigaudi*) and swim in the water column. The full list of the taxa (69 species) identified to date is 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).

ENVIRONMENTAL VARIABILITY

Physical measurements (temperature, salinity, dissolved oxygen, and pH) for each pool were taken every 2 hours for a 24-hour period in 1997, as well as on numerous occasions between December 1989 and January 2000. Individual measurements of physical variables for all rock pools were completed in less than one hour. Environmental variability was evaluated in two ways. 1) We calculated a multivariate measure of diurnal variability using PCA factor scores. 2) We calculated diurnal variability in specific physicochemical properties separately. Throughout all analyses, we used the mean SD to differentiate between low- and high-variability pools. While this division has the potential to introduce a level of subjectivity to the analyses, using the mean SD across the analyses standardizes this decision rule.

1) A multivariate score (environmental variability index, EVI) was calculated to represent several physical characteristics simultaneously. We used scores of PCA 1 produced by a Principal Component Analysis performed on the variability in physicochemical variables (standard deviations of pool temperature, salinity, dissolved oxygen, and pH) measured every two hours over a 24 hour period. Therriault and Kolasa (2000) used a similar index to investigate the effects of environmental variability on community evenness, population variability, and community structure. The index represents a gradient ranging from environmentally variable to environmentally constant rock pools (Therriault & Kolasa, 2000). The mean SD was used to differentiate between high- and low-variability pools. Thus, rock pools scoring less than the mean on the environmental variability index were considered low variability while rock pools scoring more than the mean were considered high variability.

2) We calculated diurnal variability of specific physicochemical variables (standard deviations of pool temperature, salinity, dissolved oxygen, and pH) measured every two hours over a 24-hour period to determine whether there was a general trend between specific measures of physicochemical variability and richness-variability relationships. The mean SD was used to differentiate between low- and high-environmental-variability pools. Measurements of specific physicochemical variables were made in only 40 of the 49 pools used in the analysis of richness-community variability relationships (see Figure 2); thus, all analyses for environmental variability are based on $N = 40$.

STUDY DESIGN

Temporal variation, the variation in a time series of density (Tilman, 1999), was calculated for both communi-

ties (all species combined) and populations of individual species. Year-to-year variability in community abundance was calculated as the coefficient of variation, CV, (standard deviation/mean) of abundance (untransformed data) of all species combined that share a pool (total N per sample) across all years (8 sampling dates). Year-to-year variability in population variability was calculated on a species-by-species basis for each pool, using the abundance of a species in a pool over the 8 sampling dates. These calculations are analogous to Tilman's (1996) definitions of community and population stability. Smaller values of CV represent lower variability and higher values represent greater variability. Because CV standardizes for the mean, it provides an index of year-to-year variability in abundance independent of the mean (Tilman, 1996). While use of CV is burdened with its own bias as CV tends to increase at low N values in random data sets (Walther & Kolasa, 1994) and thus requires somewhat different interpretations for species with low abundances, this should not affect our results because we restricted population analyses to the 36 most abundant species. Species richness (S) is the average richness of a rock pool across all sampling dates ($N = 8$).

Analyses were performed using linear regression (STATISTICA, version 5.5, from StatSoft). The level of significance was set at $\alpha = 0.05$ for all analyses. Residuals were tested for normality and independence.

Despite the difficulties associated with showing unequivocal relationships in natural communities, our system is particularly suitable for analyzing richness-variability relationships because (1) the pool communities are similar with respect to successional stage, (2) there are no significant richness-area effects (Therriault & Kolasa, 1999), (3) the small area of the study site implies that regional conditions and inputs are more homogenous than in other studies of natural systems, (4) species ranges extend far beyond the site boundaries, and thus there is no density decrease associated with range limits (Brown, 1984), and (5) organisms with short generation times allow us to avoid many of the confounding effects which plague studies on longer-lived species (Huston, 1997).

Results

ENVIRONMENTAL VARIABILITY

Temporal variability in community abundance and mean species richness did not change along a gradient of environmental variability, EVI ($p = 0.132$ and $p = 0.849$ respectively; Figure 1a,b). Variability in community abundance was not related to variability in temperature ($p = 0.292$), salinity ($p = 0.231$), oxygen ($p = 0.801$), or pH ($p = 0.924$). Similarly, mean species richness was not significantly related to variability in any specific physicochemical variables ($p > 0.05$).

