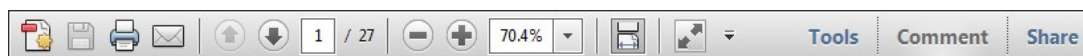
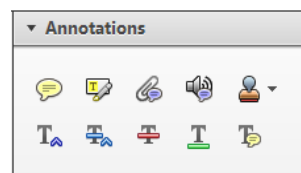


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This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the [Annotations](#) section, pictured opposite. We've picked out some of these tools below:



1. [Replace \(Ins\)](#) Tool – for replacing text.

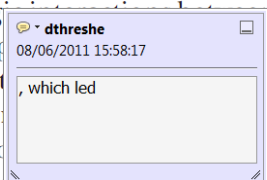


Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it

- Highlight a word or sentence.
- Click on the [Replace \(Ins\)](#) icon in the Annotations section.
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standard framework for the analysis of microeconomic behavior. Nevertheless, it also led to the development of strategic form games. The number of competitors in the industry is that the strategic form game is a main component of the model. At the level, are exogenous variables and important works on entry by firms (M henceforth) we open the 'black b



2. [Strikethrough \(Del\)](#) Tool – for deleting text.



Strikes a red line through text that is to be deleted.

How to use it

- Highlight a word or sentence.
- Click on the [Strikethrough \(Del\)](#) icon in the Annotations section.

there is no room for extra profits as mark-ups are zero and the number of firms (set) values are not determined by Blanchard and ~~Kiyotaki~~ (1987), perfect competition in general equilibrium of aggregate demand and supply in the classical framework assuming monopoly between an exogenous number of firms

3. [Add note to text](#) Tool – for highlighting a section to be changed to bold or italic.



Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the [Add note to text](#) icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

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4. [Add sticky note](#) Tool – for making notes at specific points in the text.

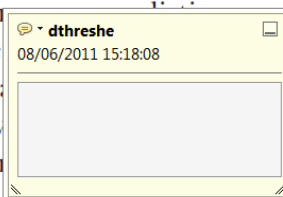


Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the [Add sticky note](#) icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
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5. **Attach File** Tool – for inserting large amounts of text or replacement figures.

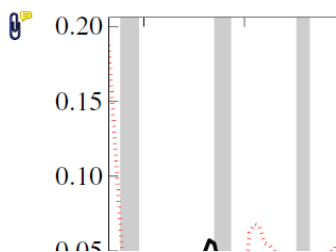


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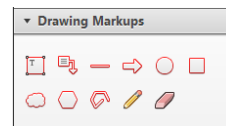
How to use it

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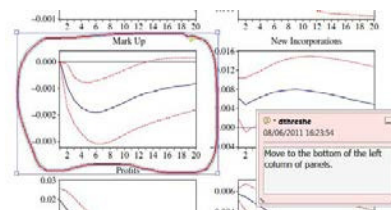


6. **Drawing Markups** Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks. Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks.



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- Double click on the shape and type any text in the red box that appears.



Compensatory dynamics stabilize aggregate community properties in response to multiple types of perturbations

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Abstract. Compensatory dynamics are an important suite of mechanisms that can stabilize community and ecosystem attributes in systems subject to environmental fluctuations. However, few experimental investigations of compensatory dynamics have addressed these mechanisms in systems of real-world complexity, and existing evidence relies heavily on correlative analyses, retrospective examination, and experiments in simple systems. We investigated the potential for compensatory dynamics to stabilize plankton communities in plankton mesocosm systems of real-world complexity. We employed four types of perturbations including two types of nutrient pulses, shading, and acidification. To quantify how communities responded to these perturbations, we used a measure of community-wide synchrony combined with spectral analysis that allowed us to assess timescale-specific community dynamics, for example, whether dynamics were synchronous at some timescales but compensatory at others. The 150-d experiment produced 32-point time series of all zooplankton taxa in the mesocosms. We then used those time series to evaluate total zooplankton biomass as an aggregate property and to evaluate community dynamics. For three of our four perturbation types, total zooplankton biomass was significantly less variable in systems with environmental variation than in constant environments. For the same three perturbation types, community-wide synchrony was much lower in fluctuating environments than in the constant environment, particularly at longer timescales (periods ≈ 60 d). Additionally, there were strong negative correlations between population temporal variances and the level of community-wide synchrony. Taken together, these results strongly imply that compensatory interactions between species stabilized total biomass in response to perturbations. Diversity did not differ significantly across either treatments or perturbation types, thus ruling out several classes of mechanisms driven by changes in diversity. We also used several pieces of secondary evidence to evaluate the particular mechanism behind compensatory responses since a wide variety of mechanisms are hypothesized to produce compensatory dynamics. We concluded that fluctuation dependent endogenous cycles that occur as a consequence of consumer–resource interactions in competitive communities were the most likely explanation for the compensatory dynamics observed in our experiment. As with our previous work, scale-dependent dynamics were also a key to understanding compensatory dynamics in these experimental communities.

