

ENVIRONMENTAL FLUCTUATIONS INDUCE SCALE-DEPENDENT COMPENSATION AND INCREASE STABILITY IN PLANKTON ECOSYSTEMS

AMY L. DOWNING,¹ BRYAN L. BROWN,² ELIZABETH M. PERRIN,¹ TIMOTHY H. KEITT,³ AND MATHEW A. LEIBOLD^{3,4}

¹*Department of Zoology, Ohio Wesleyan University, Delaware, Ohio 43015 USA*

²*Department of Forestry and Natural Resources, Clemson University, Clemson, South Carolina 29634 USA*

³*Section of Integrative Biology, University of Texas, 1 University Station C0930, Austin, Texas 78712 USA*

Abstract. The temporal stability of aggregate community and ecosystem properties is influenced by the variability of component populations, the interactions among populations, and the influence of environmental fluctuations on populations. Environmental fluctuations that enhance population variability are generally expected to destabilize community and ecosystem properties, but this will depend on the degree to which populations are synchronized in their dynamics. Here we use seminatural experimental ponds to show that reduced synchrony among zooplankton taxa increases the temporal stability of zooplankton density, abundance, and ecosystem productivity in fluctuating environments. However, asynchrony only occurs at long timescales (~80-day periods) and under recurring environmental perturbations. At shorter timescales (~10-day periods) and in constant environments, synchronous dynamics dominate. Our findings support recent theory indicating that compensatory dynamics can stabilize communities and ecosystems. They further indicate that environmental fluctuations can enhance the likelihood of long-period asynchrony and thus stabilize community and ecosystem properties despite their short term destabilizing effects.

Key words: *compensatory dynamics; ecosystem processes; food web dynamics; mesocosm; phytoplankton; stability; synchrony; wavelet analysis; zooplankton.*

INTRODUCTION

Community and ecosystem stability is largely dependent on the population dynamics of species that make up communities. Species populations can be highly variable through time in nature, influenced by both internal food web interactions and external environmental fluctuations (Ives and Cardinale 2004, Thébault and Loreau 2006). As such, variable populations can lead to more variable community and ecosystem properties. However, the degree to which these properties become destabilized may depend on the degree to which species oscillations through time are synchronous vs. compensatory (Micheli et al. 1999, Cottingham et al. 2001). Recent theoretical models of community dynamics indicate that species which show compensatory dynamics (or vary asynchronously) can stabilize ecosystems if the compensating species have similar functional roles (Doak et al. 1998, Tilman et al. 1998, Ives et al. 1999, Yachi and Loreau 1999, Ives and Cardinale 2004). Thus determining how population dynamics influence community and ecosystem dynamics requires knowing how various factors influence both the variability of

individual populations and the degree of compensation among populations.

Theory suggests that environmental fluctuations may be important for determining both the variability of individual populations and the relative degree of compensation (Ives et al. 1999, Thébault and Loreau 2005, Gonzalez and De Feo 2007). Environments experiencing fluctuations in an abiotic factor such as temperature might expect to have higher individual species variability which could destabilize populations and communities, particularly if most species respond synchronously to the fluctuations (Houlahan et al. 2007). But, if some species are more sensitive to such abiotic fluctuations and they compete strongly with less sensitive species, biotic interactions among species may facilitate asynchronous or even compensatory dynamics (Ives et al. 1999, Micheli et al. 1999, Descamps-Julien and Gonzalez 2005, Thébault and Loreau 2005). Similarly, environments experiencing fluctuations in an environmental variable such as a resource might increase species variability, but biotic interactions such as competition for resources or consumer-resource interactions may facilitate compensatory dynamics among some species (Micheli et al. 1999). Thus, patterns of synchrony and compensation will involve both the direct species responses to environmental fluctuations, and more indirect mechanisms mediated, for example, through biotic or trophic interactions (Thébault and

Manuscript received 11 October 2007; revised 1 February 2008; accepted 13 March 2008. Corresponding Editor: B. E. Kendall.

⁴ Corresponding author.
E-mail: mleibold@mail.utexas.edu

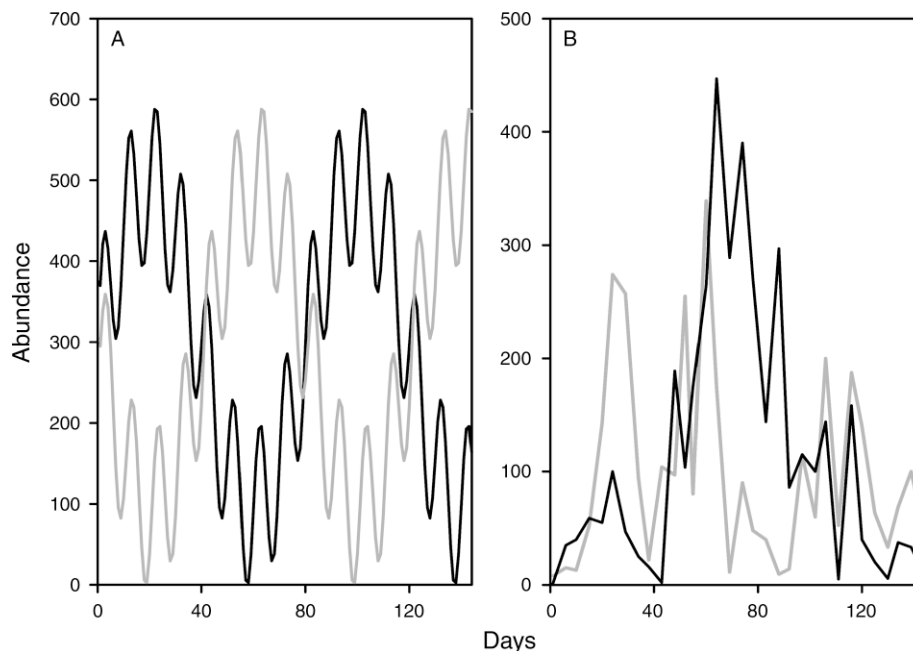


FIG. 1. (A) Simulated data demonstrating how compensatory dynamics can occur on some timescales while synchrony dominates at other scales. The two time series were created by adding together two simple sine functions of differing periods (period = $1/\text{frequency}$), and both time series have dominant frequency components with periods of 10 days and 80 days. At 10-day periods, the two series are perfectly synchronous (positively correlated); however, the two series show strong compensatory dynamics (negative correlation) at 80-day periods. (B) An example of timescale-dependent compensation involving *Scapholebris* (gray) and *Daphnia* (black) from one of our nutrient-pulsed environment mesocosms. Short-term changes in abundances are synchronous between the two zooplankton species, but changes in abundance at longer temporal scales are offset. Wavelet analysis confirms that, like the simulated series, *Scapholebris* and *Daphnia* were indeed synchronous at timescales of ~ 10 days, and showed compensation at timescales of ~ 80 days.

