LETTER

Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment

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Abstract

Theory predicts that species diversity can enhance stability of community-level biomass while simultaneously decreasing population-level stability. Enrichment can theoretically destabilize communities but effects may become weaker with increasing diversity because of the inclusion of consumer-resistant prey. Few experiments using direct manipulations of species diversity have tested these predictions. We used laboratory-based aquatic food webs to examine the effects of species composition, diversity and enrichment on temporal variability of population- and community-level biomass. We found weak effects of enrichment on population- and community-level stability. However, diversity enhanced community-level stability while species composition had no influence. In contrast, composition effects outweighed diversity effects when stability was measured at the population level. We found no negative effects of diversity on population-level stability, in opposition to theory. Our results indicate that diversity can enhance stability in multitrophic systems, but effects vary with the scale of biological organization at which stability is measured.

Keywords

Biodiversity, biomass, ecosystem functioning, portfolio effects, temporal stability, variability.

INTRODUCTION

The linkage between species diversity and the emergent properties of ecosystems continues to receive intense scientific interest. The need to comprehend the strength of such couplings has become increasingly more critical as the majority of the earth’s ecosystems are experiencing large-scale alterations and extinctions of unprecedented magnitude (Chapin et al. 2000). One component of this ongoing pursuit is the influence of species diversity and composition on the stability of population- and community-level biomass (Tilman 1999; McCann 2000; Cottingham et al. 2001; Loreau et al. 2002). Stability can take on many different meanings, but recent examinations have focused on the influence of diversity on temporal stability (or variability through time) of populations and communities (McCann 2000; Cottingham et al. 2001; Loreau et al. 2002). Emerging evidence from theoretical and empirical studies of single trophic level communities suggests an important positive effect of diversity on the temporal stability of community-level biomass (reviewed in Cottingham et al. 2001; Loreau et al. 2002). However, the role that diversity plays in the temporal variability of populations is less certain from an empirical standpoint. More importantly, the relative effects of diversity and species composition on biomass stability in more realistic food webs (i.e. multitrophic systems), remains largely unexplored.

Models of single trophic level communities show that several mechanisms may generate positive relationships between species diversity and the temporal stability of total community biomass or ‘community-level stability’ (reviewed in Tilman 1999; Cottingham et al. 2001; Hughes et al. 2002). Stabilization can occur in the absence of covariation among species populations through statistical averaging of population fluctuations or the ‘portfolio effect’ (Doak et al. 1998; Tilman et al. 1998). Assuming that variance in biomass over time of each species $i$ ($\sigma_i^2$) scales with its biomass ($m_i$) as a power function, then $\sigma_i^2 = cm_i^z$, where $c$ is a constant and $z$ is a scaling factor. If total community biomass summed across populations ($M$) is further assumed to be constant and...
independent of community diversity, then each species’ biomass in a community of \( N \) species will equal \( m_i = mN^{-1} \) and variances will equal \( \sigma_i^2 = cm_i^2 = cm^2N^{-z} \). In the absence of covariation among populations, the temporal variance of total community biomass is simply the sum of all individual biomass variances:

\[
\Sigma \sigma_i^2 = N(cm^2N^{-z}) = cm^2N^{1-z}
\]

(Tilman 1999; Hughes et al. 2002). Thus, summed variances will decrease and total biomass stability will increase with increasing species richness when \( z > 1 \). Portfolio effects are only strongly expressed when communities exhibit high species evenness (Cottingham et al. 2001) and biomass is evenly distributed among species (i.e. \( m_i = mN^{-1} \)). In communities with low evenness, total biomass variances will be more strongly influenced by population fluctuations of the dominant species.

In addition to statistical averaging, temporal variability of total community biomass also depends on how the biomasses of populations covary through time (Tilman 1999; Lehman & Tilman 2000). Species interactions (such as strong competitive effects) or differential species responses to environmental fluctuations may generate negative covariances among population biomasses through time (Tilman 1999; Yachi & Loreau 1999; Ives et al. 2000). If covariances summed across species become more negative with increasing diversity then temporal variability of community-level biomass may decrease (and stability will increase) with increasing diversity (Tilman 1999). While diversity may enhance stability of total community biomass, temporal stability of individual populations may actually decrease because of stronger compensatory responses among populations with increasing diversity (Tilman 1999; Lehman & Tilman 2000). Thus, the influence of diversity on temporal stability may depend greatly on the focal scale of biological organization. Although theory provides a foundation for comprehending diversity–temporal stability relationships, existing models have focused primarily on single trophic levels. Within multitrophic settings, predictions become more difficult to ascertain. Both positive and negative covariances are expected among species in multitrophic communities because of consumer resource interactions and indirect effects. How such complex food web interactions and species covariances vary with diversity and impact biomass stability are uncertain.