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

INTRODUCTION

It is increasingly apparent that ecological communities and the ecosystem functions that they produce can show substantial stability in the face of environmental change and variability (Steiner et al. 2011, Floder and Hillebrand 2012, de Mazancourt et al. 2013, Downing et al. 2014). Aggregate properties are characteristics of a community or ecosystem that are the products of many or all species in the system, for example total biomass, total abundance, or ecosystem functions.


Theory predicts that these aggregate properties are stabilized through time in response to environmental variation by a variety of mechanisms (Cottingham et al. 2001, Downing et al. 2014). One of the most widely discussed and poorly understood of these mechanisms is compensatory dynamics (Holling 1973, Gonzalez and Loreau 2009).

Compensatory dynamics occur when negative covariances between species stabilize aggregate community properties and ecosystem functions such that a decrease in abundance or function of one species is offset by increases from other species (Fig. 1). While many other hypothesized community stabilizing mechanisms require high diversity to function (e.g., variance–mean scaling,

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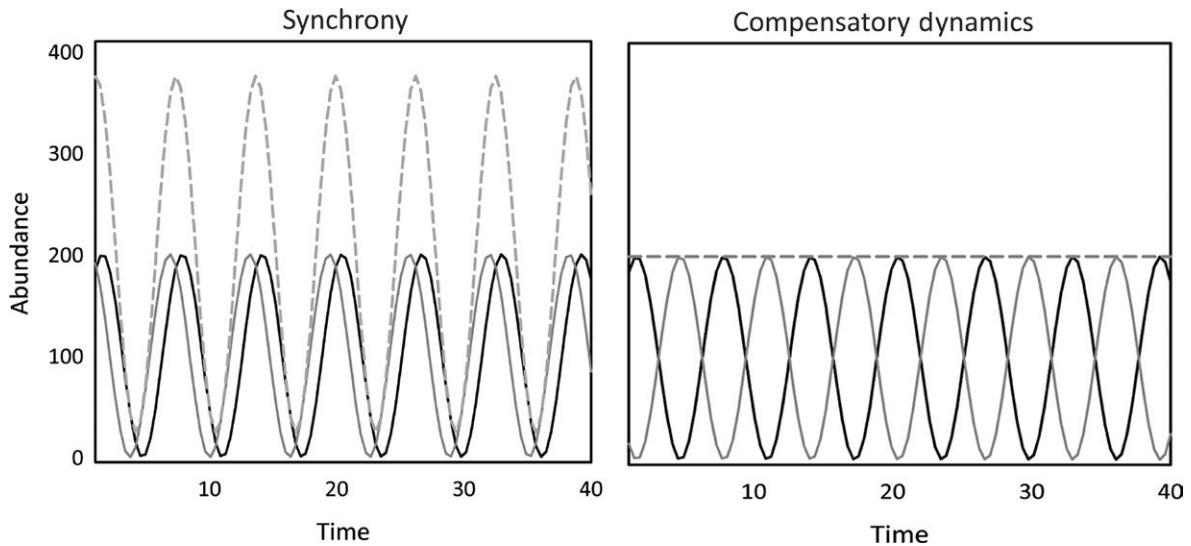


FIG. 1. Effects of synchronous dynamics and compensatory dynamics on aggregate community properties. Even though the population variance in each scenario is exactly the same, the aggregate is stabilized in the compensatory dynamics scenario because of negative covariances between species. The y-axis is shown as abundance, but could be biomass, function, etc. Units on both axes are arbitrary

insurance effects), high levels of diversity are not strictly necessary to produce stabilization of aggregate properties via compensatory dynamics (Cottingham et al. 2001, Downing et al. 2014). According to existing theory, there are three classes of mechanisms for producing compensatory dynamics: fluctuation-independent mechanisms, fluctuation-dependent endogenous mechanisms, and fluctuation-dependent exogenous mechanisms (Gonzalez and Loreau 2009). Fluctuation-independent mechanisms propose that differences in species' responses to environmental variation will lead to negative covariation among species within communities independent of the specifics of species intrinsic dynamics, thus the term "fluctuation independent" (Ives et al. 1999, Loreau and de Mazancourt 2008). On the other hand, fluctuation-dependent mechanisms are predicated on specific population dynamics (i.e., fluctuations) for the proposed mechanisms to operate (Gonzalez and Loreau 2009). In fluctuation-dependent endogenous mechanisms, systems of consumers competing for live resources generate compensatory dynamics by interactions among consumers and resources (Abrams 2006). However, compensatory dynamics through fluctuation-dependent exogenous mechanisms occur when sources of environmental variability interact with intrinsic population cycles to produce covariance between the effects of environment and the effects of competition, essentially setting up the scenario that no species can be the best under all environmental conditions (Chesson 2000, Loreau et al. 2003, Gonzalez and Loreau 2009). While this mechanism requires environmental variability, it differs from fluctuation-independent mechanisms because fluctuation-independent mechanisms are predicated on direct species responses to

environmental variability while fluctuation-dependent: exogenous mechanisms are based on the interaction between environment and consumer-resource dynamics (Gonzalez and Loreau 2009).

