Temporal stability of pond zooplankton assemblages

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SUMMARY
1. A large body of recent theory has recently developed focused on the relationship between the species diversity of competitor assemblages and the temporal stability of total competitor biomass. Many of these models predict that stability can increase with increasing diversity.
2. To explore natural relationships between zooplankton taxonomic diversity and temporal stability of total zooplankton biomass, 18 fishless, permanent ponds located in southern Michigan were surveyed over a 5 month period during a single growing season.
3. Results showed that temporal variability in total zooplankton biomass (measured as the coefficient of variation or CV) decreased with increasing mean zooplankton taxonomic richness. Thus, temporal stability increased with increasing taxonomic richness, consistent with theoretical predictions.
4. Decreases in the CV appeared to be because of portfolio effects (statistical averaging of species’ biomass fluctuations) rather than negative covariances among zooplankton taxa.
5. The CV of zooplankton biomass was also related to several environmental variables, suggesting that taxonomic richness may not be the only mediator of biomass stability. The CV decreased with increasing relative abundance of grazer-resistant algae (algae >35 μm in size) and the CV increased with increasing pond productivity.

Keywords: biomass, ecosystem functioning, species diversity, stability, zooplankton

Introduction
The relationship between species diversity and system stability is a central issue in ecological research and has recently gained renewed attention in light of widespread, human-induced alterations of global biodiversity (Tilman, 1999; McCann, 2000; Loreau et al., 2002). An essential aspect of community and ecosystem stability is the variability through time of aggregate community measures such as the total biomass of trophic levels or competitive assemblages (Tilman, 1999). Comprehending the impact of species loss on system stability is vital for predicting the reliability of such aggregate measures through time. This is especially true when aggregate measures are linked to valuable ecosystem services, such as carbon-nutrient cycling or the biomasses of harvestable and managed biota. Theory provides a rich foundation of mechanisms and predictions for the impact of species diversity on community stability (reviewed in Tilman, 1999; Cottingham, Brown & Lennon, 2001; Hughes, Ives & Norberg, 2002; Loreau et al., 2002). Despite this, documentation of diversity-stability patterns in natural systems is rare.

In this paper, I focus on the relationship between temporal variability in total competitor biomass and the richness of competing species (i.e. diversity based on presence and absence of taxa). ‘Competitor’ is used to refer to species that occupy a single trophic level (e.g. herbivorous zooplankton) and potentially compete for shared resources (e.g. algae). Theoretical explorations show that increasing species richness of competitors can enhance the temporal stability of total competitor biomass through a number of mechanisms (Doak et al., 1998; Tilman, Lehman & Bristow, 1998;
Ives, Gross & Klug, 1999; Yachi & Loreau, 1999; Ives, Klug & Gross, 2000; Ives & Hughes, 2002; reviewed in Tilman, 1999; Cottingham et al., 2001; Hughes et al., 2002; Loreau et al., 2002). Consider a common measure of temporal variability, the coefficient of variation (CV), equal to the standard deviation (σi) of the variable of interest measured through time divided by the temporal mean (μi) of that variable (CV = σi/μi). The standard deviation of competitor biomass is itself composed of the sum of all competitor species variances and covariances in biomass measured over time: σi = Σ variance + (2 × Σ covariance)1/2. Hence, biomass stability will depend on species richness if either variance or covariance components vary with species richness. Summed variances can decline with increasing species richness via statistical averaging, enhancing stability in the complete absence of species interactions; what is termed the portfolio effect (Doak et al., 1998; Tilman et al., 1998; see Discussion). However, species interactions may also influence σi by affecting how species’ biomasses covary through time.

For example, competitive effects may lead to negative covariances between some species. Alternatively, species within a trophic-level may respond differentially to environmental fluctuations and perturbations (Ives et al., 1999; Yachi & Loreau, 1999; Ives et al., 2000). If of sufficient number and/or magnitude, the sum of all covariances (Σ covariance) may be negative, decreasing temporal variability in total competitor biomass. If summed covariances become more negative with increasing species richness, stability may increase with diversity (Tilman, 1999).