In addition to the influence of species diversity, temporal variability may depend critically on system enrichment and the availability of nutrient resources. Simple predator-prey models demonstrate that enrichment can destabilize consumer–resource interactions, causing stable equilibria to become oscillatory – the classic paradox of enrichment (Rosenzweig 1971; Gilpin 1972). However, diversity may mediate such endogenously driven dynamics; theory and experiments show that increasing prey diversity and the inclusion of predator-resistant prey (or weak interactors) can counter the destabilizing effects of enrichment (Abrams & Walters 1996; Bohannan & Lenski 1999; McCauley et al. 1999). Thus, diversity and enrichment may exert interactive effects on temporal stability with negative effects of enrichment being more strongly expressed in species poor communities. However, it is important to note that prior examinations have focused on population-level stability. Whether diversity and enrichment interact to determine stability of community-level biomass is unresolved.

Although the idea that diversity enhances temporal biomass stability is a prevalent notion, strong experimental evidence is scant (Cottingham et al. 2001; Loreau et al. 2002). Fewer still are experiments that have used direct manipulations to explore such relationships within multitrophic settings (see McGrady-Steed & Morin 2000). We know of no studies that have attempted to separate the effects of species composition and diversity or examine how these factors interact with enrichment to determine stability. We investigated these issues using a laboratory-based, multitrophic aquatic system composed of bacteria, algae, heterotrophic protozoa and rotifers. We directly manipulated species diversity, composition, and enrichment and explored their effects on temporal stability at the community and population level. We show that the relative importance of species diversity vs. species composition depends on the scale of biological organization at which stability is measured. At the community-level, diversity enhanced stability in accordance with theory, with species composition having no detectable influence. In contrast, the importance of species composition overrode diversity effects when stability was measured at the population-level. Enrichment effects on both population- and community-level stability were weak and did not interact with either diversity or composition.

**METHODS**

**Experimental setup and design**

Microcosms consisted of 200 mL, loosely capped Pyrex bottles. All experiments were conducted within incubators at 22 °C under a 12 : 12 h light : dark cycle. We assembled all experimental communities to include five trophic groups: decomposers (bacteria), primary producers (single-celled algae), bacterivores (protozoa), herbivores/bacterivores (protozoa and rotifers) and omnivorous top predators (protozoa). All species in our source pool were maintained as laboratory stock cultures (for culture sources see Appendix S1). Each microcosm received one sterilized wheat seed as a slow-release carbon/nutrient source and 100 mL of nutrient medium consisting of distilled water,
sieved soil (obtained from the grounds of Rutgers University), and Protist Pellet (Carolina Biological Supply, Burlington, NC, USA) as a carbon and nutrient source. All materials were autoclave-sterilized before use.

We used a nested experimental design consisting of three diversity levels (low, medium and high) created by manipulating the number of species within four of our trophic groups: primary producers, bacterivores, herbivores/bacterivores and top predators. Diversity treatments consisted of one, two or four species per trophic group respectively. Nested within each diversity level were four unique species compositions created by randomly drawing species for each trophic group from our laboratory source pool (see Appendix S2). Diversity/composition treatments were crossed with two levels of enrichment (low and high) manipulated by varying soil and Protist Pellet concentrations. Low enrichment treatments received 0.07 g pellet L\(^{-1}\) and 0.167 g soil L\(^{-1}\) and high enrichment treatments received 0.70 g pellet L\(^{-1}\) and 1.67 g soil L\(^{-1}\). Medium concentrations equated to total phosphorus concentrations of 25.4 \(\mu\)g L\(^{-1}\) for low enrichment treatments and 145.8 \(\mu\)g L\(^{-1}\) for high enrichment treatments – values spanning the mesotrophic to hypereutrophic range (Wetzel 2001). Each treatment combination was replicated four times for a total of 96 microcosms.

