

# Removing the confounding effect of habitat specialization reveals the stabilizing contribution of diversity to species variability

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Recd 13.05.03; Accptd 04.06.03; Online 09.07.03

**Earlier studies have found that diversity,  $S$ , stabilizes the relative variability of combined biomass or abundance of species making up a community. However, the effect of  $S$  on variability of constituent species has been elusive. We hypothesize that the proportion of specialists increases with  $S$  and, because specialists are more variable, this shift in composition will mask the stabilizing effect of  $S$  on populations of species making up a community. The test uses data on variability and ecological specialization of species in 49 natural rock pool invertebrate communities. Initial analyses produced inconclusive results similar to earlier studies. However, when variability owing to species' specialization was factored out,  $S$  reduced species' abundance variability, although not in all communities. Our study explains why the stabilizing effect of diversity on populations has not been found earlier.**

**Keywords:** stability; diversity; complexity; variability; specialization

## 1. INTRODUCTION

Renewed research and debate on the relationship between diversity and stability of ecological communities is important for theoretical (McCann 2000) and practical (Loreau *et al.* 2001) reasons. Previous studies have focused on plant communities (Cottingham *et al.* 2001), and some included multitrophic assemblages in laboratory (McGrady-Steed & Morin 2000; Fox & McGrady-Steed 2002) and field experiments in artificial and natural microcosms (Romanuk & Kolasa 2002). These studies measured stability as

- (i) variability of aggregate properties such as variability of community biomass or abundance and
- (ii) variability in density or biomass of individual populations.

Although most studies show that stability increases with richness,  $S$ , for aggregate abundance (Van der Heijden *et al.* 1998; Romanuk & Kolasa 2002; reviews in McCann

2000; Cottingham *et al.* 2001; Loreau *et al.* 2001), causal mechanisms are a subject of debate (see Lhomme & Winkel 2002).

The effect of  $S$  on population variability remains unclear. First, evidence for the relationship appears to be contradictory. Empirical studies from microcosms, rock pools and grassland communities show either no (Wardle *et al.* 1999; McGrady-Steed & Morin 2000; Romanuk & Kolasa 2002) or a very weak destabilizing effect of richness on population variability (Tilman 1999). By contrast, Romanuk & Kolasa (2003) have found that richness may stabilize populations in natural communities when noise owing to spatial variability among sites is filtered out.

Theoretical predictions are equally contradictory.  $S$  should increase population variability when the scaling coefficient of mean–variance relationship,  $z$ , is less than 2 (Tilman 1999). Because, in natural populations,  $1 < z < 2$  (Murdoch & Stewart-Oaten 1989), richness should destabilize populations. However, the mean–variance relationship varies with strength of competition,  $\alpha$ , and  $S$  (McCann *et al.* 1998; Ives *et al.* 1999). Alternatively, Li & Charnov (2001) derived a scaling rule from energetic and thermodynamic arguments that predicts  $S$  to stabilize populations

$$CV = C^*(S)^{-1/2},$$

where CV is the coefficient of variation in population density of a species,  $S$  is the richness and  $C$  is a constant (figure 1a).

These conflicting expectations and evidence may arise from a yet unidentified confounding factor that affects the diversity–stability relationship. We hypothesize that if increases in  $S$  were associated with the accumulation of habitat specialists, stabilizing effects that  $S$  may have on populations would be confounded. Specifically, we hypothesize that *population variation (of individual species) will not decrease with  $S$  when analysed in a classical manner but would decrease when a function linking richness with the mean habitat specialization of species is factored out.* This hypothesis emerges from several premises as follows.

- (i) Relative variation in abundance,  $N$ , of populations making up a community decreases with  $S$ , in the absence of perturbations (figure 1a; Li & Charnov 2001).
- (ii) Relative variation in population size,  $N$ , increases with the reduction in ecological range of a species, i.e. with habitat specialization (figure 1b; Waltho & Kolasa 1994; Kolasa *et al.* 1996). Consequently, the mean population CV should increase with the number of specialists in a community—an effect opposite to the previous premise.
- (iii) Ecological range of species declines with  $S$  (figure 1c). This premise is supported indirectly in the literature and tested in the following paragraphs.

