

# Predation Alters Relationships between Biodiversity and Temporal Stability

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**ABSTRACT:** Ecologists disagree on how diversity affects stability. At the heart of the controversy is the relationship between diversity and population stability, with conflicting findings from both theoretical and empirical studies. To help reconcile these results, we propose that this relationship may depend on trophic complexity, such that positive relations tend to emerge in multitrophic but not single-trophic communities. This hypothesis is based on the premise that stabilizing weak trophic interactions restrain population oscillations associated with strong trophic interactions in diverse multitrophic communities. We tested this hypothesis using simple freshwater bacterivorous protist communities differing in diversity with and without a predatory protist species. Coupling weak and strong trophic interactions reduced population temporal variability of the strong-interacting species, supporting the stabilizing role of weak interactions. In keeping with our hypothesis, predation altered the overall effect of diversity on population temporal stability and, in particular, caused a reversal of the diversity-stability relationship (negative without predators and positive with predators) for the strong-interacting species. A similar role of predation was also observed when examining the relationship between diversity and temporal stability of community biomass. Together, these findings demonstrated strong interactive effects of trophic interactions and diversity on temporal stability of population and community properties.

**Keywords:** diversity, interaction strength, stability, temporal variability, weak interaction effect.

## Introduction

During the past 2 decades, ecologists have devoted considerable effort into understanding the relationship between biodiversity and ecosystem functioning (Kinzig et al. 2002; Loreau et al. 2002; Hooper et al. 2005; Balvanera et al. 2006). One active area of this research has aimed to elucidate the role of biodiversity for stability, particularly temporal stability, of population and community properties. Current evidence suggests possibly different diver-

sity-temporal stability patterns at different levels of ecological organization. At the community or ecosystem level, theory (Yachi and Loreau 1999; Ives and Hughes 2002; Thebault and Loreau 2005) and most empirical studies (McNaughton 1977; Dodd et al. 1994; Tilman 1996; McGrady-Steed and Morin 2000; Valone and Hoffman 2003a; Caldeira et al. 2005; Steiner et al. 2005; Romanuk et al. 2006; Tilman et al. 2006; Vogt et al. 2006; Zhang and Zhang 2006; van Ruijven and Berendse 2007; but see Petchey et al. 2002; Gonzalez and Descamps-Julien 2004; Morin and McGrady-Steed 2004; France and Duffy 2006; Zhang and Zhang 2006) indicate a positive diversity effect on temporal stability, often attributed to several community-level stabilizing mechanisms (sensu Cottingham et al. 2001). On the other hand, accompanying inconsistent theoretical predictions on the relationship between diversity and temporal stability at the population level (May 1973; De Angelis 1975; Lehman and Tilman 2000; Li and Charnov 2001; Brose et al. 2006), empirical studies have documented various relationships between the two: positive (Kolasa and Li 2003; Valone and Hoffman 2003b; Romanuk and Kolasa 2004; Romanuk et al. 2006; Vogt et al. 2006), neutral (McGrady-Steed and Morin 2000; Romanuk and Kolasa 2002; Steiner et al. 2005), and negative (Tilman 1996; Gonzalez and Descamps-Julien 2004; Tilman et al. 2006; van Ruijven and Berendse 2007). These discrepancies regarding population-level stability, coupled with the fact that little is known about mechanisms behind the different patterns among empirical studies, add further controversy to the long-standing debate on the relationship between diversity and stability (Elton 1927, 1958; MacArthur 1955; May 1973; McNaughton 1977; King and Pimm 1983; McCann 2000). As a mechanistic understanding of different diversity-stability patterns may hold the key to resolve the debate, it is imperative for experiments to move beyond depicting patterns—the main focus of existing experiments—to elucidate mechanisms influencing diversity-stability relationships.

One factor that has the potential to influence diversity-

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stability relationships is trophic interactions. Trophic interactions are often thought to be destabilizing and believed to be responsible for many striking population cycles observed in nature (Turchin 2003). Theory suggests, however, that weak trophic interactions may act to stabilize diverse communities (McCann et al. 1998; McCann 2000). According to this idea, populations in diverse food webs can attain greater temporal stability than those in depauperate webs, when sufficiently weak trophic links are present in diverse webs to dampen large population oscillations caused by strong trophic links (termed the weak interaction effect; McCann et al. 1998; McCann 2000). Besides the positive influence on population stability, this weak interaction effect may also lead to more divergent population dynamics (i.e., increased negative covariance) among species sharing predators (McCann 2000), thereby potentially contributing directly to greater community stability. In apparent agreement with this idea, natural communities, generally diverse yet apparently stable, typically exhibit skewed interaction strength distributions toward weak interactions (Paine 1992; de Ruiter et al. 1995; Raffaelli and Hall 1996; Wootton 1997). However, direct experimental evidence for the stabilizing role of weak trophic interactions remains virtually nonexistent.