All microcosms received a common bacterial community and an assemblage of heterotrophic microflagellates. We added microflagellates because they are a common experimental contaminant; thus, we equalized the probability of their inclusion in all replicates. Sterilized medium first received three species of bacteria (Serratia marcescens Bizio, Bacillus cereus Frankland and Frankland and Bacillus subtilis Ehrenberg) known to be edible by all the bacterivores in our study and a low density inoculum of microflagellates (maintained as a laboratory culture). Because non-sterile stock cultures contained additional species of bacteria, we created a pooled bacterial inoculum by filtering \(1\) mL of medium from all stock cultures through a sterile 1.2-\(\mu\)m filter to remove protists, algae and rotifers. This isolate was then added to the experimental media. To monitor for contaminants that may have passed through the 1.2-\(\mu\)m filter, we added a small volume of the inoculum to bottles containing low and high productivity sterile medium (three replicates of each concentration). We detected the following contaminants: two unknown species of unicellular green algae, Chrysopsis (an algal flagellate) and Uronema (a bacterivorous ciliate).

Two days after addition of bacteria, primary producers were added to their respective treatments (\(\approx 10^7\) cells per species, per microcosm). Bacterivores and algivores were added 4 days later (10–50 individuals per species, per microcosm). Primary consumers were allowed to respond numerically for 8 days, at which time top predators were isolated from stock cultures and added to their respective treatments (10 individuals per species, per microcosm). Hereafter, we refer to this as day 0 of the experiment. Although total biomass initially varied among our diversity/composition treatments, all populations that persisted in the microcosms exhibited increases in density in the first week of the experiment. Thus, effects of varying initial conditions were likely minimal. Beginning the second week of the experiment, we performed weekly replacements of 10% of medium from each replicate with sterile medium to replenish nutrients. We allowed the experiment to run for 22 days. This was long enough to encompass numerous generations of our species which had generations times on the order of a few hours (for bacteria and some protists) to 2 days (for rotifers).

### Measuring temporal variability

Beginning on day 5, we sampled microcosms every 3–4 days up to the final day of the experiment. To sample microcosms, bottles were first gently mixed and a small volume of medium (900–1500 \(\mu\)L) was removed and examined with a dissecting microscope. Rare taxa were enumerated by counting the entire sample volume while abundant taxa were counted in smaller subsamples. Algae and microflagellates were enumerated using a haemacytometer and a compound microscope. We measured realized species diversity based purely on species presence and absence (i.e. as species richness). To obtain measures of species biomasses, we multiplied species densities by species-specific biomass constants obtained from lab studies and published accounts (Foissner & Berger 1996). Biomass and diversity of bacteria are not considered in our analyses. In addition to realized species diversity, we also quantified mean species evenness of our communities using a modified form of Simpson’s dominance index (equation \(E_{1/D}\) in Smith & Wilson 1996). Evenness measures were first calculated for each sample date and then averaged over time to obtain a single measure for each community.

To examine temporal variability of total community biomass (biomass summed across all species), we calculated the standard deviation (SD) of \(\log_{10}\) transformed total biomass over time for each replicate (Gaston & McArdle 1994). We chose the SD over the coefficient of variation (CV) because in the latter metric covariation in mean community biomass with species diversity/composition may influence the CV independently of diversity/composition effects on biomass variance – an ‘overyielding effect’ (Hughes & Roughgarden 2000; Valone & Hoffman 2003a). Thus, we attempted to remove potential confounding effects of biomass yields from measures of community-level variability. However, results were qualitatively similar when using the CV of total biomass. Because of zero values...
we could not use log-transformed biomass to determine variability of individual populations (population-level variability). Instead, we relied upon untransformed biomass measures and calculated the CV for each population over time. CV measures were then averaged across populations to obtain a single measure of population-level variability for each replicate. To examine the influence of species covariances on diversity–stability relationships, for each replicate we calculated temporal covariances (over the course of the experiment) of species biomasses for all possible species pairings. Covariances were then summed to obtain a single community-level covariance (Tilman 1999).

Most aforementioned theory is concerned with biomass fluctuations around long-term averages or consistent trends. Because trends may also influence variability measures, we analysed detrended measures of total biomass variability by using residuals generated by linear regressions between log10 (total community biomass) and time (as the independent variable). Residuals were averaged for each microcosm and analysed in the same manner as SD measures.