RICHNESS AND VARIABILITY - GENERAL OBSERVATIONS

When all rock pools were considered, our data supported the hypothesis that total community abundance would be less variable in rock pools with more species ($r = -0.428$, $p = 0.002$, $n = 49$; Figure 2a) and that population variability in abundance would be unrelated to species richness ($p > 0.5$; Figure 2b). Environmental variability, as measured

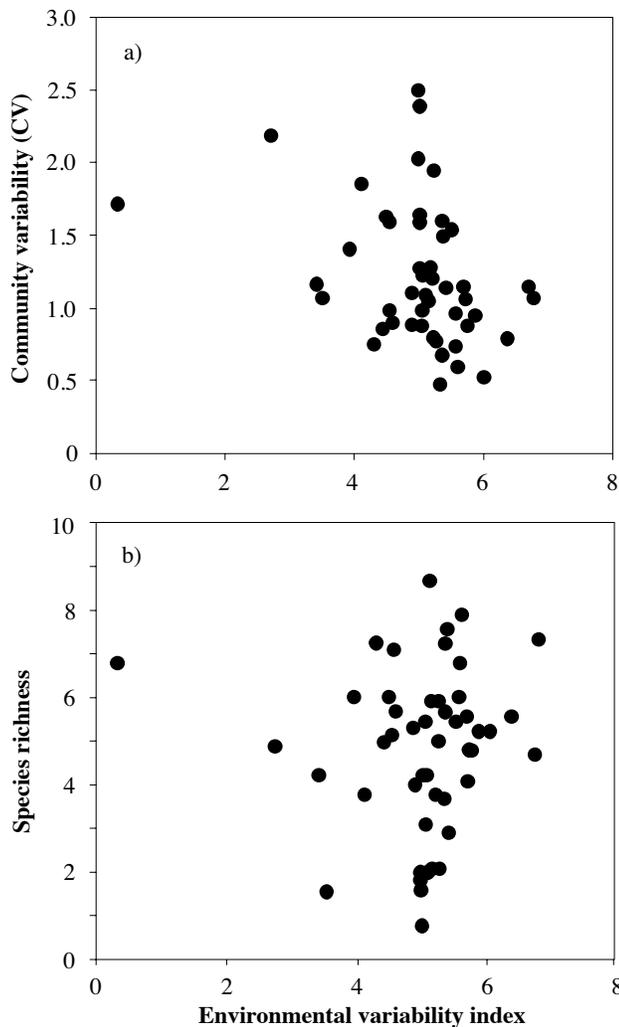


FIGURE 1. Relationship between the multivariate environmental variability index (EVI, see text) and (a) variability in total community abundance (CV) and (b) mean species richness of a pool. There is no relationship between environmental variability and species richness or variability in total communal abundance.

by the EVI, altered the relationship between richness and communal variability in abundance. In low-variability rock pools, richness and variability in community abundance were related ($r = -0.455$, $p = 0.0501$, $n = 19$; Figure 3a). There was no relationship between richness and community variability in the high environmental variability pools ($r = -0.311$, $p = 0.169$, $n = 20$; Figure 3b). In contrast, population variability was unrelated to species richness in rock pools with either low or high environmental variability ($p = 0.863$ and 0.631 respectively; Figure 4a,b).

Variability in specific physicochemical variables altered the relationship between richness and variability in community abundance. Rock pools with low variability in temperature ($r = -0.543$, $p = 0.013$, $n = 20$; Figure 5a), salinity ($r = -0.443$, $p = 0.0097$, $n = 33$; Figure 5c), oxygen ($r = -0.458$, $p = 0.0083$, $n = 32$; Figure 5e), and pH ($r = -0.506$, $p = 0.009$, $n = 25$; Figure 5g) exhibited a significant relationship between richness and variability in community abundance while rock pools with high variability in temperature ($r = -0.161$, $p = 0.582$, $n = 14$; Figure 5b), salinity ($r = -0.195$, $p = 0.673$,