If weak trophic interactions are indeed important for stabilizing diverse multitrophic communities, we might expect potentially different diversity-stability relationships in single- and multitrophic systems. Specifically, because trophic interactions are absent in single-trophic communities and more weak trophic interactions are present in more diverse multitrophic communities, positive relationships may be more likely to emerge in multitrophic than in single-trophic communities. Consistent with this hypothesis, almost all multitrophic empirical studies have reported either positive or neutral effects of diversity on population temporal stability (but see Gonzalez and Descamps-Julien 2004), contrasting with most single-trophic studies reporting negative diversity effects on population temporal stability (but see Valone and Hoffman 2003b). These findings, however, are based on observations (e.g., Valone and Hoffman 2003b), experiments that manipulated diversity in solely single-trophic systems (e.g., Tilman et al. 2006), or experiments manipulating diversity in solely multitrophic systems (e.g., Steiner et al. 2005). Rigorous experimental tests of the hypothesis, which would involve comparing diversity-stability relationships of the same communities with and without trophic interactions, are lacking.

Here, we report on a simple laboratory protist microcosm experiment that tested the above hypothesis. By manipulating the presence/absence of a predatory protist species and diversity of its bacterivorous protist prey community, we show that the relationship between prey

diversity and biomass temporal stability in the presence of predators differed from that in the absence of predators at both population and community levels. In particular, the presence of weak trophic interactions in more diverse communities stabilized population dynamics of the prey species strongly interacting with the predator, turning a negative diversity–population stability relationship without predators into a positive relationship with predators for the species.

## Material and Methods

### *Experimental Organisms*

Experimental organisms were freshwater ciliated protists, whose short generation times enabled us to collect multigenerational population dynamics essential for rigorous assessments of population and community stability (Connell and Sousa 1983). A total of four ciliated protist species were used, including one predatory ciliate (*Lacrymaria olor*) and three bacterivorous ciliates (*Colpidium striatum*, *Halteria grandinella*, and *Tetrahymena pyriformis*). All the species, including *Lacrymaria*, had generation times of <1 day under the initial conditions of the experiment (i.e., with abundant food resources). Feeding trials indicated that *Lacrymaria* was able to subsist on each of the three bacterivorous species alone or in any combination. Before the experiment, each bacterivore was cultured on a bacterial mixture consisting of *Bacillus cereus*, *Bacillus subtilis*, and *Serratia marcescens*; the same bacteria were used in the experiment. Note that our focus was on the manner in which interactions between bacterivorous and predatory protists affect the relationship between diversity and temporal stability of bacterivorous protists. This examination was facilitated by the fact that interactions of bacterivorous protists and the multispecies bacterial assemblage did not produce conspicuous protist population oscillations (see “Results”).

### *Experimental Design*

We used a two-way full factorial design, with the two factors being the absence/presence of the predator *Lacrymaria* (control and predation) and bacterivorous protist species diversity (one, two, or three species). By using a relatively small diversity gradient, this design traded off realism to allow the examination of mechanisms that may be difficult to investigate in more diverse communities. This small gradient allowed us to include every possible species composition at each diversity level: three one-species compositions (*Colpidium* [c], *Halteria* [h], and *Tetrahymena* [t]), three bispecies compositions (*Colpidium* + *Halteria* [ch], *Colpidium* + *Tetrahymena* [ct], and *Halteria* + *Tetrahymena*

[ht]), and one trispecies composition (*Colpidium* + *Halteria* + *Tetrahymena* [cht]). We replicated each treatment combination four times, for a total of 56 microcosms (7 compositions  $\times$  2 predation treatments  $\times$  4 replicates).

#### Microcosm Setup and Sampling

Microcosms consisted of 250-mL screw-capped glass bottles maintained in incubators without light at 22°C. After autoclaving, each microcosm was filled with 100 mL aqueous medium that supported the growth of bacteria. Each microcosm also received two organic, autoclaved wheat seeds as an additional carbon source. The medium, which contained 0.55 g of protozoan pellet (Carolina Biological Supply Company, Burlington, NC) per 1 L of deionized water, was autoclaved and inoculated with the three bacterial species (*B. cereus*, *B. subtilis*, and *S. marcescens*). Approximately 100 individuals of each bacterivore were added to their respective microcosms 24 h after bacterial inoculation. Ten *Lacrymaria* individuals were added into each predation microcosm 12 days after the inoculation of bacterivores. Inoculations were staggered this way so that bacterivores and predators had abundant food resources on introduction. The first sampling took place 5 days after *Lacrymaria* introduction, which was designated as day 0 of our experiment. The experiment ran for 23 days afterward, during which time microcosms functioned as semicontinuous systems, with 10% medium replacement performed each week.

We sampled microcosms every 2 or 3 days to monitor protist population dynamics. Sampling involved withdrawing ~0.35 mL medium from each microcosm and counting the number of individuals of each protist species in the samples (or diluted samples in cases of dense populations) with a stereoscopic microscope. To estimate protist body size (biovolume), we measured dimensions of 10 randomly selected individuals of each bacterivorous species with a compound microscope. Individual biovolume was calculated using appropriate formulas by Wetzel and Likens (2000).