Statistical analysis

Measures of population- and community-level variability were analysed using a mixed model ANOVA, with composition (a random effect) nested within diversity and crossed with productivity. Species compositions diverged from their initial states; this and the presence of contaminants caused realized diversity to vary within our diversity/composition treatments and between productivity levels. Consequently, we also explored the effects of realized species diversity (averaged over the experimental period) on stability measures using ANCOVA, treating productivity as a fixed effect and mean realized species diversity as a continuous covariate. Furthermore, we used nested ANOVA to examine differences in realized species diversity among our original treatments. All statistics were performed using Systat Version 8 and SAS Version 8.

RESULTS

By the first sample date, realized species diversity had declined from initial values in the medium and high diversity treatments (Fig. 1). However, significant differences among diversity treatments were still present when averaging realized diversity over the course of the experiment ($P < 0.0001$, nested ANOVA; $P < 0.0001$, all pairwise comparisons, Tukey’s HSD). Productivity also increased time-averaged realized species diversity ($P = 0.002$, nested ANOVA). No composition effects were present ($P = 0.21$) and no productivity interactions were detected (all $P > 0.07$). Results were qualitatively similar when analysing realized diversity on the final sample date and when excluding contaminant species from measures of realized species diversity. At least one of the four contaminant taxa were detected on at least one sample date in all treatment replicates with the exception of compositions 6 and 11 in which no invading species were detected over the course of the experiment. However, invaders only attained high per cent relative biomass, averaged over time, in composition 1 (64.6% ± 7.2, mean ± SE) and composition 2 (67.2% ± 10.6, mean ± SE). Invader relative biomass averaged 5.7% (± 0.85%) across the remaining treatments.

Mean species evenness declined with increasing average realized species richness (Fig. 2a; $R^2 = 0.38$, $P < 0.0001$, linear regression); no difference in slopes was detected when running regressions for low and high productivity treatments separately ($P > 0.05$). Decreases in evenness were primarily because of increasing dominance by primary producers (Fig. 2b). Time-averaged values of log10 (total consumer biomass) and log10 (total primary producer biomass) both decreased with increasing mean evenness. However, when examining 95% confidence intervals, the slope of the primary producer relationship ($R^2 = 0.391$, $P < 0.0001$, linear regression) was significantly greater than that of the weaker consumer biomass relationship ($R^2 = 0.06$, $P < 0.02$). Consequently, time-averaged per cent relative biomass of primary producers also decreased with increasing evenness ($R = -0.35$, $P = 0.0005$, Pearson correlation). Increases in algal dominance were mainly driven by two species: *Ankistrodesmus* and *Chlorella*. When
looking across all composition and enrichment treatments, presence of these two species alone or together was negatively related to species evenness ($F_{1,94} = 76.6, P < 0.00001, \text{ANOVA}$) and positively related to mean relative biomass of primary producers ($F_{1,94} = 15.8, P < 0.001, \text{ANOVA}$).

Temporal variability of community-level biomass decreased (i.e. stability increased) with increasing diversity (Fig. 3a; $F_{2,9} = 4.38, P = 0.047, \text{diversity effect, nested ANOVA}$). Mean biomass variability was higher in low diversity treatments compared with medium and high diversity levels (Fig. 3a; $P < 0.01, \text{Tukey's HSD}$); no difference between medium and high levels was detected ($P = 0.99, \text{Tukey's HSD}$). Enrichment also decreased the variability of community-level biomass (Fig. 3a,b; $F_{1,9} = 6.60, P = 0.030, \text{nested ANOVA}$). We detected no interaction between diversity and enrichment ($P = 0.27$), nor did we find any effects of species composition or a composition $\times$ enrichment interaction (Fig. 3b; all $P > 0.30$). Temporal variability of community-level biomass showed a negative relationship with mean realized species diversity (Fig. 3c). A significant effect of realized species diversity was detected when using ANCOVA ($F_{1,92} = 7.31, P = 0.008, R^2 = 0.140$). Although a weak enrichment effect was present when using ANOVA, no enrichment main effect or interaction with realized species diversity was detected when using ANCOVA ($P > 0.44$).

When examining detrended measures of community-level variability, results were qualitatively similar to those using the SD. Nested ANOVA only revealed significant negative effects of diversity ($F_{2,9} = 6.16, P = 0.021$) and enrichment ($F_{1,9} = 7.17, P = 0.025$). Moreover, ANCOVA revealed a significant effect of realized species diversity ($F_{1,92} = 7.76, P = 0.006, R^2 = 0.135$) but no effects of enrichment or an enrichment $\times$ diversity interaction ($P > 0.30$).

