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Title: Lower-level heterogeneity masks the global relationship between species richness and population variability

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Abstract

Ecological theory predicts that species richness should impact population variability. In contrast, empirical evidence suggests no or only a weak positive relationship between richness and population variability. We investigated the hypothesis that the obscuring noise of local processes, such as differences in local environmental conditions and biotic interactions, may mask the effects of richness on population variability. Using long-term data on invertebrate populations in rock pools, we considered richness-population variability relationships using three analytic resolutions in which data for two key variables, richness and population variability, were progressively averaged for each population. The resolution most useful in making predictions about the effect of richness on population variability removed the most variance in population responses arising from local processes, and allowed the detection of richness effects that would otherwise have been overlooked or underestimated. 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 abundance and, consequently, survival. Comparing results at different resolutions also provides a methodology to identify relevant detail in richness-population variability relationships.

Introduction

Species richness appears to effect variability in community abundance or biomass differently than population variability (1-5). For communities, greater richness reduces temporal variability (reviews, 6-8) through biological and statistical processes including: overyielding (9), complementarity (9-12), insurance effects (13, 14), weak interaction effects (15), statistical averaging (16), mean-variance relationships (7), or sampling effects (17). For populations, the effect of richness on variability in abundance or biomass is unclear (6, 7). Theoretical predictions are idiosyncratic, with some models predicting that richness can increase (1, 18), decrease (19-21) or have no effect on population variability (9) depending on model construction.

May (1) showed that increasing the strength and number of species interactions results in increasing population variability. Extending May's model of logistic growth Tilman (1998) showed that for a single population that experiences random variation in its environment, its variance scales linearly with mean abundance, i.e., the scaling coefficient $z = 1$ (Tilman 1998). When the average scaling coefficient for all populations in a community is $z < 2$ population variability should increase with increasing richness. If $z = 2$, species richness will have no impact on population variability. If $z > 2$ population variability should decrease as species richness increases. Populations in natural communities are expected to have scaling coefficients between 1 and 2 (Murdoch and Stewart-Oaten 1989), suggesting that if all else remains equal, populations should become more variable as richness increases.

Species richness has also been predicted to decrease population variability. Ives et al. (19) show that population variance in biomass, may either increase or decrease with strength of competition among species, α, and the number of species, S. Eigenvalues, λ_k, which measure partial correlation among species, increase with α and decrease with S. Therefore, when $\lambda_k > 0$, increasing α or decreasing S increases λ_k^2, increasing population variances. When $\lambda_k < 0$, increasing α or decreasing S initially decreases λ_k^2 but then increases λ_k^2 if λ_k becomes positive. Thus, decreasing S may initially stabilize population variances, but will eventually lead to increasing population variability (19).

In contrast to these theoretical predictions, empirical studies show non-existent or only very weak effects of richness on population variability (3, 5, 22). The only experiment detecting a significant relationship between richness and population variability was Tilman's who found that richness destabilized population abundances (3). However, only 2% of the variance in population variability was explained by richness. McGrady-Steed and Morin (4), found no relationship between richness and protist population variability in laboratory microcosms, and Romanuk and Kolasa (5) showed that population variability was unaffected by richness in natural rock pool communities.

Despite this lack of empirical support, ecologists expect populations to respond to richness. This arises from a number of logical assumptions. First, if communities are less variable in richer environments due to biological reasons, this must involve responses of populations (see 3, 19). That communities are less variable in richer environments has received considerable support (3-5, 23), suggesting that community richness may be linked to variability at the population level. For example, Ives et al (19) showed that the variance in total community biomass depends only on how species respond to environmental fluctuations. Interspecific competition and species number have little influence on community-level variances directly (19). Second, evidence is accumulating for species complementarity (9-12). Complementarity, an increase in abundance resulting from increases in richness, is composed of two distinct mechanisms: niche differentiation, the increasingly specialized use of resources as richness increases, and facilitation, the direct or indirect positive effects of adding one species on the productivity of others (4, 12, 23). If adding species facilitates higher population densities, either through niche differentiation or facilitation, populations are less likely to become locally extinct due to fluctuations at low densities (24).

Four possible population responses to increasing richness are: i) richness could increase population variability (3, 9), ii) richness could decrease population variability, a response which has yet to be shown empirically, but which has been predicted theoretically (19-21), iii) richness could have idiosyncratic effects, altering population variability differently depending on specific community attributes (25), iv) richness could have no effect on population variability (4, 5).

The paucity of data detecting population responses to richness suggests either the latter possibility or a methodological failure to detect a relationship. Population variability largely reflects interspecific and intraspecific interactions (26) and variation in the physical environment including resources (27). These "local" processes strongly vary among sites, resulting in extensive scatter (noise) in population variability values for any given S value (3-5 see also 26, 27). This noise might mask a relationship between richness and population variability. We examined whether the relationship between richness and population variability revealed if such noise could be accounted for using data from a system of tropical rock pools inhabited by zooplankton and benthic invertebrates. To accomplish this we tested the relationship between richness and population variability using three alternative resolutions of data. This method removed increasingly more noise in population responses to increasing richness and allowed us to determine the level of resolution most useful in making predictions about the effect of richness on population variability.