#### Data Analysis

To answer the question of how *Lacrymaria* predation influences the diversity-stability relationship of its protist prey community, our analysis necessarily focused on the dynamics of bacterivorous protist species (for *Lacrymaria* population dynamics, see fig. A1 in the online edition of the *American Naturalist*). We calculated population biovolumes of each bacterivorous protist species by multiplying its population density (recorded as number of individuals/mL + 1 for later log transformation) by its mean individual biovolume, and we calculated community bio-

volumes of bacterivorous protists by summing population biovolumes of component species in the community. We used the standard deviation of log-transformed values of biovolume ( $SD [\log_{10} (\text{biovolume})]$ ) as the metric of temporal variability: the smaller the temporal variability, the greater the temporal stability. This metric yields similar information as coefficient of variation of untransformed biovolume data ( $CV [\text{biovolume}]$ ), but compared with CV, it tends to be less affected by skewed distributions (McArdle et al. 1990); results based on the two metrics were qualitatively similar. For each bacterivorous species, we estimated the strength of its interaction with *Lacrymaria* as the ratio of its population temporal variability in the corresponding *Lacrymaria*-present predation and *Lacrymaria*-free control treatments (i.e., those that contained no other bacterivores). This metric is most relevant for our investigation of population dynamics and stability, and it yielded similar results to the log response ratio of population densities, one of the most frequently used metrics of interaction strength (Berlow et al. 2004), measured after day 4 of our experiment (i.e., after predators started to limit prey abundance; see fig. B1 in the online edition of the *American Naturalist*). We calculated temporal variability using both undetrended data and linearly detrended data but reported only results based on the undetrended data, since the two approaches produced similar results. In six predation microcosms (2 c, 2 h, and 2 ch), *Lacrymaria* failed to establish (likely as a result of demographic stochasticity), and we excluded data from these microcosms from statistical analyses. Two control microcosms (1 ct and 1 t) were also excluded as a result of unexpected species extinction and human error, respectively.

We used ANOVA to test for differences among bacterivorous species in the strength of their interactions with *Lacrymaria*, with significant differences followed by a Tukey's HSD test for multiple comparisons. We used ANCOVA to test for the effect of predation and species diversity on temporal variability, with the presence/absence of *Lacrymaria* as the categorical variable, and bacterivore diversity as the continuous variable. A significant interaction between the two variables would indicate that predation altered the effect of diversity on temporal variability. In addition to ANCOVA, we also performed separate linear regressions for the control and predation treatments to delineate the trend of the diversity-variability relationship within each treatment. These analyses were done for population temporal variability at the species level, average-across-species population temporal variability at the microcosm level, and community temporal variability at the microcosm level. To assess potential community-level stabilizing mechanisms at work, we examined how summed variances and covariances of protist population biovol-

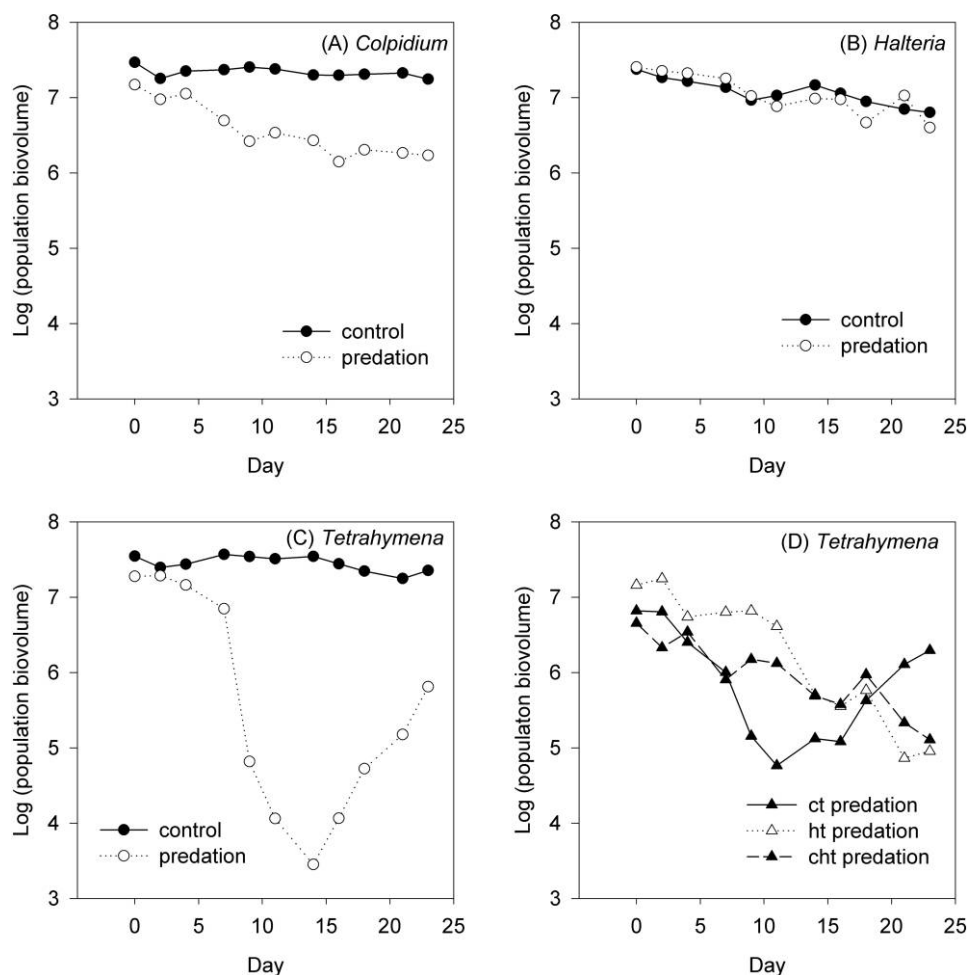
umes and average (over time) total protist community biovolumes changed with diversity, again using ANCOVA and linear regressions. All analyses were done with log-transformed biovolume data.