We found no effects of species diversity or a diversity $\times$ enrichment interaction on mean population-level variability (Fig. 4a; $P > 0.44$, nested ANOVA). However, population-level variability varied among species compositions (Fig. 4b; $F_{9,8} = 3.54, P = 0.037, \text{nested ANOVA}$), independent of enrichment level ($P = 0.49$, composition $\times$ enrichment interaction, nested ANOVA). Composition effects were largely driven by two compositions of unusually high and low variability: compositions 1 and 7 respectively (Fig. 4b). In pair-wise comparisons among compositions, significant differences were only detected for the following contrasts: 1 vs. 2, 1 vs. 3, 1 vs. 7, 4 vs. 7 and 5 vs. 7 (Fig. 4b; all $P < 0.054$; Tukey's HSD). As with community-level variability, mean population-level variability decreased with increasing enrichment (Fig. 4a,b; $F_{1,9} = 11.09, P = 0.009, \text{nested ANOVA}$). When analysing results using ANCOVA, no effects of mean realized species diversity or enrichment were detected (Fig. 4c; all $P > 0.14$). However, a very weak
Figure 3  Temporal variability of community-level biomass as a function of: (a) species diversity and enrichment; (b) species composition and enrichment; (c) average realized species diversity; the solid line is the linear regression line for low enrichment treatments, the dashed line is the linear regression line for high enrichment treatments. In panel (b) vertical dashed lines demarcate low, medium and high diversity treatments (from left to right). Shown are mean values ± 1 SE.

Figure 4  Temporal variability of population-level biomass as a function of: (a) species diversity and enrichment; (b) species composition and enrichment; (c) average realized species diversity (regression lines as in Fig. 3c). In panel (b) dashed lines demarcate low, medium and high diversity treatments (from left to right). Shown are mean values ± 1 SE.
negative relationship was detected when using linear regression to analyse both low and high productivity treatments together ($R^2 = 0.044$, $P = 0.04$).

Negative summed covariances among populations were prevalent among our communities with 64 of 96 micro-cosms exhibiting negative values. However, summed covariances showed no relationship with average realized species diversity when analysing enrichment levels together (Fig. 5; $P = 0.67$, linear regression) or separately (low enrichment: $P = 0.09$, linear regression; high enrichment: $P = 0.10$, linear regression). Population biomass–variance scaling was consistent with the operation of portfolio effects. When examining the relationship between temporal variances and time-averaged biomasses for all species present in our microcosms, the slope on the log–log scale (equivalent to the scaling factor, $\gamma$) was estimated to be 1.55 (Fig. 6; $R^2 = 0.96$, $P < 0.00001$, linear regression). Slopes from separate regressions for the low and high productivity treatments did not differ ($P > 0.05$).

DISCUSSION

Consistent with theory, temporal stability of community-level biomass increased with increasing diversity. Both ANCOVA and nested ANOVA revealed significant negative effects of diversity on temporal biomass variability. In contrast to species diversity effects, species composition appeared to have little influence on temporal variability of total community biomass, suggesting that the number of species present within a food web rather than their identities may be of greater importance for understanding and predicting biomass variability at this level of biological organization. Our results further suggest that diversity effects on stability may be asymptotic, with strong stabilizing effects only emerging at relatively low diversity levels. Presence of a positive diversity–stability relationship in our study complements previous observational (Romanuk & Kolasa 2002; Valone & Hoffman 2003a; Steiner 2005) and experimental studies (Dodd et al. 1994; Tilman 1996) of community biomass stability in single trophic level systems. However, note that none of the latter experiments directly manipulated species diversity, relying instead on indirect manipulations via nutrient additions. To our knowledge, only one previous study has used a multitrophic level system to examine diversity effects on temporal variability of an aggregate ecosystem property (McGrady-Steed et al. 1997). However, that study focused on temporal variability of community-level respiration, making its link to existing stability theory unclear. Thus, our experiment provides the first strong evidence that diversity effects on temporal biomass stability can extend to more complex food webs.

Several factors may account for a positive relationship between diversity and community-level stability. First, species interactions (such as exploitative competition) can generate compensatory dynamics and negative covariances among species populations through time; as some species
decrease in biomass over time, other populations may increase, decreasing overall temporal variability at the community level. To account for a positive diversity–stability relationship, temporal covariances summed across species must become more negative with increasing diversity (Tilman 1999). This was clearly not the case in our study; although negative summed covariances were prevalent among our food webs, no relationship between summed covariances and realized species diversity was detected. One possible explanation is that environmental perturbations from our sampling and medium replacement regimes were not strong enough to generate compensatory responses among species. Hence, direct imposition of stronger environmental variation could produce different results.