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 (5, 28-34). The study site covered an area 50m 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 (29) 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 = 56 ± 35.0 SD), 10 to 188 cm in width (mean = 32.9 ± 26.8 SD), and in depth from 1-37 cm (mean = 12.8 ± 8.3 SD). Elevation above sea level ranged from 1-235 cm (mean = 76.6 ± 80.1 SD) at high tide, with the tide rarely exceeding 30 cm. Seven pools were tidal (although tidal flooding was not daily). The remaining 45 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 rigaudi*, and several fresh and brackish water ostracods. Most species were benthic animals ranging from 0.6mm - 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 other animals were found transient visitors, including gastropods (Littorinidae and Neritidae), hermit crabs, and the brachyuran crabs *Pachygrapsus* sp. (28).

There are no pronounced species-area effects on abundance or species richness. 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 in richness and abundance were low due to the relatively constant annual temperature (5) and accounted for < 2% of the variability in density and none of the variability in species richness (unpublished data).

Pool communities experienced high colonization and desiccation. Following desiccation and refilling fauna was rapidly re-established. A range of 0.4-17.6 copepods per ml^{-1} was counted in the detritus layer 24h after rain, although their source was not determined (28). The system-wide mean species richness was 5.73 ± 2.69 SD per pool, with an abundance of 1606 ± 2964 SD; ranging from zero to > 50,000 individuals per liter. In colonization experiments involving 20 natural pools with no initial *in situ* sources of individuals, comparable mean species richness was attained within 6 months or earlier. Furthermore, 27 artificial pools exposed only to colonization accumulated 13 species after only 17 days (unpublished data), indicating that dispersal could completely reconstitute the fauna within 12-month long sampling intervals. The pool communities dry out frequently (33).

Of the 49 pools, 31 were found dry on one or more dates and 18 have never been found dry. On any one sampling date 7% of pools are without water.

Methods

Sampling

Each pool sample consisted of 500ml of water and sediments. Water was thoroughly stirred to dislodge organisms from pool sides and bottom to ensure a homogenous sample. Next, a variety of locations (water surface, pool bottom, pool sides, water column) were sampled using a 100 ml dip container. Organisms were caught in a 63µm net with a collecting container and immediately preserved in 50% ethanol. Overall, 392 samples were collected from 49 pools over 8 censuses, with 365 containing organisms. Sixty-nine species were identified and counted totaling > 300,000 individuals from all samples.

Data Analysis

We applied three alternative analyses that successively removed more noise arising from local processes. The "high noise" analysis preserved variance arising from local process and is analogous to the calculation of species or population variability presented in (3-5). The "intermediate noise" analysis reduced variance in richness for each population while preserving the range of population variability responses at each richness value. The "low noise" analysis reduced both richness and population variance.

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}).

$$S_{local} = \sum S / D \qquad (1)$$

where, S_{local} is the local richness, S is richness observed on a single date, and D is the number of census dates. For example, the harpacticoid copepod *Nitocra spinipes* was

counted 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}).

$$S_{region} = \sum_{1-i}^{p} S_i / D \qquad (2)$$

Where S_{region} is the mean of richness values experienced by local populations of a species, S_i is the richness of an *i*'s pool when the population was present in that pool, and *p* is the number of pools populations of a given species have occurred in. 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). 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.

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:

$$CV_{local} = StDev(N_k) / \left[(\sum_{k=1}^{D} N_k) / D \right] \qquad (3)$$

where CV_{local} is the coefficient of variation in population abundance of species N_k is a population size on date k, *D* is the number of sampling dates ($D = 8$).

Regional population variability was determined as:

$$CV_{landscape} = \left[StDev\left(\sum_{p=1}^{P} N_p \right) \right] \Big/ \left[\left(\sum_{k=1}^{D} \sum_{p=1}^{P} N_p \right) \Big/ D \right] \quad (4)$$

where CV_{region} is the coefficient of variation in population abundances summed over all pools, N_p is abundance of that species in a pool p on one date, D is the number of sampling dates (D=8). 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, $S_{region} = aCV_{region} + b$.

Results

The regression analysis yielding the best resolution was that removing 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; Fig. 1, (e) solid line). Although S_{region} was also negatively related to CV_{local}, it explained only 5% of the variance (p = 0.00001, n = 390, Fig. 2a). In contrast, no relationship was detected between S_{local} and CV_{local} (p = 0.715, n = 390, Fig. 2b) in spite of the high power of the test. Because abundant species vary less in relative terms (35), 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; Fig. 1, (a) dotted line). As groups of populations with lower density were added into the regression (Fig. 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, Fig. 3a). Thus, richness may affect the variability of high-density populations differently than low-density populations. This hypothesis is supported by an alternative analysis where populations were iteratively added into the regression analyses in reverse order (Fig. 3b). Populations with low-density ranks were more variable in pools with higher S_{region} (Fig. 3b). Thus, richness appears to strongly affect the variability of high-ranking populations, but low-ranking populations were less affected. There is

even some suggestion that low-ranking populations became more variable as richness increased.