Loreau 2005). These indirect mechanisms are likely to be complex since there can be numerous pathways for such indirect effects to affect a given group of species and each of these may have different lags in the response of the organisms involved. For example, Greenman and Benton (2005) show that the particular effects of environmental fluctuations on compensation/synchrony and the timescale at which it happens depend on the properties of the entire network of interacting species.

Despite recent advances in theory, relatively little empirical work exists to determine if populations oscillate synchronously or asynchronously in reasonably diverse ecosystems (Houlahan et al. 2007) and importantly, whether populations are likely to respond synchronously or asynchronously to environmental fluctuations (Descamps-Julien and Gonzalez 2005). Asynchronous or compensatory dynamics have sometimes been shown to stabilize ecosystem properties (Tilman 1996, Naeem and Li 1997, Havens and Carlson 1998, Fischer et al. 2001, Bai et al. 2004), however, other evidence suggests that compensatory dynamics have little or no role for ecosystem stability (Klug et al. 2000, Steiner 2005, Steiner et al. 2005). In a laboratory study, environmental fluctuations led to decreased ecosystem variability by increasing compensation among species engaged in competitive interactions (Gonzalez and

Descamps-Julien 2004). However, this experimental study used a simple system consisting of a single rotifer predator and six species of algal prey (Gonzalez and Descamps-Julien 2004). No study to date has experimentally demonstrated compensatory dynamics driven by environmental fluctuations in systems approaching realistic diversities or trophic structures.

One possible reason for such disparities in the empirical data is that oscillation patterns can be complex and most data is not complete enough to detect such complex temporal patterns (Vasseur et al. 2005). For example, species may oscillate synchronously at one timescale, but asynchronously or with compensatory dynamics at a different timescale (Keitt and Fischer 2006, Vasseur and Gaedke 2007; see Fig. 1A). Detecting such a pattern requires detailed time-series data over a reasonably long time frame and statistical methods adequate to identify patterns at different scales. Most empirical work to date relies on relatively short timescales (e.g., weeks or months) or relatively infrequent (e.g., monthly or yearly) sampling of long-lived organisms (e.g., plants), making it difficult to detect complex relationships between species populations.

A further complication is that much previous work on natural (non-experimental) populations has simply focused on the presence or absence of compensatory

dynamics (i.e., negative correlations) between functionally similar species rather than on the degree of synchrony (i.e., the relative strength of positive correlations) between functionally similar species. This is important because most of the evidence indicates a strong tendency toward synchrony between functionally similar species in nature (Houlahan et al. 2007). Thus it is possible that increased stability under some conditions, such as under fluctuating environments, is not due to the influence of overall compensatory dynamics but rather could result from reductions in the degree of synchrony instead.

Here we provide an experimental test of how environmental fluctuations influence population dynamics and, in turn, community and ecosystem stability. Specifically, we examined the population dynamics of zooplankton in replicate pond mesocosms subjected to nutrient pulses. Previous work in these experimental systems shows that plankton mesocosms correspond well with natural ponds with respect to trophic structure, stoichiometry, productivity, and respiration (Hall et al. 2005). The seasonal dynamics of the mesocosms mimics those occurring in natural ponds, starting with small populations (inoculated in the mesocosms but hatching from resting stages in nature) that develop fairly rapidly (within a month or so) and then show oscillations. These systems have also been shown to have strong endogenous plant-herbivore oscillations characterized by a periodicity of about 20–30 days (Leibold et al. 2005) which are common in naturally occurring communities (McCauley et al. 1999). Generation times of plankton communities are short, allowing reasonable time-series data for population dynamics to be generated over a single field season. Thus, the experimental pond mesocosms appear to approach the complexity, dynamics and functioning of natural plankton ecosystems and provide a good model system to test predictions about compensatory dynamics from theory. Finally, we use statistical methods based on wavelet analysis (Daubechies 1992, Mallat 1999, Keitt and Fischer 2006) to decompose the experimental time series into dynamics at multiple temporal scales, allowing us to examine the importance of compensation vs. synchrony at each of these scales.

METHODS

To explore the effects of population dynamics on community and ecosystem properties, we created replicate pond ecosystems in mesocosms with naturally diverse assemblages of algae and zooplankton. Mesocosms consisted of 300-L polyethylene tanks with 1-mm screen mesh lids to control the immigration by larger organisms. 20 L of silica sand was added as a bottom substrate and the mesocosms were filled with well water. Inoculae of microbes, algae, and zooplankton from 10 local ponds were added in mid April and every other week thereafter to simulate colonization from nearby ponds in the metacommunity, and to provide the

opportunity for mesocosm zooplankton communities to track changes in natural pond communities. All mesocosms were maintained under nutrient inputs typical of eutrophic ponds in southern Michigan. Target water-column concentrations for the mesocosms were established as 150 $\mu\text{g P/L}$ and 2250 $\mu\text{g N/L}$ in the form of NaH_2PO_4 and NaHNO_3 .

Previous research in these mesocosms indicates that nitrogen and phosphorous are lost from the water column to the sediments and mesocosm walls at rates of approximately 5% per day (or 35% per week) of target levels. Therefore, to maintain constant nutrient levels in the water column, approximately 35% of the target nutrient levels must be replaced on a weekly basis. All mesocosms received the same total nutrients over the course of the experiment, but individual treatments differed in the pattern of nutrient addition. We established four treatments beginning 1 May, in which the frequency of nutrient input was varied in order to generate different degrees of environmental fluctuations. Each treatment was replicated four times. Nutrient inputs to mesocosms occurred in two forms: in the “constant” treatment we added weekly total nitrogen and phosphorus inputs at a constant rate (i.e., constant drip) via peristaltic pumps; in the remaining three treatments, we added a one week nutrient supply (35% of target N and P levels) as pulses delivered via pipette. These pulses were delivered every 7, 14, or 21 days resulting in three different pulsed treatments. In the N and P 7-day pulsed treatment, the entire weekly nutrient input was delivered as a pulse once a week. In the 14- and 21-day pulsed communities, a constant drip was necessary to maintain the same average target weekly nutrient input as the other treatments. Thus the size of each pulse (35% of the target N and P levels) was identical for each pulsed treatment, but the frequency of the pulse varied. The hand-delivered pulses simulate naturally occurring nutrient pulses associated with rainfall events, while ensuring that total average nutrient inputs were identical to the constant environment (Cottingham and Schindler 2000). In the biweekly and triweekly addition treatments, two replicates were first pulsed in the first week of the experiment and the other two were first pulsed in the second week in order to prevent any unintended correlations between nutrient pulses and environmental fluctuations due to weather fronts. All mesocosms were maintained outdoors and were subject to identical natural environmental fluctuations such as those due to weather. Therefore, the pulsed nutrient additions represented the only form of environmental forcing that was unique among treatments.