Briefly, most communities contain many more habitat specialists than generalists (Gaston 1994). Data on diversity gradients, succession and colonization suggest that  $S$  increases primarily by adding habitat specialists (Brown 1995). Because distribution and abundance are strongly correlated at multiple scales (Bock 1987; Warren & Gaston 1997), generalists are more likely to reach a habitat patch first, with the subsequent growth of  $S$  driven primarily by specialists.

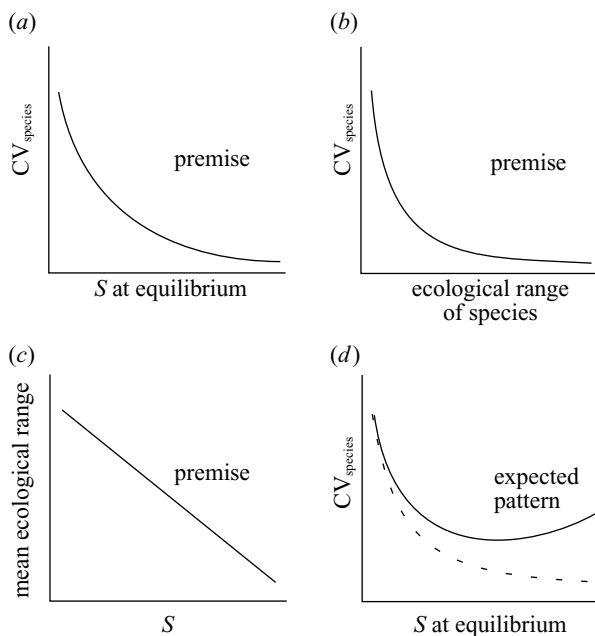


Figure 1. Premises leading to the hypothesis formulation. (a) CV increases with habitat specialization of species (reduction in ecological range); (b) Li & Charnov (2001) model: CV decreases with  $S$ ; (c) mean ecological range of species declines with community  $S$ ; (d) modified expectations of Li & Charnov (2001) model (b) after relationships shown in (a) and (c) are factored in; when the increase in variation owing to habitat specialists is large enough, the relationship between richness and stability may become undetectable.

These three premises, considered in conjunction, lead us to modify the predictions of the Li & Charnov (2001) model. Instead of the relation shown in figure 1a, the expected pattern of relative variation of populations becomes a combination of a decrease in variability postulated in (i) and an increase in variability owing to interaction between higher variability of specialists (ii) and a community growth by accumulating specialists (iii), with net variability actually increasing with  $S$  when  $S$  becomes large.

This paper tests the hypothesis formulated earlier, including premise (iii). Specifically, we aim to answer two distinct questions as follows.

- (1) Does mean ecological specialization of communities increase with  $S$ ?
- (2) Is the relationship between species richness and mean population variability in communities detectable once the species variability is standardized with respect to specialization?

## 2. MATERIAL AND METHODS

### (a) Data

We obtained annual abundance data on 70 species of invertebrates from 49 natural rock pool communities on the coast of Jamaica. Animals retained on a 60  $\mu\text{m}$  net were identified to species and counted (more than 200 000 individuals). Rock pool morphometry and physico-chemical conditions were recorded repeatedly (temperature, salinity, conductivity, pH, dissolved  $\text{O}_2$ , light on pool surface and bottom, nutrients, chlorophyll, water hardness)—see Kolasa *et al.* (1998) for additional taxonomic and sampling information.

### (b) Community range

The simplest way of showing that species-rich communities increase their proportion of specialists is to examine community ecological range,  $R_{\text{com}}$  as a function of  $S$ .  $R_{\text{com}}$  is the mean ecological range of constituent species. We chose two ways of estimating  $R_{\text{com}}$ : one based on pool abiotic characteristics and one on occupancy. We applied the Rotenberry & Wiens (1980) niche breadth estimate but, like Litvak & Hansell (1990), we used principal component analysis (PCA) scores from physico-chemical pool attributes in species' niche calculations (see electronic Appendix A: available on The Royal Society's Publications Web site).