### Results

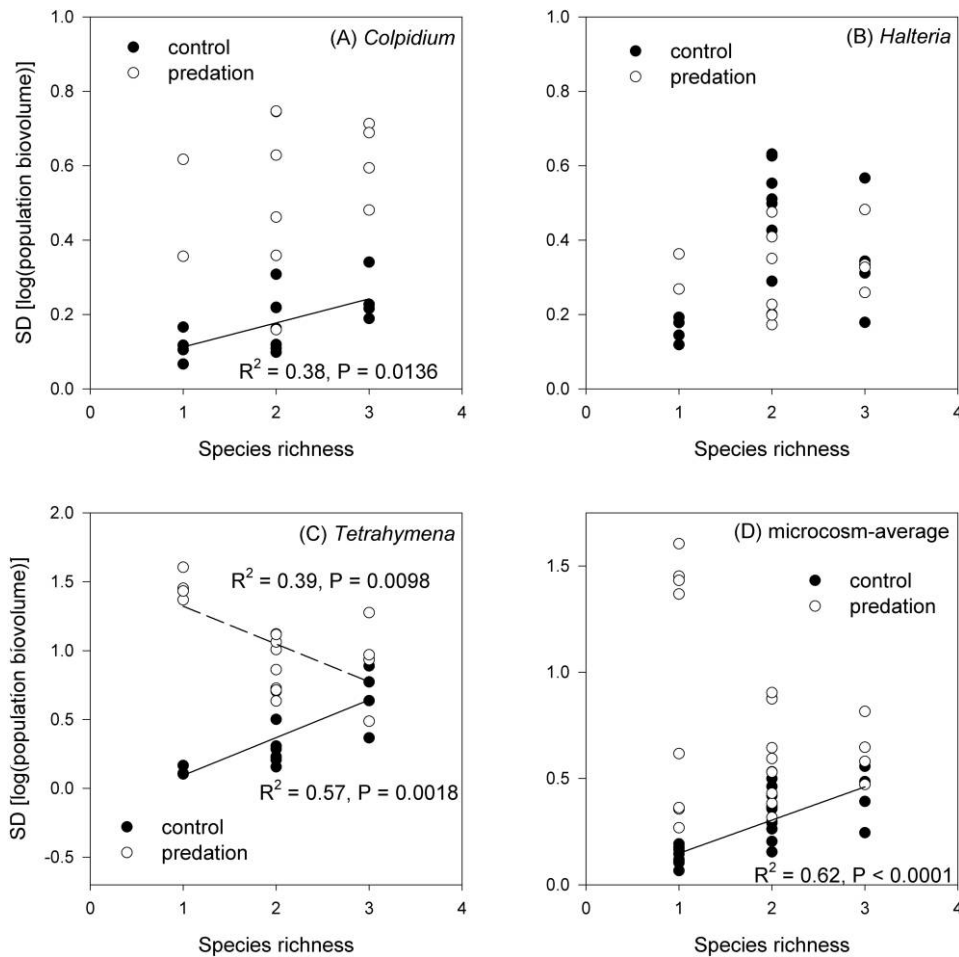
In the absence of *Lacrymaria*, *Colpidium*, *Halteria*, and *Tetrahymena* showed similar population dynamics that lacked large-magnitude fluctuations (fig. 1A, 1B, 1C). The three species, however, exhibited quite different dynamics when interacting with *Lacrymaria*. *Colpidium* abundance declined and temporal variability increased modestly in the presence of *Lacrymaria* (figs. 1A, 2A). *Lacrymaria* predation, however, appeared to have little, if any, effect on

*Halteria* (figs. 1B, 2B). By contrast, *Lacrymaria* caused large oscillations in *Tetrahymena* abundance over several orders of magnitude (figs. 1C, 2C). Accordingly, ANOVA revealed a significant species effect on interaction strength ( $F = 79.47$ ,  $df = 2, 5$ ,  $P = .0002$ ), with *Tetrahymena* demonstrating significantly stronger interactions with *Lacrymaria* than *Colpidium* and *Halteria* (fig. 3; Tukey's HSD test).