Positive diversity–stability relationships can also arise in the absence of compensatory dynamics and negative summed covariances through the operation of portfolio effects (Doak et al. 1998). Stabilization through this mechanism depends on the manner in which temporal variances of individual populations scale with their mean biomasses, with portfolio effects only emerging with scaling constants (\(z\)) greater than one (Tilman 1999). When examining all populations in our microcosms, regression produced a \(z\) estimate of 1.55, suggesting that portfolio effects may underlie the positive diversity–stability relationship exposed in our study. This estimate is also consistent with prior studies that have shown that \(z\) commonly ranges between 1 and 2 (Tilman 1999).

While biomass–variance scaling in our study was consistent with the existence of portfolio effects, this result must be viewed cautiously. First, a major assumption of the portfolio effects model is that total community biomass is fixed and independent of species diversity. Thus, abundances of individual species decrease with increasing species diversity. This assumption was not upheld in our experiment. Time-averaged biomasses of populations did not decrease with realized species diversity (\(R^2 < 0.0001, P = 0.82\), linear regression) and a weak but significant positive relationship between time-averaged total community biomass (on the log10 scale) and realized diversity was present (\(R^2 = 0.090, P = 0.004\), linear regression). Finally, the strength of statistical averaging as a stabilizing force decreases with decreasing species evenness (Gottingham et al. 2001). In our study, mean species evenness declined with increasing average realized species diversity, due largely to increasing relative biomass of primary producers and the algal species Ankistrodesmus and Chlorella. Increased incidence and dominance by these two species with increasing species diversity is evidence of a selection effect – that is, an enhanced probability of inclusion of dominant species with increasing diversity (Tilman 1999) – although other facilitative factors cannot be dismissed such as stronger top-down control of herbivores or increased nutrient regeneration at higher diversities. Rather than destabilizing community-level biomass, decreased evenness likely enhanced community-level stability in our study. When measuring population-level variability of primary producers and consumers separately, the mean population-level CV of primary producers was significantly lower than that of consumers across food webs (\(P < 0.0001\), t-test). Moreover, the presence of Ankistrodesmus and Chlorella was negatively related to community-level variability, regardless of diversity or enrichment level (\(F_{1,91} = 8.75, P = 0.004\), ANOVA).

Thus, enhanced dominance by species with inherently lower population-level variability could underlie the positive relationship between species diversity and community-level stability.

Prior studies have shown that variability in community biomass can decrease with increasing species diversity (Loreau et al. 2002), yet few have quantified species covariances or searched for evidence of portfolio effects. Those studies that have sought causal mechanisms have generated results consistent with ours; negative species covariances appear to play little part in diversity–variability relations (e.g. Tilman 1999; Petchey et al. 2002; Valone & Hoffman 2003a; Steiner 2005). Moreover, mean biomass–variance relationships commonly scale with \(z\) values consistent with the presence of portfolio effects (Tilman et al. 1998; Petchey et al. 2002; Steiner 2005). The degree to which changes in species evenness may drive diversity–stability relationships is less known empirically. Although studies have shown that evenness may decline with increasing species richness (e.g. Weiher & Keddy 1999; Mulder et al. 2004), we know of only one study that showed that such a negative relationship was also linked to increased community-level stability (Valone & Hoffman 2003a). If declines in evenness with increasing species diversity are commonly associated with dominance by species with inherently low population-level variability then this may be an important general explanation for positive diversity–stability relationships in nature. These results and ours do not negate the potential influence of species covariances on temporal stability, but they do call into question the role of compensatory dynamics in the generation of positive diversity–stability relationships.