Tanks were sampled 32 times at even intervals of 4–5 days beginning 7 May and continuing through 24 September. Sampling consisted of collecting 16 samples of 750 mL using a tube sampler to integrate over the depth of the water column evenly distributed over the area of the mesocosm and pooling these into a single

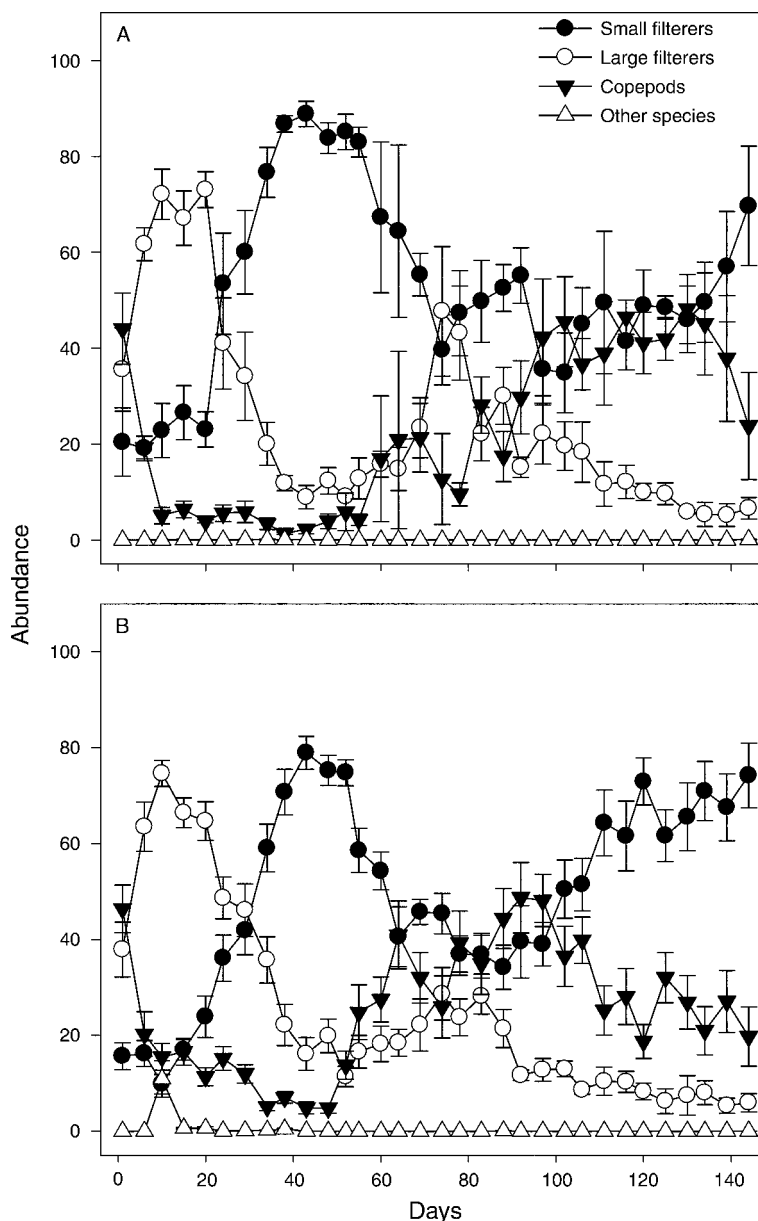


FIG. 2. Time series for relative abundances of functional groups in the experimental mesocosms showing the similarity between (A) the constant environments and (B) the pulsed environments. Points represent means across replicates (\pm SE). The nutrient-pulsed environments were averaged across all three nutrient-pulse treatments due to similarities across the pulsed treatments and for consistency with later analyses.

bucket. A 300-mL sample was collected for phytoplankton analysis. The remainder was collected on an 80- μ m mesh, handpicked to remove unwanted particulates (e.g., clumps of detritus, sand, etc.) and preserved in sucrose Lugols solution for later microscopic enumeration in the lab. Biomass was estimated by applying published length-mass regressions to abundance data. Productivity was evaluated by collecting a 500-mL integrated water column sample in the morning, evening, and subsequent morning at dawn and dusk in which O_2 concentrations were measured using a YSI

meter (YSI, Yellow Springs, Ohio, USA). From oxygen data, gross productivity was measured by calculating hourly respiration at night and correcting estimates of net hourly productivity during the day by addition.

We examined total zooplankton density, density of individual component species, primary productivity, and community respiration by treatments using one-way ANOVA and planned linear contrasts of the constant environment vs. the three pulsed environments to evaluate differences among treatments. We also examined variability in total zooplankton density, zooplank-

TABLE 1. Percentage of total zooplankton abundance represented by individual taxa in the control and pulsed treatments.

Taxon	Constant (%)	Pulsed (%)
<i>Chydorus</i>	19.5	13.1
Nauplii	16.7	21.8
<i>Daphnia</i>	15.9	14.4
<i>Bosmina</i>	13.0	6.7
<i>Ceriodaphnia</i>	12.8	18.5
<i>Scapholebris</i>	12.8	9.4
<i>Alona</i>	2.5	4.4
Cylopoids	2.3	3.4
<i>Diaphanosoma</i>	1.8	1.7
<i>Simocephalus</i>	1.5	2.9
Copepodites	0.7	3.4
Calanoids	0.2	0.3

Note: Percentages represent average abundances across the entire 144 days of the experiment.

ton biomass, and net primary productivity by performing one-way ANOVA with planned contrasts on the coefficient of variation (CV) for each treatment (Cottingham et al. 2001).

To evaluate the degree of synchrony or compensation in the plankton community as a function of treatment, we used a variance ratio method (Frost et al. 1995) combined with wavelet analysis (Torrence and Webster 1999, Keitt and Urban 2005, Keitt and Fischer 2006). Wavelet analysis is a method of quantitatively partitioning variance from a time series into time "scales." Each scale represents a specific frequency or period (the inverse of frequency), and thus the wavelet transform identifies how much variance in a time series can be accounted for by oscillations of a given frequency. Wavelet analysis is a true variance conserving technique in that the sum of variance across all timescales equals the untransformed variance. Wavelet coefficients are also independent across timescales, making them appropriate and useful predictors or response variables in statistical models or analyses.