The manner in which *Lacrymaria* predation influenced the relationship between diversity and population temporal variability differed among the three bacterivores. Population variability of *Colpidium* increased with diversity in the absence of *Lacrymaria* (fig. 2A; table C1 in the online edition of the *American Naturalist*) but was unaffected by diversity in the presence of *Lacrymaria* (fig. 2A; table C1). ANCOVA, however, failed to detect an inter-



**Figure 1:** Population dynamics of *Colpidium* (A), *Halteria* (B), and *Tetrahymena* (C, D) from representative replicates. Log-transformed biovolumes were originally measured as  $\mu\text{m}^3/\text{mL}$ . In A–C, filled circles denote the predation-free controls, and open circles denote the predation treatment. In D, solid lines represent the predation treatment with *Colpidium* and *Tetrahymena* (ct) as the prey, dotted lines represent the predation treatment with *Halteria* and *Tetrahymena* (ht) as the prey, and dashed lines represent the predation treatment with *Colpidium*, *Halteria*, and *Tetrahymena* (cht) as the prey.

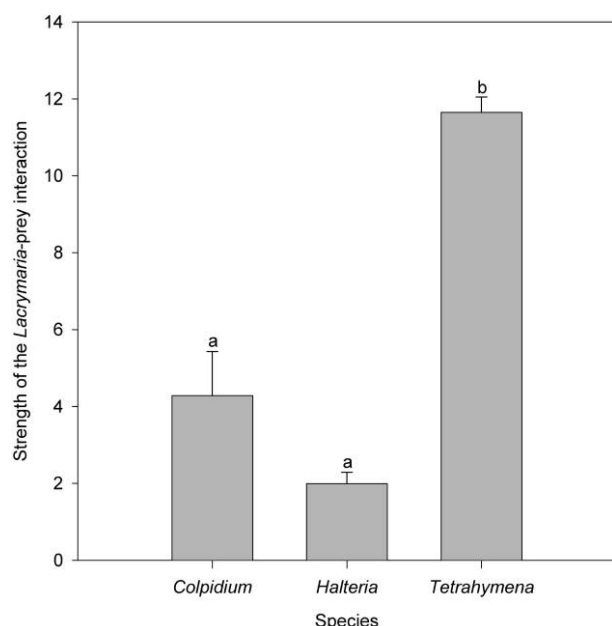


**Figure 2:** Population temporal variability, measured as standard deviation of log-transformed population biovolume, as a function of species richness of the bacterivorous protist community. Log-transformed biovolumes were originally measured as  $\mu\text{m}^3/\text{mL}$ . A, *Colpidium*. B, *Halteria*. C, *Tetrahymena*. D, Microcosm average (averaged across species). Solid lines are linear regression lines for the controls (filled circles), and dashed lines are regression lines for the predation treatment (open circles). Only statistically significant regression lines are shown.

active effect of predation and diversity (table C2). Population variability of *Halteria* showed little response to changes in diversity, regardless of the presence/absence of *Lacrymaria* (fig. 2B; tables C1, C2). In contrast, *Lacrymaria* predation changed the diversity–population variability relationship for *Tetrahymena* (significant predation  $\times$  diversity term in ANCOVA; table C2). While population variability of *Tetrahymena* increased with diversity when *Lacrymaria* was absent (fig. 2C; table C1), it decreased with diversity when *Lacrymaria* was present (fig. 1C, 1D; fig. 2C; table C1). When averaged across species, population temporal variability was again an increasing function of diversity when *Lacrymaria* was absent (fig. 2D; table C3) but was not a significant function of diversity when *Lacrymaria* was present (table C3), again resulting in a sig-

nificant predation  $\times$  diversity term in ANCOVA (table C4).

The relationship between diversity and temporal variability of total community biovolumes also depended on the presence/absence of predators (significant predation  $\times$  diversity term in ANCOVA; table C5). Increasing diversity reduced community variability when *Lacrymaria* was present but had no effect on community variability when *Lacrymaria* was absent (fig. 4; table C6). When examining possible mechanisms leading to this pattern, we found that predation did not modify the effect of diversity on summed variances (fig. 5A; tables C7, C8) but led to increased summed covariances (fig. 5B) and total community biovolumes (fig. 5C; table C9) with diversity, contrasting with no effect of diversity on summed covariances



**Figure 3:** Strength of interactions between *Lacrymaria* and *Colpidium*, *Halteria*, and *Tetrahymena*. Different letters indicate significant differences in a Tukey's HSD test at a significance level of 0.05. Error bars represent +SE.