We define the community ecological range based on occupancy as

$$R_{\text{com}} = \frac{\sum_{i=1}^{S_{\text{pool}}} p_i}{S_{\text{pool}}},$$

where  $S_{\text{pool}}$  is pool richness,  $p_i$  is the range of an  $i$ th species measured as the mean occupancy for seven sampling dates.

The relationship between the colonization sequence and species specialization was examined by creating a hypothetical community assembled from the regional species pool of invertebrates found in 49 rock pools (see electronic Appendix A).

### (c) Population stability

Following others, we use coefficients of variation, CV, to measure population stability (Cottingham *et al.* 2001). We obtained three distinct measures of variation.

#### (i) Raw CVs

Raw CVs were calculated for each of two consecutive dates and for each species in each pool separately, as recommended by Gaston & McArdle (1994) to reduce the bias caused by temporal autocorrelation. The number of CVs per species varied depending on the number of pools occupied. These high-resolution CVs served as foundation for most analyses. We also obtained low-resolution CVs based on seven-date instead of two-date means.

#### (ii) Detrended CVs

To remove the effect of habitat specialists (figure 1b), we used residuals from the fitted equation ( $\text{CV} = -0.002p + 1.3847$ ,  $r^2 = 0.518$ ,  $n = 69$ ) that describes CV dependence on ecological range of species (defined as  $p$ , pool occupancy at any single date), after adding a constant of  $|-1.3312|$  equal to the lowest residual to remove negative values while retaining the range of values.

#### (iii) Community CVs

Finally, we averaged species' detrended CVs in each pool for each of the six pairs of dates. While retaining the non-aggregated nature of the data, we obtained six independent community CVs to characterize each pool. These pool community-wide means are independent of habitat specialization, irrespective of  $S$ .

### (d) Pool community stability

The Li & Charnov (2001) model is valid for communities in equilibrium. We assumed that highly variable populations indicate pools away from equilibrium. We created an index of community variability independent of  $N$  and unrelated to community CV (see electronic Appendix A).

## 3. RESULTS

### (a) Community range

Species-rich pools include a larger share of habitat specialists (figure 2a). Different measures of habitat specialization coincide (figure 2b). The simulation of community assembly showed that colonization sequence was from habitat generalists to specialists, with the mean community range declining with  $S$  (see figure 5 in electronic Appendix A). Both findings support the premise (iii) (figure 1c).

### (b) Population stability

Raw CVs based on adjacent dates, the high-resolution analysis, increased insignificantly with  $S$  ( $r^2 = 0.0019$ ,  $p < 0.4803$ ). When CV was calculated across all seven