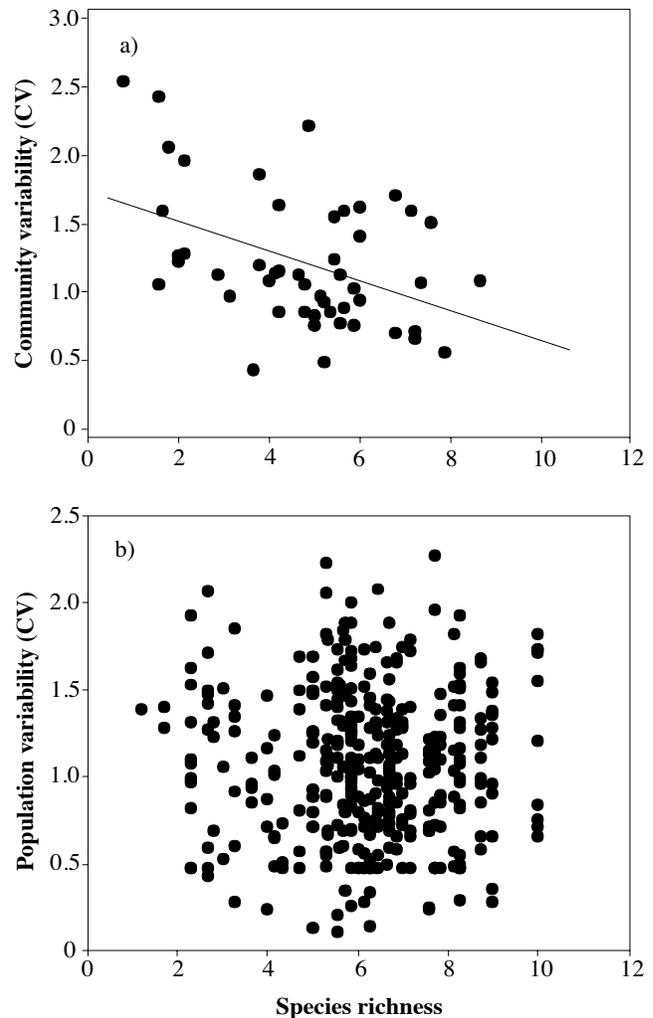


FIGURE 2. Relationship between richness and (a) variability of combined community abundance and (b) variability of populations of individual species in each pool. Variability is expressed as coefficients of variation (CV). Each point represents (a) one rock pool community or (b) one individual species in a rock pool.

$n = 6$; Figure 5d), oxygen ($r = -0.063$, $p = 0.891$, $n = 9$; Figure 5f), and pH ($r = -0.154$, $p = 0.583$, $n = 15$; Figure 5h) did not.

As diurnal changes in salinity are correlated with pool depth and exposure (*i.e.*, shading) and represent in part the rate of evaporation and desiccation in the rock pools, we further considered the effects of annual variability in salinity on richness-variability relationships. Similar to our results for diurnal variability in salinity, rock pools with low annual variability in salinity showed a strong richness-variability relationship ($r = -0.537$, $p = 0.004$, $n = 26$) while rock pools with high annual variability in salinity did not ($r = -0.288$, $p = 0.218$, $n = 20$).

To determine whether using the mean SD as the cut-off point to separate low- versus high-variability pools was biasing the analysis, we added pools to the regression analysis in order of their variability in each physicochemical variable (Figure 6). The average explained variance (explained variance was averaged for temperature, salinity, oxygen, and pH) for the relationship between species richness and