Discussion

Our results show that changing the resolution at which variability is analyzed allows detection of richness effects (26, 27). There was no relationship between S_{local} and CV_{local} (the high variance analysis). In contrast, S_{region} was significantly correlated with both CV_{local} and CV_{region}. The scale which removed the most variance arising from local processes, CV_{region} (the low variance analysis), resulted in the most sensitive test, and allowed discrimination of ecological patterns which otherwise were statistically invisible (high variance analysis; Fig. 2b) or underestimated (intermediate variance analysis; Fig. 2a). Thus, as local differences are removed from the calculations of both richness and population variability, the explained variance between richness and population variability dramatically increased. The obscuring effects of local processes may be especially pronounced in populations with high variability such as these rock pools, where population CVs exceed 50% of the mean (range = 0.51 to 2.89, mean = 1.35 ± 0.545 SD).

Population variability significantly declined in richer environments supporting the hypothesis that populations are stabilized by richness. It is of interest, however, whether this pattern of decreasing variability in richer environments is a result of statistical averaging (16) or is biologically generated. The role of statistical as opposed to biological mechanisms in generating richness-variability relationships has been the subject of considerable debate (see 7). In particular, statistical averaging or portfolio an effect, i.e. the sum of several randomly and independently varying items is less variable (has lower variance) than the average item, have been proposed to decrease variability in richer communities independently of direct compensation between species (16). The question then is whether averaging effects could be invoked to explain reductions in population variability in richer environments. Averaging effects could be invoked if more pools were averaged together for populations with higher exposure richness. However, occupancy is negatively correlated with the exposure richness of populations ($r^2 = 0.262$, p < 0.005, n =28; Fig. 4). Thus, unlike richness-community variability relationships where reductions in variability can be explained in part by the results of statistical averaging (16), 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 (Fig. 1) was obtained by the method of collapsing variance (where no pattern was visible otherwise; Fig. 2b) suggests a biological reality regardless of the statistical method for achieving resolution.

One biological mechanism highly relevant to richness and variability is competition (26 and references therein). Differences in the response of individual species to environmental fluctuations are hypothesized to encourage negative covariance between species which, in turn, results in increasing population variability and decreasing community variability in richer environments (26). In rock pools we see a different pattern of responses, with both population variability (this paper) and community variability (5) decreasing as richness increases. This pattern has been predicted theoretically. Ives et al. (19) have shown that species number may have diverse effects on variability measured at the population level, but there are no 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 (19). 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, stabilizing effects of richness on populations of component species could yield more stable communities in richer environments.

There are two 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 (3, 4, 22, 36, 37). The possible implications of multiple trophic levels should not be discounted (7). Others (19) however suggest that there should be no qualitative difference in richness-variability relationships for multi-trophic communities. Secondly, species richness was not artificially manipulated (5). Instead, we used a natural richness gradient to test the relationship

between richness and population variability. Such unmanipulated communities have much greater variation than experimental systems, which could preclude detecting any clear richness-variability relationships. Remarkably, results obtained utilizing the procedures developed here, appear to be quite unambiguous compared to those reported in any previous studies (cf. 3, 4).

We previously showed that, in natural aquatic rock pools, communities with more species are less variable than species-poor communities (5). Furthermore, when the full range of variance arising from local processes is preserved in the model, population variability is unrelated to richness (*sensu* 3-5; Fig. 2b). Our work (5) supported the majority of studies that species-rich communities are less variable in their aggregated density than species-poor communities, and that there is no or only a weak relationship between richness and population variability (2-4). However, removing noise from local processes exposes strong effects of richness on population variability and its dependence on density. That richness could stabilize populations has been hypothesized theoretically (19), but this important hypothesis has had no prior empirical support.

Acknowledgements

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Figure 1. Low variance model. Population variability (CV_{region}) is negatively correlated with average richness, S_{region}. Each dot represents one population. 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 ($r^2 = 0.0164$, p = 0.032, n = 28).

Figure 2a-b. Temporal variability of populations in each rock pool as a function of richness. A) Intermediate variance model. Population variability (CV_{region}) 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 thus 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 variance model. Population variability (CV_{local}) of each population in each rock pools as a function of local richness, S_{local}.

Figure 3a-b. Contributions of each population into the model for population variability (CV_{region}) according to rank in density. a) Explained variance at each step with populations added into the model from the highest to the lowest rank. b) Explained variance at each step with populations added into the model from the lowest to the highest rank.

Figure 4. Average richness, S_{region} as a function of pool occupancy. Pool occupancy significantly correlates with S_{region} (total pools over 8 sampling dates, n = 365. The relationship remained strong when the most broadly distributed populations (occupancy >200) were removed from the analysis ($r^2 = 0.245$, p < 0.01, n = 26; dotted line).