Prior to calculating variance ratios, we wavelet transformed all time series which allowed us to partition variability from the time series into specific timescales. We then examined the variance ratio at each of 17 timescales (i.e., oscillation periods) to examine how synchrony or compensation varied with timescale (Keitt and Fischer 2006). Wavelet transformations were performed using the Morlet wavelet with six octaves and four voices, and implemented using the *cwt* function in the *Rwave* package of the R programming environment (R Development Core Team 2004). Since the Morlet is complex valued, we examined results based on both real and imaginary parts and found little difference, thus our results focus on the real part. To reduce wrap-around and end effects, we zero padded the ends of our time series and chose not to examine seven of the 24 frequency components (the two smallest and five largest). We also compared results based on the Morlet wavelet to results based on a complex-valued, second-order derivative of Gaussian wavelet and found them

comparable. After wavelet transformation of the data, we calculated variance ratios at each timescale based on Frost et al. (1995). We then graphically determined specific timescales of interest, and used one-way ANOVA and planned linear contrasts (constant vs. three pulsed treatments) to evaluate treatment differences in the wavelet transformed variance ratio at those scales. We also examined pairwise correlations among all zooplankton species in wavelet transformed data at the same timescales to identify the zooplankton species that led to differences in compensatory or synchronous dynamics between the constant and pulsed environments.

We also employed wavelet analysis to examine the possible role of climate as an external driver of community variability. We calculated both the wavelet covariance and the wavelet coherence which is similar to a cross correlation in wavelet space between zooplankton density and temperature. We specifically looked for strong signals of covariance and/or coherence that might occur at the same timescales as strong signals from our variance ratio analysis.

RESULTS

The nutrient pulses created significant differences in total zooplankton density across the four treatment levels (one-way ANOVA, $F_{3,12} = 6.47$, $P = 0.007$). Density of total zooplankton was 914 ± 71 individuals/L (mean \pm SE) for the constant environment, and 1013 ± 130 , 1326 ± 261 , and 1849 ± 141 for the one-, two-, and three-week pulse perturbations, respectively. Post-hoc analysis with Tukey's *h*sd revealed that the three-week pulsed treatment had significantly higher total zooplankton density than either the constant environment or the one-week pulsed treatment, but that no other treatment combinations differed from one another. Despite differences in total abundance, zooplankton community composition at the level of functional group was generally quite similar between treatments (Fig. 2, Table 1). In all treatments, there was a shift from relative dominance by large filtering cladocerans to dominance by small filtering copepods within the first 60 days of the experiment, reflecting seasonal trends commonly observed in the surrounding natural ponds. For the remainder of the experiment, copepods and small filtering cladocerans were codominant groups, with large filtering cladocerans comprising a relatively small fraction of total abundance (Fig. 2). All treatments maintained these compositional similarities at the level of functional group despite wide-ranging differences in composition at the species level (Table 1).

Temporal variability (CV) of several aggregate community and ecosystem properties was significantly reduced in treatments that received nutrient pulses compared to the constant environment (Fig. 3). Variability in total zooplankton density was lower in all three pulsed treatments when compared to the constant environment (CV \pm SE: constant = 1.08 ± 0.10 ; one-

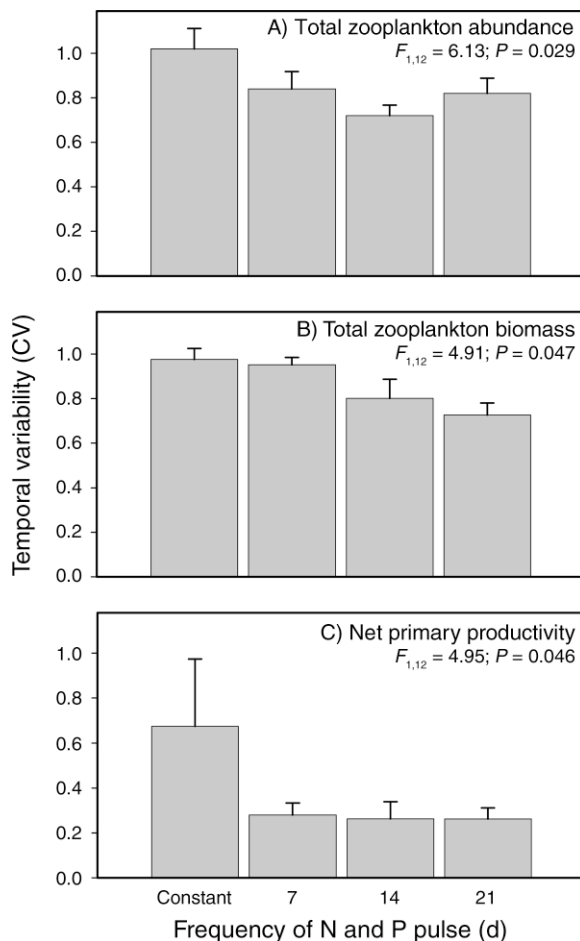


FIG. 3. Temporal variability in (A) total zooplankton abundance, (B) total zooplankton biomass, and (C) net ecosystem productivity for the four treatment groups during the plankton mesocosm experiment. Temporal variability was calculated as the temporal coefficient of variation within a treatment. Error bars represent 1 standard error of the mean. F values and probabilities represent results of planned linear contrasts (constant vs. three pulsed treatments).

week pulse = 0.87 ± 0.08 ; two-week pulse = 0.77 ± 0.07 ; three-week pulse = 0.90 ± 0.071). One-way ANOVA gave a Type I error probability of 0.10 ($F_{3,12} = 2.48$) for differences between means based on our design, but a planned linear contrast between the constant environment and the three pulsed environments gave a Type I error probability of 0.029 ($F_{1,12} = 6.13$) of true differences between the constant and pulsed environments (Fig. 3A). We found a similar result for the temporal variability of total zooplankton biomass (CV \pm SE: constant = 0.98 ± 0.049 ; one-week pulse = 0.95 ± 0.033 ; two-week pulse = 0.80 ± 0.086 ; three-week pulse = 0.73 ± 0.054). One-way ANOVA gave a Type I error probability of 0.030 for a difference among treatment means and a Tukey's post hoc analysis of means revealed that these differences were between the constant environment treatment and the three-week pulsed

treatment ($P = 0.045$), and the one-week and three-week pulsed treatments ($P = 0.074$). Planned linear contrasts for the difference in variability between the constant and pulsed environments gave a probability of a Type I error as 0.047 ($F_{1,12} = 4.91$; Fig. 3B).