Although temporal stability of total competitor biomass may increase with increasing species richness, numerous other factors may independently influence the stability of populations and communities. For instance, system productivity and enrichment have long been thought to affect negatively the stability of populations. Simple consumer-resource models show that such systems are more prone to exhibit unstable-oscillatory dynamics under enriched conditions; what is commonly known as the paradox of enrichment (Rosenzweig, 1971; Gilpin, 1972; McCauley & Murdoch, 1990). How such consumer-prey dynamics scale up to whole consumer assemblages and total consumer biomass is unknown. More recently, theoretical and empirical research has shown that increasing prey diversity and inclusion of inedible or consumer-resistant prey species (or weak interactors) can stabilise consumer–prey dynamics (Abrams & Walters, 1996; McCann, Hastings & Huxel, 1998; Bohannan & Lenski, 1999; McCauley et al., 1999; Petchey, 2000). Thus, the prevalence of grazer-resistant algal-prey could stabilise zooplankton dynamics (e.g. McCauley et al., 1999). These investigations have not considered complex consumer assemblages or effects on community-level biomass.

Studies that have used survey/observational data to examine natural relationships between species richness and variability in trophic level biomass are surprisingly rare. Here I present results from a field survey of pond zooplankton communities in southern Michigan. Using this data set, I explore the relationship between mean zooplankton taxonomic richness and temporal stability of total zooplankton biomass. I also examine several other limnological variables that may have affected these stability measures.

**Methods**

All ponds were found within 100 km of the W. K. Kellogg Biological Station (Hickory Corners, MI, U.S.A.), were fishless, and permanent in the 1–2 years prior to the study (personal observation). Ponds were sampled monthly in 1998, beginning in late April and ending in late August. For methodological details see Steiner (2002) and Steiner (2004). In most cases, zooplankton were collected at mid-day with integrated tube samplers that extended to the pond bottom, with the exception of ponds approximately <0.5 m in depth (which were sampled with a 2 L hand pitcher). Samples were collected at several points, at even intervals, along a qualitative transect spanning from approximately 1 m in the pond from edge to the centre of each pond. At each sample point along the transect, the water column was sampled and the water poured through a 60 μm sieve to retain zooplankton; this was then repeated and a sample of equal volume poured through a separate 60 μm sieve. Thus, two replicate zooplankton samples were taken, each integrating spatial variation in the pond. Total sample volume varied among ponds and ranged between 24 and 108 L. Larger sample volumes obtained in a subset of the study ponds spanning a range of productivities revealed that sample volumes of 10–24 L were adequate for detecting the majority (>80%) of zooplankton taxa. Zooplankton were preserved in acid Lugol’s solution and later identified to

genus or species, excepting copepods, which were classed as calanoid or cyclopoid. Rotifers were identified to genus or species with the exception of members of the Notommatidae and Proalidae, which were identified to family, and the Bdelloidea, which were identified to the level of Order. Protozoa and copepod nauplii were not counted. In each sample, up to 50 randomly chosen individuals of each taxon were measured to obtain dry mass estimates using published length-mass regressions (McCauley, 1984). Because of low water levels, zooplankton could not be sampled in eight ponds in August.

In addition to zooplankton, several additional biotic and abiotic variables were measured monthly in the ponds. Oxygen concentration, pH and temperature were measured along transects using a Horiba U-10 multi-probe (Horiba Ltd., Kyoto, Japan). Pond water (1.5 L total) was collected at each sample point along the transect using the same samplers used to collect zooplankton, pooled and immediately placed on ice, for later analysis of total phosphorus, total zooplankton, pooled and immediately placed on ice, the transect using the same samplers used to collect zooplankton, pooled and immediately placed on ice.