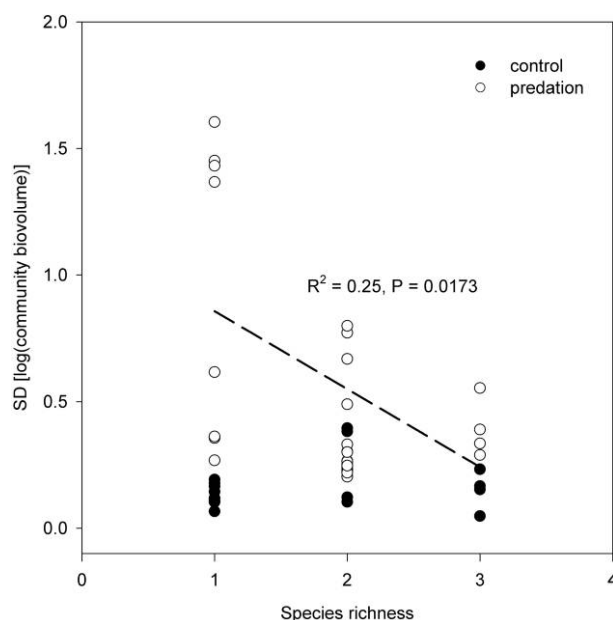
(fig. 5B; significant predation  $\times$  diversity term in ANOVA; table C7) and total community biovolumes (fig. 5C; table C9; significant predation  $\times$  diversity term in ANCOVA; table C7) in the controls. Because greater community-level stability entails reduced summed variances, reduced summed covariances, or increased total community biovolume, these data indicated that the positive diversity–community stability relationship in the predation treatment arose primarily from the overyielding effect (the increase of community biomass with increasing species diversity).

### Discussion

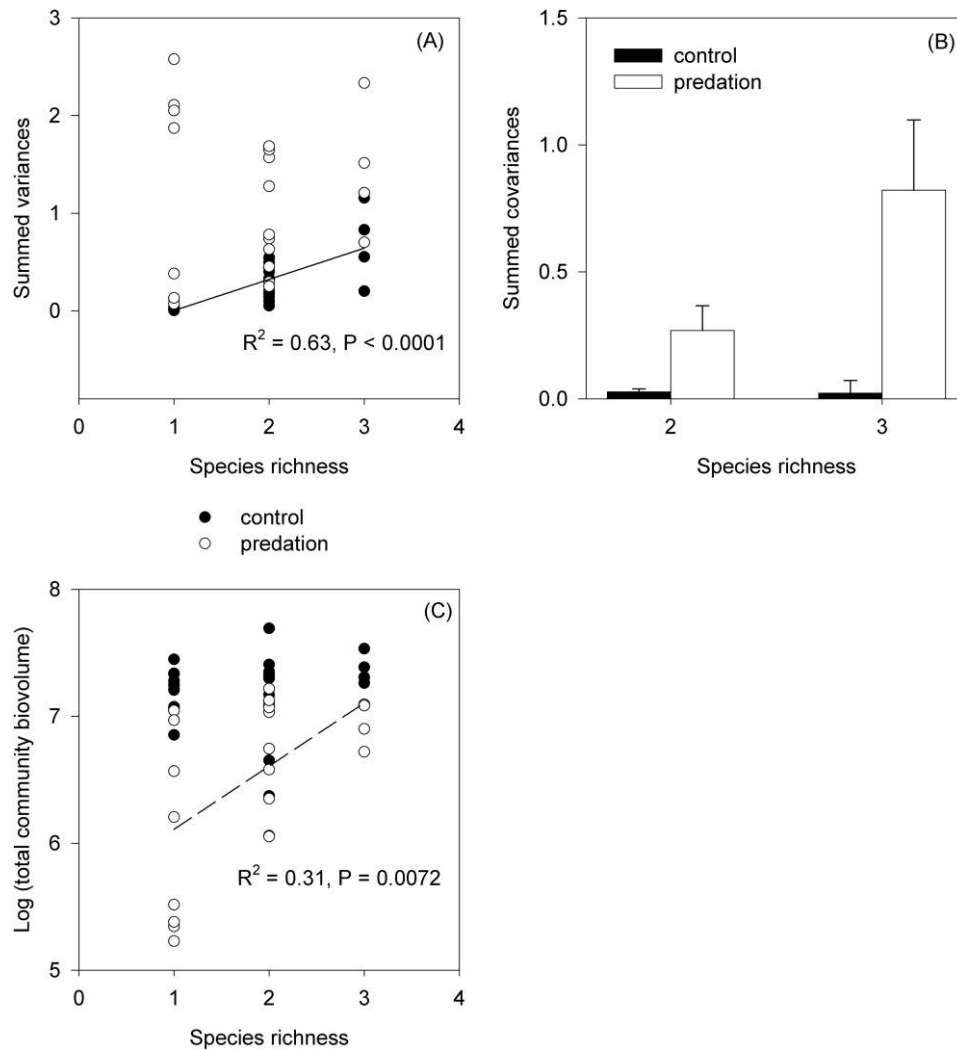
The question of how diversity influences stability has interested ecologists since early last century (Elton 1927, 1958; MacArthur 1955; May 1973; McNaughton 1977) and remains a topic of contention (McCann 2000; Ives and Carpenter 2007). The presence of multiple concepts of stability (Pimm 1984; McCann 2000; Ives and Carpenter 2007) and potentially different diversity–stability relationships at different levels of ecological organization (May 1973; King and Pimm 1983; Tilman 1996) have contributed to historical controversy surrounding this issue. However, recent diversity–stability studies, which are not plagued by these complications, still produced mixed

results. To help resolve this issue, we propose that the diversity–stability relationship may take possibly different forms in single- and multitrophic communities. Consistent with this hypothesis, our experiment shows that predation altered the effects of diversity on both population- and community-level temporal stability.