As with the previous density and biomass of zooplankton, there were differences in temporal variability of net primary productivity of algae between the constant and pulsed environments (Fig. 3C). Despite a large difference in the magnitude of mean temporal variability among treatments (CV \pm SE: constant = 33.8 ± 14.9 ; one-week pulse = 14.0 ± 2.7 ; two-week pulse = 13.1 ± 3.8 ; three-week pulse = 13.1 ± 2.5), one-way ANOVA suggested that there were no differences across the treatments ($F_{3,12} = 1.65$, $P = 0.23$) because of high within-treatment variability. However, a planned linear contrast produced a Type I error rate of 0.046 ($F_{1,12} = 4.95$) for differences between the constant and pulsed environments (Fig. 3C).

In order to explore potential mechanisms behind the reduced variability of total zooplankton biomass and density in the pulsed environments, we looked at the average variability of individual taxa, and the relative amount of synchrony and compensation among zooplankton species within our experimental communities. MANOVA suggested that there were no effects of nutrient pulsing on the variability (CV) of individual taxa (MANOVA, Wilks' lambda $F_{36,3.68} = 0.87$, $P = 0.65$), indicating that fluctuating environments did not lead to more variable populations of individual species on average. The results of the variance ratio analysis, designed to detect the degree of synchrony or compensation among species, indicated that treatment differ-

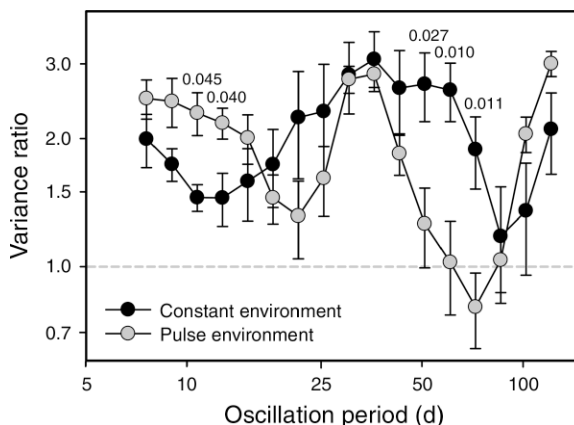


FIG. 4. Variance ratios (VR) of the zooplankton community across a range of frequencies (measured as days per cycle). Error bars represent one standard error of the mean. A VR > 1 (above dashed line) indicates synchrony among members of the functional group, while a VR < 1 (below dashed line) indicates compensation. Numbers above points are Type I error rates from planned linear contrasts for the difference between VR in the constant vs. pulsed environment at selected timescales. Scales were selected for analysis based on visual inspection of the data.

TABLE 2. Mean pairwise correlations between species in the constant treatment are above the diagonal, and pulsed treatments are below the diagonal at timescales of (A) ~11 days and (B) ~60 days.

Pulsed environment	Constant environment					
	Cer	Sca	Dap	Chy	Bos	Alo
A) 11-day period†						
Cer	1	0.21 (0.09)	-0.05 (0.06)	0.19 (0.17)	0.41 (0.01)	0.35 (0.17)
Sca	-0.06 (0.05)	1	-0.20 (0.06)	0.37 (0.07)	-0.21 (0.03)	0.42 (0.14)
Dap	0.25 (0.13)	0.08 (0.03)	1	-0.53 (0)	0.41 (0.12)	- 0.32 (0.07)
Chy	0.21 (0.09)	0.17 (0.06)	0.21 (0.06)	1	-0.02 (0.15)	0.58 (0.18)
Bos	0.37 (0.11)	-0.10 (0.03)	0.48 (0.07)	0.02 (0.14)	1	-0.19 (0.03)
Alo	0.23 (0.11)	0.08 (0.11)	0.19 (0.05)	0.45 (0.15)	0.14 (0.18)	1
Cal	0.14 (0.06)	0.01 (0.08)	0.25 (0.03)	0.00 (0.13)	0.12 (0.06)	0.07 (0.10)
Cyc	0.15 (0.05)	0.16 (0.06)	0.16 (0.07)	0.32 (0.08)	0.05 (0.06)	0.46 (0.05)
Cop	0.21 (0.04)	0.06 (0.09)	0.18 (0.05)	0.28 (0.08)	0.10 (0.09)	0.54 (0.12)
Nau	0.07 (0.08)	0.22 (0.15)	0.12 (0.07)	0.25 (0.05)	-0.01 (0.06)	0.39 (0.16)
Sim	0.22 (0.09)	0.27 (0.10)	0.15 (0.05)	0.30 (0.08)	0.08 (0.07)	0.45 (0.12)
Dia	-0.08 (0.05)	0.44 (0.11)	0.06 (0.02)	0.13 (0.03)	-0.09 (0.01)	0.03 (0.05)
B) 60-day period‡						
Cer	1	-0.24 (0.36)	0.90 (0.01)	0.87 (0.23)	0.91 (0.14)	0.76 (0.4)
Sca	-0.83 (0.30)	1	-0.25 (0.34)	-0.17 (0.35)	-0.09 (0.32)	-0.34 (0.32)
Dap	0.70 (0.17)	-0.60 (0.10)	1	0.94 (0.07)	0.95 (0.02)	0.76 (0.17)
Chy	0.62 (0.22)	-0.60 (0.05)	0.75 (0.07)	1	0.95 (0.01)	0.83 (0.04)
Bos	0.72 (0.19)	-0.67 (0.06)	0.79 (0.12)	0.69 (0.1)	1	0.71 (0.05)
Alo	0.46 (0.26)	-0.48 (0.15)	0.27 (0.11)	0.45 (0.19)	0.45 (0.14)	1
Cal	0.56 (0.20)	-0.45 (0.13)	0.70 (0.07)	0.55 (0.23)	0.59 (0.24)	0.16 (0.17)
Cyc	0.20 (0.15)	-0.32 (0.30)	-0.08 (0.09)	0.09 (0.19)	0.01 (0.12)	0.37 (0.17)
Cop	0.04 (0.21)	-0.13 (0.27)	-0.16 (0.08)	-0.16 (0.31)	0.00 (0.17)	0.22 (0.23)
Nau	0.03 (0.27)	-0.12 (0.24)	-0.20 (0.09)	-0.15 (0.21)	-0.08 (0.16)	0.36 (0.15)
Sim	0.32 (0.21)	-0.31 (0.14)	-0.06 (0.06)	0.02 (0.16)	0.05 (0.23)	0.57 (0.12)
Dia	-0.76 (0.21)	0.83 (0.02)	-0.52 (0.04)	-0.49 (0.09)	-0.60 (0.06)	-0.65 (0.05)

Notes: Standard errors for each correlation are given in parentheses. Correlations >0.30 are shown in boldface type and those <-0.30 are in italics. Taxa abbreviations are: Cer, *Ceriodaphnia*; Sca, *Scapholebris*; Dap, *Daphnia*; Chy, *Chydorus*; Bos, *Bosmina*; Alo, *Alona*; Cal, Calanoids; Cyc, Cyclopoids; Cop, Copepodites; Nau, Nauplii; Sim, *Simocephalus*; Dia, *Diaphanosoma*.