To explore effects of variable zooplankton composition among ponds, I performed a separate PCA based on the covariance matrix of log10 (x + 1) transformed biomass measures of the major zooplankton groups encountered in the survey (a constant was added because of zero values). I focused on the most frequently occurring groups, averaging biomass over the sample period for each pond. These included Daphnia pulex Leydig, Diaphanosoma brachyurum Liévin, Ceriodaphnia spp., Scapholeberis spp., Bosmina logirostris Müller, Chydorus sphaericus Müller, Alona spp., Pleuroxus spp., calanoid copepods, cyclopoid copepods, rotifers (all taxa combined), and Chaoborus spp. To examine the effect of weak interactors (grazer-resistant algal-prey) on biomass stability, I calculated mean relative abundance of the >35-μm chlorophyll a fraction (calculated as mean >35-μm chlorophyll a divided by mean total chlorophyll a). Relationships between biomass variability (the CV) and explanatory variables were explored using ordinary least squares linear regressions.

Results

A total of 79 zooplankton taxa was encountered in the survey. As predicted by theory, biomass stability increased with zooplankton taxonomic richness. Temporal variation in zooplankton biomass, as measured by the coefficient of variation, was negatively related to mean zooplankton taxonomic richness (Fig. 1; $R^2 = 0.394$, $P = 0.005$).

Principal components analysis of environmental variables generated two PCA axes accounting for 54.2 and 24.1% of variation in the data set. The first PCA axis represented a general productivity gradient with
total phosphorus, total chlorophyll $a$, <35 $\mu m$ chlorophyll $a$ and >35-$\mu m$ chlorophyll $a$ correlating positively and seston C : P and N : P correlating negatively with axis scores (Table 1; $P < 0.05$, Bonferroni adjusted). Oxygen concentration, pH and temperature were negatively correlated with the second PCA axis (Table 1; $P < 0.05$, Bonferroni adjusted).

PCA of zooplankton composition produced a single PCA axis accounting for 51.5% of variation in the data. *Daphnia pulex* and *Chaoborus* were strongly and positively correlated with axis 1 (Table 2). *Diaphanosoma* and *Bosmina* were strongly and negatively correlated with axis 1 (Table 2).

I used multiple linear regressions to explore the effects of mean taxonomic richness, mean relative abundance of >35-$\mu m$ chlorophyll $a$, environmental PCA axes 1 and 2, and zooplankton PCA axis 1 on the CV of total zooplankton biomass. When running the complete regression model, none of the independent variables were significant at the $P < 0.05$ level (all $P > 0.10$), although the entire model was significant at $P = 0.052$ ($R^2 = 0.560$). In both forward and backward stepwise regressions, only mean zooplankton taxonomic richness was retained in the model ($R^2 = 0.394$, $P = 0.005$). The low number of ponds may have limited the power to detect significant relationships. As a precaution, I ran separate linear regressions with each of the explanatory variables. The CV of zooplankton biomass was unrelated to either zooplankton PCA axis 1 ($R^2 = 0.092$, $P = 0.22$) or environmental PCA axis 2 (pH, temperature and oxygen) ($R^2 = 0.001$, $P = 0.91$). The biomass CV decreased with increasing relative abundance of >35-$\mu m$ chlorophyll a (Fig. 2; $R^2 = 0.317$, $P = 0.014$) and tended to decrease with increasing values of environmental PCA axis 1 (pond productivity) (Fig. 3; $R^2 = 0.204$, $P = 0.060$).

**Discussion**

Consistent with model predictions, temporal variation in zooplankton biomass decreased with increasing taxonomic richness. As shown theoretically, numerous mechanisms may underlie this relationship. First, Doak *et al.* (1998) and Tilman *et al.* (1998) showed that

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**Table 1** Results of the PCA of pond environmental variables. Shown are axis loadings.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Axis 1</th>
<th>Axis 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log$_{10}$TP</td>
<td>0.926*</td>
<td>0.029</td>
</tr>
<tr>
<td>Log$_{10}$Total Chl-$a$</td>
<td>0.946*</td>
<td>-0.115</td>
</tr>
<tr>
<td>Log$_{10}$&lt;35-$\mu m$ Chl-$a$</td>
<td>0.912*</td>
<td>-0.214</td>
</tr>
<tr>
<td>Log$_{10}$&gt;35-$\mu m$ Chl-$a$</td>
<td>0.889*</td>
<td>0.055</td>
</tr>
<tr>
<td>Seston C : P</td>
<td>-0.851*</td>
<td>0.180</td>
</tr>
<tr>
<td>Seston N : P</td>
<td>-0.670*</td>
<td>0.426</td>
</tr>
<tr>
<td>pH</td>
<td>-0.457</td>
<td>-0.644*</td>
</tr>
<tr>
<td>Temperature</td>
<td>-0.319</td>
<td>-0.790*</td>
</tr>
<tr>
<td>Oxygen concentration</td>
<td>-0.130</td>
<td>-0.923*</td>
</tr>
</tbody>
</table>

*Variables that were significantly correlated with each axis ($P < 0.05$, Bonferroni adjusted).