Our experiment provided compelling evidence for the weak interaction effect (McCann et al. 1998; McCann 2000). *Tetrahymena*, the species that demonstrated the strongest interaction with *Lacrymaria* among the three bacterivores, exhibited large population cycles while being the only prey of *Lacrymaria* (fig. 1C). When coupled with weaker *Lacrymaria*–*Colpidium* and/or *Lacrymaria*–*Halteria* interactions in more diverse communities, the *Lacrymaria*–*Tetrahymena* interaction appeared weakened, causing *Tetrahymena* populations to oscillate with considerably smaller magnitude (fig. 1D). This result contrasts sharply with the finding of another microcosm experiment that adding more bacterivorous protist species in the presence of a protist predator destabilized population dynamics (Luckinbill 1979). Luckinbill's (1979) experiment, however, was based on a system in which all bacterivorous species interacted strongly with the predator, hence supporting predictions of classic food web models that did



**Figure 4:** Community temporal variability, measured as the standard deviation of log-transformed total community biovolume, as a function of species richness of the bacterivorous protist community. Log-transformed biovolumes were originally measured as  $\mu\text{m}^3/\text{mL}$ . The dashed line represents the linear regression line for the predation treatment (open circles). The regression model for the control treatment (filled circles) was not statistically significant.



**Figure 5:** Summed variances (A), summed covariances (B), and average (over time) total community biovolumes (C) as a function of species richness of the bacterivorous protist community. Log-transformed biovolumes were originally measured as  $\mu\text{m}^3/\text{mL}$ . Solid lines are linear regression lines for the controls (filled circles), and dashed lines are regression lines for the predation treatment (open circles). Only statistically significant regression lines are shown. In B, error bars represent  $\pm$ SE.

not specifically consider the role of weak trophic interactions (May 1973). These results thus lend support to the idea that weak interactions may play a pivotal role in stabilizing diverse natural communities (McCann et al. 1998; McCann 2000), which typically contain many weak interactions and few strong interactions (Paine 1992; de Ruiter et al. 1995; Raffaelli and Hall 1996; Wootton 1997). We suspect that this weak interaction effect may be particularly strong in aquatic ecosystems, where fast biomass turnover and strong top-down control (Shurin et al. 2006) offer ample opportunities for abundant strong interactions to be buffered by much more abundant weak interactions. Note that the weak interaction effect may have also op-

erated in the bacteria-bacterivore subsystem of the three-trophic-level food webs that we studied. Our experiment indicated that all the bacterivores maintained relatively stable dynamics when interacting with the multispecies bacterial assemblage. Results from a separate experiment, however, showed that several bacterivorous protist species, including *Tetrahymena*, showed strongly oscillatory dynamics when *Serratia* was available as the only prey bacterium (L. Jiang, unpublished data). A plausible scenario is that weak interactions between bacterivorous protists and other bacteria may have prevented population oscillations associated with strong protist-*Serratia* interactions in our experiment. Further experimentation would be nec-

essary to confirm this proposition. Finally, it is noteworthy that the weak interaction effect may also operate at the within-species level. As an example, similar to what we found here, Yoshida et al. (2003, 2007) showed that the interactions of multiple clones of an algal species with a rotifer produced more stable dynamics than the interactions of a single algal clone with the rotifer.

Theory suggests that increasing diversity tends to reduce population stability in competitive communities (Lehman and Tilman 2000). The few single-trophic experiments, all conducted in plant communities, supported this prediction (Tilman et al. 2006; van Ruijven and Berendse 2007). In our experiment, two of the three bacterivorous protist species showed reduced population stability with increasing diversity in the absence of predators (a similar but nonsignificant trend holds for the other species; table C1), and average population stability showed the same pattern. Our results may thus be considered as supporting negative diversity–population stability relationships in competitive communities. We note, however, that competition for biotic resources (e.g., bacteria in our experiment) may not always be treated the same as competition for abiotic resources (e.g., plants competing for soil nutrients). In particular, consumer–resource interactions based on biotic resources, but not those based on abiotic resources, can produce population oscillations. Here, potential complications associated with this difference have been avoided by the stable interactions between protists and the multispecies bacterial assemblage. Indeed, stable protist–bacteria interactions have made it possible to model competition between bacterivorous protists using simple Lotka–Volterra models, without explicitly considering bacterial dynamics (Gause 1934; Vandermeer 1969; Jiang and Morin 2004).