† The grand mean of pairwise correlations for the constant environment was 0.12 ± 0.03 (mean \pm SE) compared to a mean of 0.17 ± 0.02 in the pulsed environment.

‡ The grand mean of pairwise correlations for the constant environment was 0.18 ± 0.06 compared to a mean of 0.06 ± 0.06 in the pulsed environment.

ences in population dynamics were apparent at two timescale windows approximately centered around 11 and 60 days (Fig. 4). Interestingly, the effects of the pulsed perturbations on compensation in the zooplankton community differed qualitatively at short vs. long timescales (Fig. 4; see Fig. 1 for an example of what this analysis indicates in terms of individual species' time series). At oscillation periods close to 10 days, we observed significantly more synchrony (indicated by a higher variance ratio) in the pulsed environments relative to the constant environments (Fig. 4). In contrast, at longer timescales (approximately 45–80 day periods) there was much higher synchrony in the constant environments (Fig. 4). Additionally, at periods of approximately 60 days, the variance ratio analysis indicated that there was a considerable degree of compensation between species in zooplankton communities in the pulsed environments. In contrast, zooplankton species in the constant environments showed a high level of synchrony at the same timescale (Fig. 4).

To determine which species within the zooplankton community were oscillating synchronously or asynchronously with respect to one another, we calculated community correlation matrices for wavelet-transformed species abundances at the timescales identified

by the variance ratio analysis (11- and 60-day periods; Table 2). We found that short-term pairwise dynamics (11-day period) were strongly synchronous in both pulsed and constant treatments except for *Daphnia pulex* which showed compensation with some species in the constant environments (Table 2A). Conversely, at longer timescales we found that there were a greater number of negative pairwise correlations in the pulsed environments relative to the constant environments, and that the average correlation across all species pairs was significantly less positive (i.e., less synchronous) in the pulsed treatments (Table 2B). Negative correlations in the pulsed treatments largely involved the abundant species *Scapholebris mucronata* (Table 1). *Diaphanosoma* was also frequently negatively correlated with other taxa, but on average composed <2% of total zooplankton in our communities (Table 1).

There was no indication that climate acted as an external driver of community variability at the key scales identified in the variance ratio analysis. By far the strongest signal of climate using either wavelet covariance or wavelet coherence occurred at timescales ≈ 150 days, a period that clearly corresponds to the long-term changes in temperature through the course of the experiment. We found no significant climatic variability

TABLE 2. Extended.

Constant environment					
Cal	Cyc	Cop	Nau	Sim	Dia
0.03 (0.01)	0.34 (0.08)	−0.25 (0.08)	−0.06 (0.06)	0.19 (0.16)	0.30 (0.02)
0.11 (0.01)	0.65 (0.23)	0.23 (0.17)	0.16 (0.05)	0.43 (0.05)	0.31 (0.06)
0.09 (0.14)	−0.08 (0.16)	−0.02 (0.12)	0.27 (0.01)	0.17 (0.09)	−0.08 (0)
0.03 (0.24)	0.41 (0.19)	0.24 (0.11)	−0.03 (0.05)	0.04 (0.21)	−0.03 (0.01)
0.18 (0.17)	−0.17 (0.01)	−0.19 (0.16)	0.06 (0.01)	−0.09 (0.08)	0.00 (0)
−0.21 (0.03)	0.69 (0.03)	−0.06 (0.05)	0.08 (0.04)	0.38 (0.05)	0.08 (0.01)
1	−0.22 (0.03)	0.28 (0.17)	−0.10 (0.07)	−0.08 (0.11)	0.17 (0.02)
0.17 (0.10)	1	0.09 (0.11)	0.38 (0.12)	0.66 (0.05)	0.14 (0.02)
0.16 (0.07)	0.43 (0.13)	1	0.23 (0.08)	0.10 (0.15)	−0.03 (0.05)
−0.19 (0.10)	0.10 (0.14)	0.46 (0.10)	1	0.16 (0.23)	0.14 (0.24)
−0.11 (0.11)	0.30 (0.10)	0.12 (0.17)	0.39 (0.13)	1	0.18 (0.02)
0.07 (0.07)	0.21 (0.02)	−0.05 (0.09)	0.02 (0.08)	0.26 (0.09)	1
0.90 (0.05)	0.29 (0.16)	−0.03 (0.07)	−0.54 (0.19)	0.38 (0)	−0.65 (0.23)
−0.18 (0.20)	0.04 (0.20)	−0.05 (0.42)	0.28 (0.20)	−0.40 (0.35)	0.25 (0.23)
0.96 (0.01)	0.40 (0.25)	−0.07 (0.04)	−0.36 (0.03)	0.12 (0.03)	−0.38 (0.08)
0.95 (0.16)	0.48 (0.26)	0.00 (0.45)	−0.26 (0.24)	0.16 (0.27)	−0.32 (0.02)
0.94 (0.04)	0.38 (0.17)	−0.03 (0.16)	−0.37 (0.12)	0.18 (0.16)	−0.39 (0.05)
0.72 (0.17)	0.20 (0.27)	−0.16 (0.31)	−0.40 (0.16)	0.22 (0.44)	−0.38 (0.19)
1	0.48 (0.36)	0.01 (0.24)	−0.29 (0.11)	0.12 (0.13)	−0.37 (0.27)
0.13 (0.21)	1	0.58 (0)	0.36 (0.16)	0.10 (0.21)	0.00 (0.48)
−0.15 (0.17)	0.57 (0.11)	1	0.30 (0.28)	0.52 (0.21)	−0.12 (0.47)
−0.16 (0.07)	0.34 (0.15)	0.64 (0.05)	1	−0.31 (0.27)	0.62 (0.19)
−0.04 (0.06)	0.29 (0.08)	0.32 (0.06)	0.40 (0.13)	1	−0.58 (0.18)
−0.48 (0.08)	−0.35 (0.27)	−0.13 (0.34)	−0.22 (0.17)	−0.59 (0.07)	1

that corresponded to either of the two important community level timescales (~ 10 days and ~ 50 – 80 days), and no indications of treatment differences at these timescales.