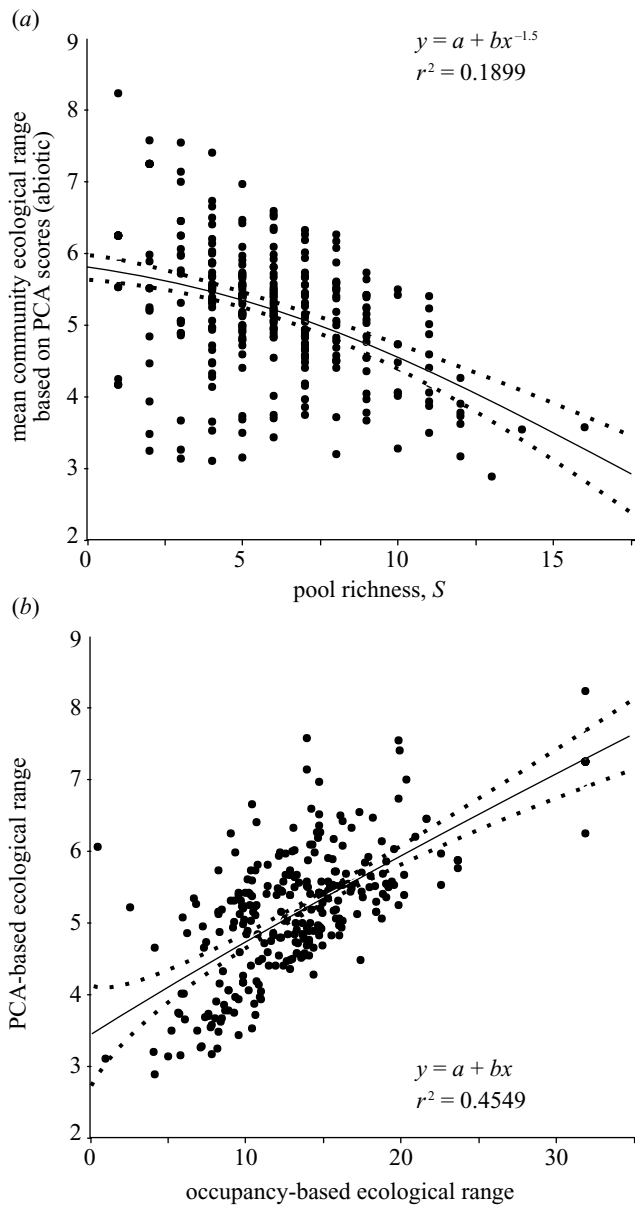


Figure 2. Measures of ecological range (habitat specialization) are related to  $S$  and each other in the rock pool communities. (a) Community specialization increases with  $S$ . Each point is a mean ecological range,  $R_{com}$ , of one community based on the niche breadth measure of Rotenberry & Wiens (1980;  $n = 305$ ,  $r^2 = 0.19$ ,  $p < 0.0000$ );  $a = 5.799$ ,  $b = -0.039$ . (b) The relationship between the previous and occupancy-based measure of ecological range ( $n = 305$ ,  $r^2 = 0.45$ ,  $p < 0.0000$ );  $a = 3.583$ ,  $b = 0.118$ .

dates, the low-resolution analysis, a negative relationship emerged between richness and variation (figure 3). The differing results produced by each method imply a statistical effect, which may be unrelated to those discussed by Doak *et al.* (1998) and Ives *et al.* (1999).

To test our hypothesis that a shift in community specialization correlated with  $S$  interferes with the detection of diversity–stability relationship, we removed variability owing to habitat specialists using detrended CVs and the index of community stability as a covariate. As postulated (figure 1*d*),  $S$  affected the population’s variability and this effect becomes stronger when highly variable communities are dropped from the analysis (figure 4; see electronic

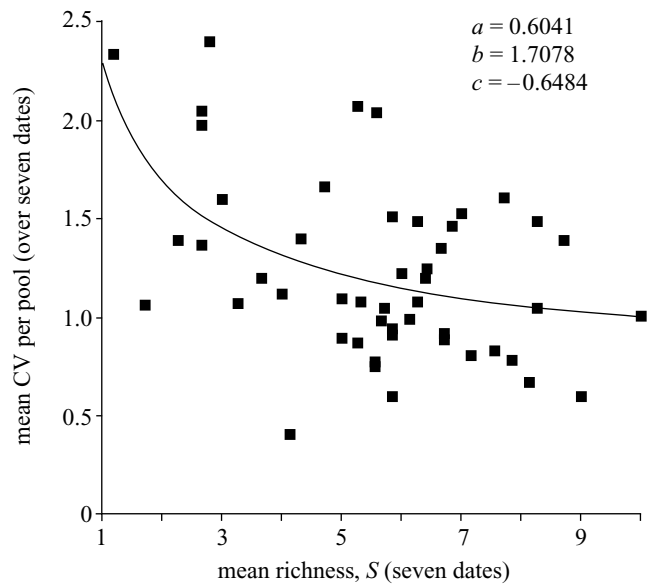


Figure 3. The effect of  $S$  on population CV in pool communities (low-resolution analysis). CVs are fitted by a curvilinear function suggested by Doak *et al.* (1998):  $CV = a + bx^c$  ( $r^2 = 0.2249$ ,  $F_{2,49} = 6.68$ ,  $p < 0.003$ ).