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**Table 2** Results of the PCA of log$_{10}$ transformed zooplankton biomass. Shown are axis loadings.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Axis 1</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Daphnia pulex</em></td>
<td>0.786*</td>
</tr>
<tr>
<td><em>Diaphanosoma brachyurum</em></td>
<td>-0.698*</td>
</tr>
<tr>
<td><em>Ceriodaphnia</em></td>
<td>-0.083</td>
</tr>
<tr>
<td><em>Chydorus sphaericus</em></td>
<td>-0.130</td>
</tr>
<tr>
<td><em>Scapholeberis</em></td>
<td>0.007</td>
</tr>
<tr>
<td><em>Bosmina longirostris</em></td>
<td>-0.817*</td>
</tr>
<tr>
<td><em>Alona</em></td>
<td>0.001</td>
</tr>
<tr>
<td><em>Pleuroxus</em></td>
<td>0.003</td>
</tr>
<tr>
<td>Calanoid copepods</td>
<td>-0.327</td>
</tr>
<tr>
<td>Cyclopoid copepods</td>
<td>0.170</td>
</tr>
<tr>
<td>Rotifers</td>
<td>0.016</td>
</tr>
<tr>
<td><em>Chaoborus</em></td>
<td>0.532*</td>
</tr>
</tbody>
</table>

*Variables that were significantly correlated with each axis ($P < 0.05$, Bonferroni adjusted).
Species diversity and biomass stability

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Species richness effects can occur in the absence of competition and species interactions because of statistical averaging or the ‘portfolio effect’. They assumed that temporal variance in biomass of each species i scales with its biomass (mi) as a power function: variancei = cmizi, where c is a constant and z is a scaling factor. In the absence of species interactions and assuming that species fluctuations are independent of one another, the variance of consumer biomass summed across all species in a community is a nonlinear function of species richness (N): Σvariance = cmiziN1−z (for details see Doak et al., 1998; Tilman et al., 1998; Hughes et al., 2002). Hence, summed variances will decrease, and stability will increase, with increasing species richness when z > 1. Using nonlinear regressions, z in my ponds was estimated to be 1.447 (R² = 0.969, P < 0.05) and summed variances were negatively related to taxonomic richness on the log-log scale (Fig. 4; r = −0.484, P = 0.042), indicating that portfolio effects were occurring. This z estimate is similar to previous studies that have shown that z commonly ranges between 1 and 2 (Tilman, 1999).

Strong effects of interspecific competition are well-documented among zooplankton species (reviewed in DeMott, 1989) and are known to occur in a subset of the ponds included in the present investigation (Steiner, 2003b). When analysing temporal covariances of zooplankton species biomass in the study ponds, negative terms were frequent and summed covariances averaged across ponds tended to be

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Fig. 2 The relationship between the temporal coefficient of variation (CV) of total zooplankton biomass and mean relative abundance of chlorophyll a of algae greater than 35 µm in size (the grazer resistant fraction) for all 18 ponds. The 95% confidence interval is shown.

Fig. 3 The relationship between the temporal coefficient of variation (CV) of total zooplankton biomass and environmental PCA axis 1 (increasing pond productivity) for all 18 ponds. The 95% confidence interval is shown.