DISCUSSION

Community and ecosystem stability were enhanced in environments experiencing increased environmental fluctuations. In our study, zooplankton populations oscillated strongly in all treatments, resembling naturally occurring plankton ecosystems that typically show strong population oscillations due primarily to consumer-resource dynamics (McCauley et al. 1999, Leibold et al. 2005). However, community and ecosystem properties were stabilized in fluctuating environments primarily through reduced overall synchrony between oscillating zooplankton populations at long timescales (50–80 days), though we did detect some compensatory dynamics as well (Fig. 4). Previous attempts to document the role of compensatory dynamics in stabilizing community responses to environmental fluctuations (Fischer et al. 2001, Vasseur et al. 2005) may have underestimated the importance of community dynamics since the reduction of synchrony rather than the presence of compensation may actually provide the stabilizing mechanism (see also Huber and Gaedke 2006). The ubiquity of synchronous oscillations in natural communities has been reasonably well documented (Houlahan et al. 2007), and the largely synchronous dynamics observed in this experiment

resemble the dynamics observed in natural communities. Our results also indicate that reduced synchrony may be more important for stabilizing ecosystems than previously thought and that such reduced synchrony may be heavily timescale dependent. While a number of studies (Klug et al. 2000, Fischer et al. 2001, Bai et al. 2004, Descamps-Julien and Gonzalez 2005, Vasseur et al. 2005, Huber and Gaedke 2006) suggest a role for compensatory dynamics in fluctuating environments, Gonzalez and Descamps-Julien (2004) is the only study to previously show a reduction of aggregate community variance due to compensatory interactions between species in an experimental setting. Our study confirms their findings, while also showing that the effects can be strongly timescale dependent, and can occur in reasonably complex communities that more closely resemble natural communities than the simple lab settings previously studied.

There are at least three mechanisms that might possibly explain the observed lower variability in fluctuating environments compared to constant ones. The first possibility is that fluctuating environments reduce both the amplitude and the likelihood of fluctuations in individual species for unknown or complex reasons. However, our finding of equal average population variance across all treatments does not provide support for this mechanism. A second mechanism is destructive interference of internal population oscillations by exogenous forcing. Theory on oscillators shows that if the period of nutrient pulses is similar to

the period of internal population oscillations, fluctuations can enhance the magnitude of population oscillations. If, on the other hand, the periods of fluctuations differ from those of the internal dynamics, fluctuations will dampen the magnitude of internal oscillations due to mechanical resonance. We have no evidence that destructive interference occurred as we did not observe any sensitivity of population variability in pulsed treatments to the period of imposed environmental fluctuations despite having one of these pulses occurring at or near the internal frequency of the system of 21 days (see Leibold et al. 2005). Finally, compensatory dynamics among functionally similar species may lead to lower variability in aggregate properties. Our data are most consistent with this general mechanism because (1) aggregate properties such as total zooplankton density and biomass are stabilized in pulsed ecosystems while the variability of individual species density is the same across treatments, (2) the differences across treatments involve changes in relative composition at the species level rather than changes in community structure or overall species richness (Fig. 2, Table 1), (3) the component species involved in asynchrony and compensation can be easily identified as functionally similar zooplankton species (Table 2), and (4) the timescale at which asynchronous and compensatory dynamics occur in pulsed ecosystems is consistent with mechanisms that can create such dynamics.

By partitioning the variance of community time series into component timescales through wavelet analysis, we can interpret mechanisms responsible for changes in synchrony that we observe at different timescales in the different treatments. The mechanisms operating in our study are likely different and more complex than those observed in previous work on compensation because these previous studies focused primarily on the direct effects of environmental fluctuations on populations at a single timescale. For example, Fischer et al. (2001) showed that acid-tolerant species compensated with acid-sensitive species over long timescales (multiple years) during acidification and neutralization of lakes via a process that might be termed "environmental tracking." Tilman (1996) found that drought-tolerant plants compensated with drought-sensitive species over many years in a grassland community subject to natural variation in rainfall. By comparison, in our study the changes in zooplankton population dynamics observed likely involve more complex responses to the imposed environmental fluctuations. First, the nutrient additions affect zooplankton dynamics indirectly by altering the dynamics of their phytoplankton resources. Second, the recurring nutrient pulses likely alter endogenous zooplankton-phytoplankton dynamics that occur on relatively similar timescales. Third, the mechanisms that drive treatment differences in synchrony at short timescales (7–15 days) are different than the mechanisms driving treatment differences at longer timescales (50–80 days).

We observed that the constant treatments were significantly less synchronous than pulsed ecosystems at short timescales (7–15 days), however, the reduction in synchrony relative to pulsed ecosystems was modest. Indeed, both pulsed and constant ecosystems have variance ratios greater than 1 at short timescales, indicating a predominance of synchronous dynamics in all ecosystems (Fig. 4). The mechanism behind the increase in synchrony in the pulsed ecosystems at short timescales appears to be an immediate growth response by the plankton to the recurring nutrient pulses. Generation times for the dominant cladoceran zooplankton species in our experiment range between one and three weeks: similar to timescale of both the nutrient pulses, suggesting that the pulses may interact with reproduction cycles to generate higher synchrony in pulsed ecosystems at the 7–15 day timescale. Copepods, on the other hand, tend to have longer generation times between one and two months. While increased synchrony in pulsed ecosystems has the potential to destabilize aggregate properties, the modest treatment differences do not appear strong enough to cause a significant change at the aggregate level.

The reduced synchrony in the pulsed environments that we observe at periods of 50–80 days is stronger than the reduction observed at shorter timescales in the constant environment, and results in variance ratios less than or equal to 1 in pulsed ecosystems, indicating a major shift toward compensatory dynamics. One possible mechanism that has been credited for producing compensation at longer timescales within trophic levels in previous work is direct consumer-resource interactions (Micheli et al. 1999, Klug et al. 2000, Fischer et al. 2001). This mechanism is not likely responsible for the patterns observed at the timescale of 50–80 days because typical consumer-resource interactions in our pond mesocosms have previously been shown to result in synchronous dynamics over periods of 20–30 days, reflecting correlated increases and decreases between resources and their consumers (Leibold et al. 2005). Such consumer-resource oscillations appear in our results as peaks at about a 30-day period of synchrony common to both control and pulsed treatments (Fig. 4). Instead of direct consumer-resource interactions, we suggest that the increase in asynchrony and compensation we observed at the 50–80-day timescale likely involves less direct food web interactions. One such interaction may involve unmeasured community fluctuations in the phytoplankton. Recent theoretical work (e.g., Gragnani et al. 1999, Abrams and Matsuda 2003, Abrams et al. 2003, Yoshida et al. 2003) shows that oscillations involving three or more taxa (or potentially clonal genotypes) can occur in which compensation between prey that differ in edibility or predators that differ in consumption of prey compensate with each other when they oscillate. Theory predicts that these oscillations should have longer period lengths than the pairwise predator-prey oscillations that would otherwise

occur (Greenman and Benton 2005). It thus seems likely that the reduced synchrony and increased compensation we observed at relatively long timescales involves such shifts in food web dynamics mediated via shifts in plankton communities, although we cannot document these since we did not sample the phytoplankton adequately to do so.