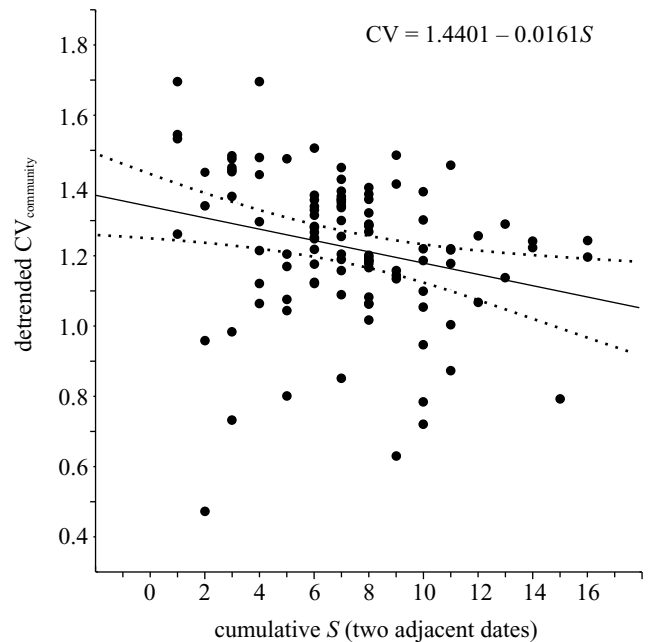


Figure 4. The effect of  $S$  on detrended CVs of individual populations (high-resolution analysis: CV calculated for date pairs) in stable pools after the effect of habitat specialists has been removed to calculate mean pool scores: the relative variation decreases with the number of species (adj.  $R^2 = 0.0850$ ,  $F_{2,236} = 12.05$ ,  $p = 0.00001$ ; not shown). This effect is stronger when the analysis is restricted to the stable 50% of the pools (adj.  $R^2 = 0.1316$ ,  $F_{2,113} = 9.71$ ,  $p < 0.0001$ ; shown in figure).

Appendix A). The observed reduction in species variability could be due to a statistical artefact if  $S$  and  $N$  were positively correlated, which is commonly observed, and CV values declined with  $N$ , but this is not the case—detrended CV values are unrelated to  $N$  ( $r^2 = 0.0026$ ,  $p = 0.417$ ).

#### 4. DISCUSSION

We found that the relationship between population CVs and  $S$  depends on analytical resolution. Specifically, low-resolution analysis produced a negative diversity–stability relationship, but high-resolution analysis revealed no diversity–stability relationship (CVs increased insignificantly). We confirmed that mean specialization of species in a community increases with  $S$ , at least in the system of rock pool communities. When variability owing to species' specialization was factored out,  $S$  also reduced the variability of individual populations. This reduction was stronger when only pools with modest absolute abundance variability (standard deviations) were retained in the analysis.

The first observation reflects larger temporal scale and thus evokes statistical averaging suggested earlier for aggregate properties (cf. Lhomme & Winkel 2002), even though the specifics of our methods are different. Furthermore, others have also reported the absence of a relationship between  $S$  and population CV (Tilman 1999; McGrady-Steed & Morin 2000; Romanuk & Kolasa 2002). Thus, up to this point our results are in agreement with previous studies.

The new finding, and the test of our hypothesis, is that the community-wide mean specialization of species increases with  $S$  and that the variability associated with the specialization masks the effect of  $S$  alone. Although the stabilizing effect of richness on local populations of individual species was weak (22% and 13% of the variance was explained, respectively, in low- and high-resolution analyses) and largely restricted to pools with overall modest variability in absolute abundance, even a weak stabilizing effect may have significant consequences. It is likely to affect the probability of local extinctions (Bengtsson & Milbrink 1995), the strength and predictability of species interactions, indirect effects, the persistence of species over landscape of patches or ecosystem functioning (cf. Loreau *et al.* 2001). The determination that  $S$  reduces the CV of constituent populations has potential implications for ecological theory. As species specialization appears to be responsible for the lack of a *prima facie* relationship between richness and population variability, models that test or examine this relationship using species of different specialization levels may lead to erroneous conclusions. Future analyses of community complexity and stability should explicitly account for the substantial differences in variability among species of distinct specialization.

#### Acknowledgements

The authors thank E. L. Charnov, M. Fuller, S. Naeem, F. Schläpfer, T. Romanuk, S. Dudley, T. Therriault, C. M. Wood, A. Hayward, two anonymous reviewers and undergraduates at McMaster University for comments and assistance in this research. This research has been funded by the NSERC (J.K.), NSF and DOE/Sandia National Laboratories (B.-L.).

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