Although positive effects of diversity on community-level stability are documented (Loreau et al. 2002), the relationship between population-level stability and diversity is less clear. In a study of grasslands systems, Tilman (1996) demonstrated that contrasting diversity effects could emerge depending on the level of biological organization at which stability is measured; diversity can enhance stability of total community biomass while stability of individual populations may decrease with increasing diversity because of stronger compensatory dynamics at higher diversity levels. These results were later upheld by predictions from theoretical
work (Lehman & Tilman 2000). Although intriguing, subsequent studies have failed to support a general negative relationship between diversity and population-level stability with some studies finding no relationship (McGrady-Steed & Morin 2000; Romanuk & Kolasa 2002; Kolasa & Li 2003) and others a positive diversity effect (Valone & Hoffman 2003b). Similarly, we found no support for contrasting diversity–stability relationships as predicted by Tilman (1996) and Lehman & Tilman (2000). Although diversity enhanced stability of community-level biomass, no effect of diversity was detected when examining variability at the population level. Indeed, the general trend (although weak) was a positive effect of diversity on population-level stability.

While species diversity did not shape population-level stability of our food webs, we did uncover significant effects of species composition. Hence, the identity of species present appeared to play a stronger role in determining the overall stability of populations, in contrast to community-level stability. However, we should point out that composition effects in our experiment were driven by two treatments of especially high and low variability (compositions 1 and 7 respectively). Composition 1 was dominated by two contaminant algal species. Thus, variability in this composition was influenced by two species not originally included in the experimental design. In composition 7, top predators failed to persist for the majority of the experimental duration. Past studies have shown that removal of top predators can have a stabilizing effect on populations (Lawler & Morin 1993; Halpern et al. 2005). Thus, reduced food chain length in this composition may have driven low population-level CVs. Do our results mean compositional effects would be rare in more natural settings? It is difficult to assess given the relatively small number of compositions we employed. Furthermore, the limited species pool that was available to us meant that some species inevitably were included in multiple compositions of a given diversity level; this was especially true in our high diversity treatments. Greater compositional similarity would weaken differences among our composition treatments. Thus, it is plausible that in natural communities with richer species source pools, compositional effects on population-level stability would be more pronounced.

We also investigated the impact of system enrichment on population- and community-level stability. Enrichment is known to influence the structure of natural communities, potentially affecting patterns of species diversity, composition and relative abundance – factors which in themselves may influence stability. However, enrichment may also alter temporal stability independent of effects on community structure. For example, simple predator-prey models predict increased population variability under enriched conditions (Rosenzweig 1971; Gilpin 1972). However, more recent studies show that diversity can counter the destabilizing effects of enrichment by increasing the presence of predator-resistant species or ‘weak interactors’ (e.g. Abrams & Walters 1996; Bohannan & Lenski 1999; McCauley et al. 1999). This occurs because weak interactors may channel resources away from more susceptible prey reducing their effective carrying capacity. Consequently, we hypothesized that enrichment and diversity would interact to determine stability. In contrast, we found no destabilizing effects of enrichment. Nor did we find an interactive effect of enrichment with diversity. To the contrary, both population- and community-level stability increased in high enrichment treatments (Figs 3a and 4a). While intriguing, this paradoxical outcome became statistically insignificant when analysing realized species diversity effects using ANCOVA (Figs 3c and 4c). A plausible explanation is that enrichment effects on stability were simply mediated by enrichment effects on species diversity. When analysing average realized species diversity using nested ANOVA, we found that enrichment increased diversity across all composition treatments. Thus, enrichment of ecosystems may influence stability through indirect effects on the diversity and composition of communities, but it may have little direct influence on either population or community-level variability.

Attaining the capacity to predict the impact of species loss on the temporal variability and reliability of population- and community-level biomass may be of vital importance to the management of ecosystems and their sustainability. This is especially so if such measures are directly related to the biomass of harvestable or managed biota, or if coupled to important ecosystem services such as carbon and nutrient cycling. Unfortunately, evidence for diversity effects on temporal biomass stability have, to date, focused almost exclusively on single trophic level systems. Moreover, the majority of past studies have not directly manipulated diversity and composition. Our study shows clearly that both species diversity and composition play important roles as predictors of stability in food webs. However, the focal level of biological organization at which stability is measured will play a major part in the relative importance of these two facets of community structure. Thus, our results add to the growing body of evidence showing that the biotic makeup of a community can influence stability and that these effects extend to more complex and realistic food webs. However, additional long-term studies of natural multitrophic communities are needed to determine the generality of our findings and their applicability to the management of natural ecosystems.

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**SUPPLEMENTARY MATERIAL**

The following supplementary material is available online for this article from http://www.Blackwell-Synergy.com:

**Appendix S1** Species lists and culture sources.

**Appendix S2** Species combinations of all composition treatments.

**REFERENCES**


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