In contrast to the negative diversity effect on population stability in the controls, diversity did not affect average population stability in the predation treatment. This pattern was strongly influenced by the weak interaction effect, which led to a reversal of the diversity–stability relationship (i.e., negative without predators and positive with predators) for the species strongly interacting with the predator. While obtained for simple laboratory communities, these results may possibly apply to more diverse natural communities, given that both are characterized by more weak than strong interactions. The stabilizing role of weak trophic interactions also provides a plausible explanation for the positive (Kolasa and Li 2003; Romanuk and Kolasa 2004; Romanuk et al. 2006; Vogt et al. 2006) and neutral (McGrady-Steed and Morin 2000; Romanuk and Kolasa 2002; Steiner et al. 2005) diversity–average population stability relationships reported for more diverse multitrophic communities. Some of these studies also reported the relationship between diversity and population temporal stability at the individual species level, which may sometimes

differ from the relationship between diversity and average-across-species population temporal stability (e.g., Romanuk et al. 2006; Vogt et al. 2006). In a microcosm experiment using multitrophic rock pool invertebrate communities, for instance, Vogt et al. (2006) showed that whereas population stability of seven species and average population stability increased with diversity, two species showed little change in stability with diversity. One possible explanation for this pattern, based on our experiment, is that the relationship at the species level is linked to the strength of trophic interactions. Species characterized by strong trophic interactions may be more likely to exhibit positive relationships as a result of the weak interaction effect (e.g., *Tetrahymena* in our experiment), whereas those characterized by weak interactions may be more likely to exhibit nonpositive relationships (e.g., *Colpidium* and *Halteria* in our experiment). Quantifying the strength of interactions among species, in addition to their stability, will be necessary for future experiments to further test this hypothesis.

Although theory and most experimental studies support a positive effect of diversity on temporal stability of competitive communities (e.g., Ives and Hughes 2002; Tilman et al. 2006), diversity did not influence community stability in the controls. While uncommon, this lack of diversity effect on community stability has previously been reported (Petchey et al. 2002; Zhang and Zhang 2006). When examining potential contributing community-level mechanisms, we found that summed covariances and total community biovolumes changed little with diversity and that summed variances in fact increased with diversity (fig. 5). Note that increased summed variances with diversity, largely driven by the increased population variability with diversity (correlation coefficient between summed variances and average population variability = 0.92), do not necessarily mean that the portfolio effect (the statistical phenomenon that aggregate properties of several variables may be less variable than any single variable; Tilman et al. 1998) was absent. The slope of the mean-variance relations in the controls was in fact 1.47, indicating that the portfolio effect did operate to stabilize community biomass. The destabilizing diversity effect on populations apparently overrode the stabilizing portfolio effect on communities, resulting in increased summed variances with diversity (see also Petchey et al. 2002).

Unlike the predator-absent controls, increasing diversity had a positive effect on community stability in the predation treatment. Also unlike the controls, summed variances were not an increasing function of diversity, and both summed covariances and total community biovolume became increasing functions of diversity in the presence of predators (fig. 5). These community-level mechanisms are again linked to the weak interaction effect. First,



the weak interaction effect reduced the magnitude of population fluctuations of the strong-interacting species in diverse communities; this, along with the portfolio effect (slope of the mean-variance relation = 1.16), helped neutralize the diversity–summed variances relationship. Second, by preventing large population declines, the weak interaction effect effectively increased community biomass in multispecies communities relative to the monocultures of the strong-interacting species. Note that this mechanism cannot be completely separated from the potentially positive effect of predator-mediated nutrient recycling on prey biomass (De Angelis 1992). The increased community biomass with diversity resulted in the overyielding effect as the primary cause of the positive diversity–community stability relationship in the predation treatment. The increased covariances at high diversities, however, ran counter to the idea that the weak interaction effect may lead to increasingly negative covariances (McCann 2000). McCann's (2000) prediction, however, was based on the assumption that predators practice optimal foraging strategies involving prey switching. It is possible that the single-celled protist predator in our experiment did not adopt this practice, causing similar density responses of different prey species to predation.

### Conclusions

This study demonstrates that the form of the diversity–temporal stability relationship at both population and community levels depended on system trophic complexity. Variation in the trophic complexity of ecological communities in which studies are conducted may thus provide a possible explanation for conflicting empirical findings on the diversity–temporal stability relationship. Equally important, this study demonstrated the importance of weak trophic interactions for stabilizing population and community dynamics, lending support to the idea that weak interactions may act as the “glue” that holds diverse natural communities together (McCann et al. 1998). In our experiment, predation altered the effect of diversity on stability because it brought more weak interactions that mitigated impacts of strong interactions to more diverse multitrophic communities. The same logic can potentially explain the nonnegative diversity–population stability relationships often reported for more speciose multitrophic systems. We recognize that this study represents only an initial attempt to understand the role of trophic interactions on diversity-stability relationships using a simple laboratory system, and we encourage more experiments to be conducted in a variety of natural systems to test the generality of this result. A particularly interesting but rarely experimentally explored question is how predator diversity (compared with prey diversity studied here) influences

ecological stability. Answers to this question carry significant implications for understanding the consequences of the scenario of predators generally experiencing greater extinction risks than their prey (Purvis et al. 2000).

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