Interest in compensatory dynamics in complex communities has come largely from an interest in explaining why diverse communities may have more stable aggregate properties (such as total consumer density) than less diverse communities, even though individual species may be more variable in highly diverse communities. Our experiment cannot directly address this question because we did not manipulate diversity, but compensation among species such as that we document here cannot occur in single species communities and may be unlikely in depauperate ones. Nevertheless, our experiment shows that there can be strong effects of recurrent environmental fluctuations on compensation in naturally diverse plankton assemblages driven by nutrient pulses and that compensation in this system only occurs at specific timescales and not others. Future work should look at how closely changes in diversity of functionally similar species influences oscillations among species.

ACKNOWLEDGMENTS

The paper is a Kellogg Biological Station contribution, and was supported by the National Science Foundation (DEB-0521954 to M. Leibold and A. Downing). We thank several anonymous reviewers and Andrew Gonzalez and Chad Brassil for valuable comments on previous versions of the manuscript.

LITERATURE CITED

- Abrams, P. A., C. E. Brassil, and R. D. Holt. 2003. Dynamics and responses to mortality rates of competing predators undergoing predator-prey cycles. *Theoretical Population Biology* 64:163–176.
- Abrams, P. A., and H. Matsuda. 2003. Population dynamical consequences of reduced predator switching at low total prey densities. *Population Ecology* 45:175–185.
- Bai, Y., X. Han, J. Wu, Z. Chen, and L. Li. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* 431:181–184.
- Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters* 4:72–85.
- Cottingham, K. L., and D. E. Schindler. 2000. Effects of grazer community structure on phytoplankton response to nutrient pulses. *Ecology* 81:183–200.
- Daubechies, I. 1992. Ten lectures on wavelets. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania, USA.
- Descamps-Julien, B., and A. Gonzalez. 2005. Stable coexistence in a fluctuating environment: an experimental demonstration. *Ecology* 86:2815–2824.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist* 151:264–276.
- Fischer, J. M., T. M. Frost, and A. R. Ives. 2001. Compensatory dynamics in zooplankton community responses to acidification: measurement and mechanisms. *Ecological Applications* 11:1060–1072.
- Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1995. Species compensation and complementarity in ecosystem function. Pages 224–239 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Gonzalez, A., and A. De Feo. 2007. Environmental variability modulates the insurance effects of diversity in nonequilibrium communities. Pages 159–177 in D. Vassuer and K. McCann, editors. *The impact of environmental variability on ecological systems*. Springer, New York, New York, USA.
- Gonzalez, A., and B. Descamps-Julien. 2004. Population and community variability in randomly fluctuating environments. *Oikos* 106:105–116.
- Gragnani, A., M. Scheffer, and S. Rinaldi. 1999. Top-down control of cyanobacteria: a theoretical analysis. *American Naturalist* 153:59–72.
- Greenman, J. V., and T. G. Benton. 2005. The frequency spectrum of structured discrete time population models: its properties and their ecological implications. *Oikos* 110:369–389.
- Hall, S. R., V. H. Smith, D. A. Lytle, and M. A. Leibold. 2005. Constraints on primary producer N:P stoichiometry along N:P supply ratio gradients. *Ecology* 86:1894–1904.
- Havens, K. E., and R. E. Carlson. 1998. Functional complementarity in plankton communities along a gradient of acid stress. *Environmental Pollution* 101:427–436.
- Houlahan, J. E., et al. 2007. Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Sciences (USA)* 104:3273–3277.
- Huber, V., and U. Gaedke. 2006. The role of predation for seasonal variability patterns among phytoplankton and ciliates. *Oikos* 114:265–276.
- Ives, A. R., and B. J. Cardinale. 2004. Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* 429:174–177.
- Ives, A. R., K. Gross, and J. L. Klug. 1999. Stability and variability in competitive communities. *Science* 286:542–544.
- Keitt, T. H., and J. M. Fischer. 2006. Detection of scale-specific community dynamics using wavelets. *Ecology* 87:2895–2904.
- Keitt, T. H., and D. L. Urban. 2005. Scale-specific inference using wavelets. *Ecology* 86:2497–2504.
- Klug, J. L., J. M. Fischer, A. R. Ives, and B. Dennis. 2000. Compensatory dynamics in planktonic community responses to pH perturbations. *Ecology* 81:387–398.
- Leibold, M. A., S. R. Hall, and O. N. Bjornstad. 2005. Food web architecture and its effects on consumer resource oscillations in experimental pond ecosystems. Pages 37–47 in P. C. De Ruiter, V. Wolters, and J. C. Moore, editors. *Dynamic food webs: multispecies assemblages, ecosystem development and environmental change*. Academic Press, San Diego, California, USA.
- Mallat, S. G. 1999. A wavelet tour of signal processing. Second edition. Academic Press, San Diego, California, USA.
- McCauley, E., R. M. Nisbet, W. W. Murdoch, A. M. de Roos, and W. S. C. Gurney. 1999. Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments. *Nature* 402:653–656.
- Micheli, F., K. L. Cottingham, J. Bascompte, O. N. Bjornstad, G. L. Eckert, J. M. Fischer, T. H. Keitt, B. E. Kendall, J. L. Klug, and J. A. Rusak. 1999. The dual nature of community variability. *Oikos* 85:161–169.
- Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390:507–509.
- R Development Core Team. 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Steiner, C. F. 2005. Temporal stability of pond zooplankton assemblages. *Freshwater Biology* 50:105–112.

- Steiner, C. F., Z. T. Long, J. A. Krumins, and P. J. Morin. 2005. Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. *Ecology Letters* 8:819–828.
- Thébault, E., and M. Loreau. 2005. Trophic interactions and the relationship between species diversity and ecosystem stability. *American Naturalist* 166:E95–E114.
- Thébault, E., and M. Loreau. 2006. The relationship between biodiversity and ecosystem functioning in food webs. *Ecological Research* 21:17–25.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77:350–363.
- Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity–stability relationships: statistical inevitability or ecological consequence? *American Naturalist* 151:277–292.
- Torrence, C., and P. Webster. 1999. Interdecadal changes in the ENSO-Monsoon system. *Journal of Climate* 12:2679–2690.
- Vasseur, D. A., and U. Gaedke. 2007. Spectral analysis unmasks synchronous and compensatory dynamics in plankton communities. *Ecology* 88:2058–2071.
- Vasseur, D. A., U. Gaedke, and K. S. McCann. 2005. A seasonal alternation of coherent and compensatory dynamics occurs in phytoplankton. *Oikos* 110:507–514.
- Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences (USA)* 96:1463–1468.
- Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, and N. G. Hairston. 2003. Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* 424:303–306.