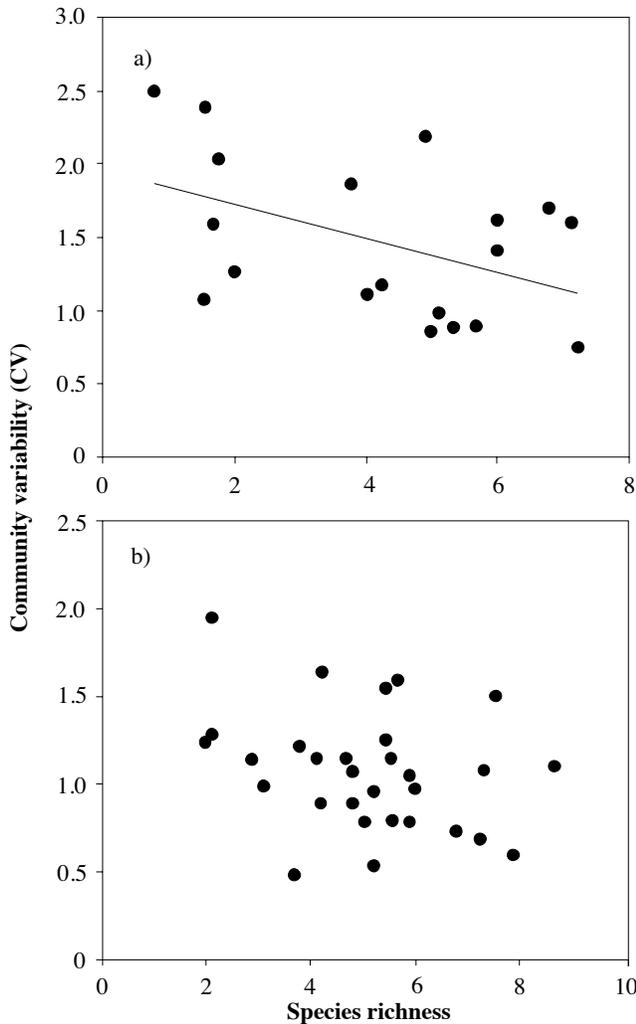


FIGURE 3. Relationship between richness and variability of total communal abundance in (a) low-variability rock pools (low EVI) and (b) high-variability rock pools (high EVI). The regression line is shown for the statistically significant trend only.

community variability decreased as more variable pools were included in the analyses (Figure 6).

Discussion

When all rock pools are considered, the results support the hypothesis that community variability is negatively related to species richness. In contrast, population variability appears to be unrelated to species richness. This concurs with the majority of empirical and theoretical evidence, which has shown community biomass to be stabilized by species richness (McNaughton, 1977; Tilman & Downing, 1994; Tilman, 1996; Naeem & Li, 1997; Yachi & Loreau, 1999; Lehman & Tilman, 2000; McGrady-Steed & Morin, 2000).

Evidence for the destabilizing effect of species richness on population variability (May, 1973; Pimm, 1979; Lehman & Tilman, 2000) is less clear. McGrady-Steed and Morin (2000) found no difference in variability of the majority of populations along an experimental richness gradient. In contrast, Peterson (1975) found that species variability of

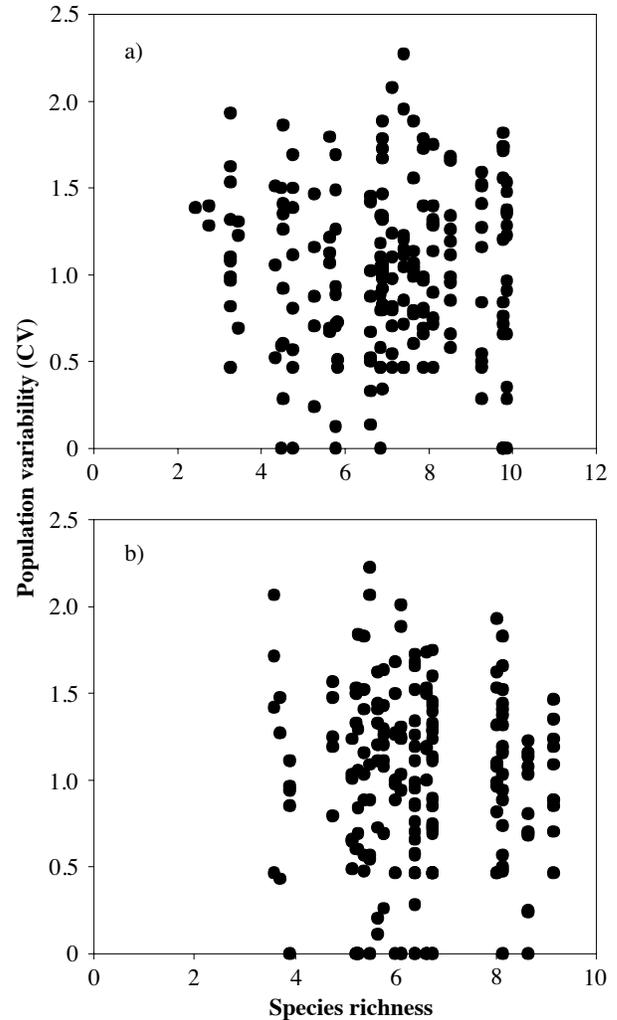


FIGURE 4. Relationship between richness and population variability in (a) low-variability rock pools (EVI) and (b) high-variability rock pools (EVI). Each point represents one individual species in a rock pool.

benthic invertebrates was lower in more diverse (and less disturbed) sites. In contrast yet again, Tilman (1996) showed an increase in population variability with increasing species richness. Thus, there exists a range of empirical results for the effects of richness on population variability, many of which are not consistent with theoretical predictions (King & Pimm, 1983; Lehman & Tilman, 2000). Furthermore, environmental variability did not alter richness-population variability relationships. In all cases, population variability was unrelated to species richness. This suggests either that negative covariances between populations did not change as a result of environmental variability or that the richness-variability relationship reported here is not a function of species richness *per se* in the rock pools, but is related to factors that determine or covary with species richness (Sankaran & McNaughton, 1999).