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Fig. 4 The relationship between the sum of temporal variances in zooplankton biomass (summed across taxa) and mean zooplankton taxonomic richness. The 95% confidence interval is shown.
negative (mean = −0.0024); although covariances averaged across ponds did not differ from zero \( P = 0.872, \text{one-way t-test} \). Negative covariances are indicative of competition effects. Alternatively, negative covariances could be driven by species responding differently to external perturbations (Yachi & Loreau, 1999). Regardless of underlying mechanisms, negative covariances will increase stability of zooplankton communities by reducing net variances in total community biomass. However, in order for such covariances to account for the observed stability-richness relationship (Fig. 1), the sum of covariances must become more negative with increasing species richness. This was not the case in the present data set; no relationship between mean taxonomic richness and summed covariances was apparent among ponds \( r = 0.039, P = 0.877 \). Thus, portfolio effects are a more likely explanation for observed patterns.

One potential criticism of this study is that several zooplankton taxa were not identified to the species level. The measures of taxonomic richness were meant as correlates or indices of true species richness and would fail only if certain taxa were highly speciose. As the majority of zooplankton was identified to a high level of taxonomic resolution (either species or genus), the probability of a strong bias in the data set seems minimal. Of greatest concern are the copepods, in which course levels of identification were used (either calanoid or cyclopoid). However, previous studies that have identified copepods to the level of species in these ponds have consistently found only one species of calanoid copepod and up two species of cyclopoid copepod (J. Shurin, University of British Columbia, personal communication). Hence, it seems unlikely that a finer taxonomic resolution would greatly alter the results. Another potential criticism is that microzooplankton, such as protozoa and small species of rotifers that passed through the sampling sieve, were not included in measures of taxonomic richness. Inclusion of such taxa would affect the results if species richness within these groups varied systematically among the ponds. As I am unable to assess the magnitude of this potential problem, some caution is warranted. Finally, zooplankton sample volumes varied among ponds. Thus, it is possible that rare zooplankton taxa were missed in some samples, potentially confounding species richness effects with a sample size effect. However, in the year following the survey, collector curves comparing the total number of zooplankton taxa encountered with total sample volume were generated for a number of the study ponds spanning a range of productivities. These revealed that sample volumes of 10–24 L were often adequate for detecting the majority (>80%) of zooplankton taxa. Sample volumes collected for the present investigation were all equal to or greater than 24 L. Finally, no relationship between mean zooplankton taxonomic richness and mean sample volume was detected either on the arithmetic scale \( P = 0.33 \), Pearson correlation or logarithmic scale \( P = 0.12 \), Pearson correlation), further indicating that a sampling artefact was unlikely.

Although biomass stability increased with zooplankton taxonomic richness, numerous factors covaried among the study ponds and may have influenced observed variation. Thus, the diversity effect is not the only viable explanatory hypothesis. Regressions showed that temporal stability of biomass increased with increasing relative abundance of grazer-resistant algae (>35-μm chlorophyll a). This observation is qualitatively consistent with recent investigations that have shown that the presence of weak interactors and inedible prey can stabilise community dynamics (Abrams & Walters, 1996; McCann et al., 1998; Bohannan & Lenski, 1999; McCauley et al., 1999). However, enrichment is also thought exert an important destabilising influence on community dynamics, causing stable consumer-resource dynamics to become temporally variable (Rosenzweig, 1971; Gilpin, 1972). My results were consistent with this hypothesis as well; the CV of zooplankton biomass increased (i.e. stability decreased) with increasing system enrichment.

A handful of empirical studies has examined the relationship between species diversity and ecosystem stability. Although there are exceptions, many of these investigations show that the relationship between temporal variability of community-level biomass and species richness is negative (reviewed in Loreau et al., 2002; Schmid, Joshi & Schlaper, 2002). This study provides further evidence that diversity may play an important role in maintaining the temporal stability of aggregate community measures. However, this conclusion must be tempered by the caveat that other environmental variables in the study ponds may have driven the diversity-stability relationship. Making inferences from natural pattern can be problematic as numerous factors commonly covary and exhibit
collinearity among sample sites. In my study system, it is difficult to assess the relative importance of potential driving mechanisms. While one of the above-named factors (taxonomic richness, productivity, or the prevalence of grazer resistant algae) may have been the true mediator of biomass stability, it is also possible that all three interacted to generate observed variability. Only direct experimental manipulations in conjunction with proper control of extraneous environmental factors will offer stronger insights.

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References


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