Community variability declined with increasing species richness when all rock pools were considered without a distinction between physically variable and stable ones. However, the relationship between community variability and species richness was not the same across rock pools

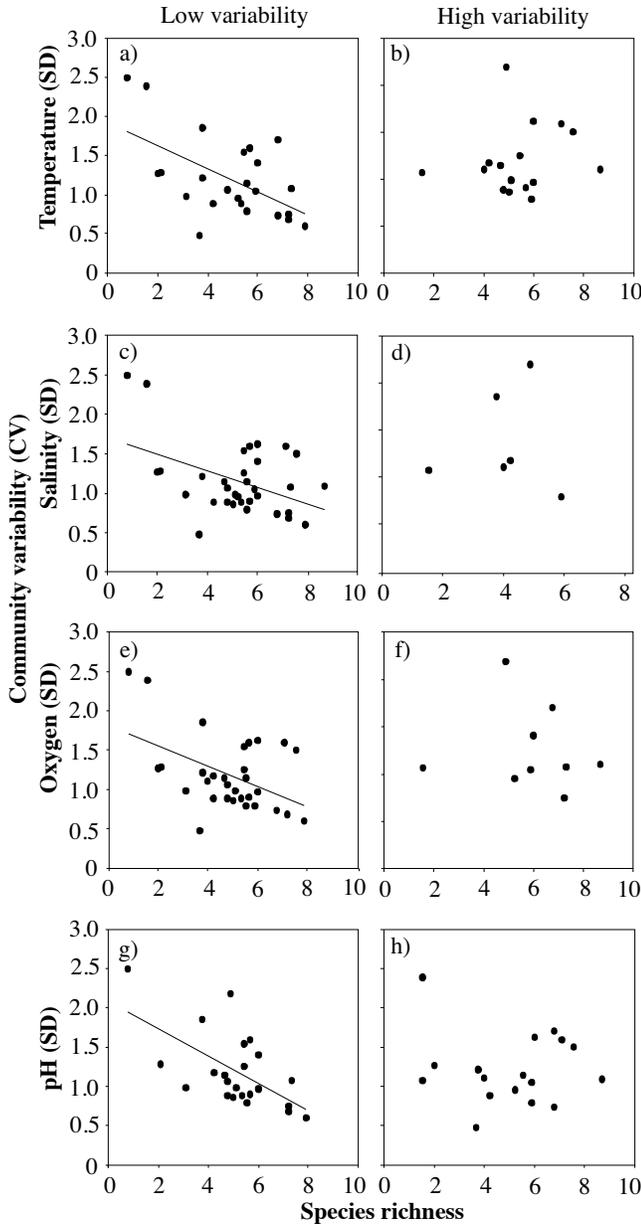


FIGURE 5. Relationship between richness and variability of total community abundance in rock pools with (a) low and (b) high variability in temperature, (c) low and (d) high variability in salinity, (e) low and (f) high variability in oxygen, and (g) low and (h) high variability in pH. The regression line is shown for the statistically significant trend only.

along the gradient of environmental variability. Temporal variability of total community abundance was significantly related to species richness only in the low-environmental-variability rock pools. Whether the trend of variability decreasing with species richness in low-environmental-variability rock pools is due to species richness per se or other determinants (Sankaran & McNaughton, 1999) cannot be conclusively resolved using a simple correlation approach. However, the presence of a trend in the low-environmental-variability pools, when compared to the lack of a significant relationship in the high-environmental-variability pools, is intriguing. Ross *et al.* (1985) found that community variability was lower in sites with lower relative environmental

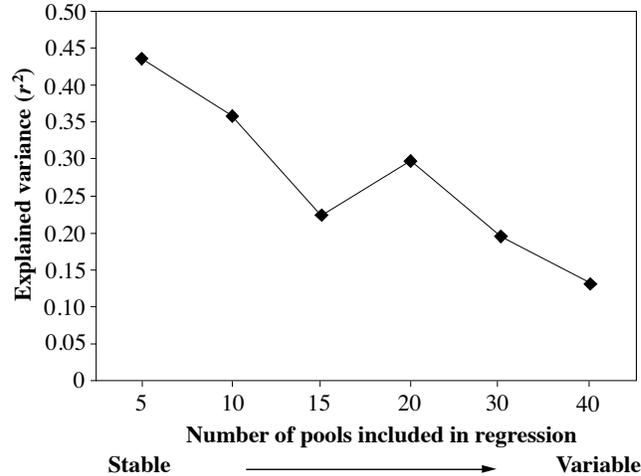


FIGURE 6. Relationship between the mean explained variance (y-axis) in the relationships between species richness and community variability (CV) for all physicochemical variables and the number of pools included in the analysis (x-axis). Pools were added to the regression analysis in order of their variability for each physicochemical property, such that for $n = 5$, the r^2 shown refers to the average explained variance of temperature, salinity, oxygen, and pH for the 5 most stable pools in each of these variables. As N increases, more variable pools are included in the analysis.

variability. Peterson (1975) found that community variability was similar in both disturbed and undisturbed sites but that species variability was lower in the more diverse, low disturbance sites. Tilman (1996) found strong richness-variability relationships in both drought and non-drought years. The range of results, while not entirely consistent, seems to give some support to the notion of a destabilizing effect of environmental variability, at least on the communal, aggregated measure of abundance.

Richness-variability relationships were also affected by variability in specific physicochemical variables. Variability in communal abundance was only related to richness in rock pools with low variability in temperature, oxygen, and pH, and low variability in salinity (both annual and diurnal). Temperature and salinity are both external variables that may force richness-variability relationships through decreasing the number of species in a pool. Species richness decreases with both increasing maximum temperature and maximum salinity in the rock pools (Therriault & Kolasa, 1999). While many freshwater species are able to tolerate low levels of salinity, few are able to tolerate hypersaline conditions (Hutchinson, 1967). Variability in temperature is also a sign of poorer conditions (higher frequency of desiccation) and has adverse direct effects on many organisms (Hutchinson, 1967). Variability in salinity also has been seen to increase year-to-year variability in species richness (Romanuk & Kolasa, pers. obs.).

In contrast to temperature and salinity, variability in oxygen and pH are largely due to biotic factors. Dissolved oxygen and pH are strongly correlated, with correlation explaining > 80% of variance, and can be used as a surrogate measure of pool productivity (Wetzel, 1983). Rock pools with low variability in oxygen and pH showed strong richness-variability relationships while richness was unrelated to community variability in pools with high variability in oxygen and pH. High variability in pH and oxygen may

act similarly to variability in temperature and salinity, forcing species richness to decline due to harsher conditions.

It is important to note, however, that variability in total communal abundance and species richness were unrelated to physicochemical variability in any of the specific variables we measured. This was confirmed by both the regressions presented earlier and by additional multivariate analyses in which we used temporal variability in community abundance as the dependent variable and both (1) mean species richness and (2) variability in each physicochemical variable (temperature, salinity, pH, and oxygen) separately as independent variables. In all four regressions, mean species richness was the only variable significantly related to temporal variability in community abundance. This indicates that physicochemical variability may be affecting the relationships between species richness and community variability independently of the effects of physicochemical variability on species richness or community variability per se. When pools are added into the regression analysis according to their variability in specific physicochemical measures (Figure 6), very stable pools show a strong relationship between richness and variability. Adding pools that are increasingly variable results in increasingly less explained variance, from an average of 44% explained variance in very stable pools to 13% for all pools (Figure 6). This analysis confirms that environmental variability modulates the relationship between richness and community variability in a systematic way and is not overly sensitive to the cut-off used to separate low- versus high-variability pools. However, the analysis also sounds a warning that the results are scale-dependent and that studies that are based on experiments or data analyzed for one scale only may lead to spurious or biased conclusions.

Our results are consistent with the hypothesis that community variability is lower in speciose communities. This hypothesis, however, was not supported for environmentally variable pools (as measured by the multivariate index) or for pools with high variability in specific physicochemical variables. In contrast, population variability of individual species was unrelated to richness across the range of situations. Whether these patterns are directly caused by environmental variability remains an open question. However, the presence of richness-variability relationships in the less variable rock pools and not in the more variable rock pools suggests that environmental variability may play an important role in modulating richness-variability relationships.

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