Considerable correlative evidence for compensatory dynamics exists from a wide range of systems (e.g., Havens and Carlson 1998, Fischer et al. 2001, Bai et al. 2004, Vasseur et al. 2005, Vasseur and Gaedke 2007, Valdivia et al. 2013). However experimental demonstrations of compensatory dynamics are in short supply. This shortcoming is particularly true for controlled experiments performed in systems with realistic levels of diversity. Experiments in two different algal microcosm systems have clearly demonstrated compensatory dynamics but, in both cases, communities consisted of few species relative to their counterpart natural communities (Gonzalez and Descamps-Julien 2004, Romanuk et al. 2010). The European diversity-function experiment BIODEPTH demonstrated compensatory dynamics in experimentally manipulated grass communities. However, evidence of compensatory dynamics was only strong for two-species treatments (Hector et al. 2010). Two sets of experiments using plankton mesocosms with near-natural diversity have generated compensatory dynamics in response to perturbations and demonstrated that these compensatory responses involved many of the species in the experimental communities (Downing et al. 2008, Howeth and Leibold 2013). Compensatory dynamics have also been implicated in stabilizing aggregate properties in several whole-ecosystem perturbation studies, including lakes subjected to experimental pH manipulations (Fischer et al. 2001, Keitt and Fischer 2006), grassland plants subjected to fertilization treatments

(Tilman 1996), and grasses in response to plowing (Grman et al. 2010). However, there is also some evidence suggesting that compensatory dynamics may be a rare phenomenon in nature. Many studies have explicitly searched for evidence of compensatory dynamics and failed to find them (Klug et al. 2000, Steiner 2005, Steiner et al. 2005). An analysis of 41 time-series data sets from natural communities concluded that strong negative covariances indicative of compensatory dynamics were extremely rare (Houlahan et al. 2007), though these conclusions have been criticized for overly simplistic methodology (Loreau and de Mazancourt 2008, Gonzalez and Loreau 2009). However, a recent investigation of similar scope using robust analytical methodologies found that synchronous dynamics were far more prevalent in natural plankton systems than compensatory dynamics, especially over large spatial and temporal scales (Vasseur et al. 2014). These differences among results may stem from a variety of causes including methodological error, or real differences between systems based on factors like trophic state, dominant organisms, or system complexity (Gonzalez and Loreau 2009).

A recent key insight regarding compensatory dynamics is that they may be timescale dependent, i.e., species may be synchronous at one timescale and compensatory at other timescales (Vasseur et al. 2005, 2014, Keitt and Fischer 2006, Downing et al. 2008). In such cases, without examining community dynamics using a timescale-specific methodology (e.g., spectral analysis), combining multiple dynamics across scales within a single time series can mask compensatory effects (Keitt and Fischer 2006, Downing et al. 2008). Timescale-specific dynamics may also explain why compensatory dynamics appear rare in examinations of raw time series (e.g., Houlahan et al. 2007), though some studies that do employ timescale specific methodologies also identify compensatory dynamics only rarely (Vasseur et al. 2014).

Here we present the results of a suite of coupled experiments that demonstrate stabilization of aggregate community properties in realistically diverse plankton communities. We previously reported results from a subset of our work in which compensatory dynamics stabilized total biomass and net primary productivity in response to a nutrient pulse perturbation (Downing et al. 2008). In this report, we expand on those results and demonstrate their generality across a range of perturbations. As with our previous results, we utilized spectral transformations of our time series data to investigate timescale-specific community dynamics. We also used ancillary evidence from these experiments to evaluate the mechanisms that produced compensatory dynamics when they were detected. We used the specific characteristics of these mechanisms (described in detail in Gonzalez and Loreau 2009) to try to address which mechanism was most likely to be responsible for our results.

METHODS

Mesocosm establishment and manipulation

We created replicate pond ecosystems in mesocosms with naturally diverse assemblages of algae and zooplankton in order to explore the effects of perturbations on community and ecosystem properties. Mesocosms were 300-L polyethylene tanks with mesh lids (1 mm) to prevent foreign immigration into the tanks. The mesocosms were filled with well water and contained 20 L of silica sand as substrate. We inoculated the mesocosms with microbes, algae, and zooplankton from 10 local ponds in mid April and biweekly thereafter to simulate colonization from nearby ponds that tracked changes in natural pond communities. Prior to the application of experimental perturbations, all mesocosms were maintained under nutrient inputs typical of eutrophic ponds in Southern Michigan, reaching target levels of 150 μg P/L and 2250 μg N/L in the form of NaH_2PO_4 and NaHNO_3 .

To maintain constant nutrient levels in the water column of the mesocosms, we replaced 35% of the target nutrients on a weekly basis. Replacement rates were based on previous research in these mesocosm systems indicating 30–35% per week of target levels of nitrogen and phosphorous were lost from the water column to the sediments and mesocosm walls (i.e., a loss of 675 μg N/L and 45 μg P/L per week). As a result, all mesocosms received the same total amount of replacement nutrients and differed only in addition schedule. All mesocosms were maintained outdoors and were subject to identical ambient environmental variability so the perturbation treatments represented the only form of environmental forcing that was unique among treatments.

We used pulses of nutrients, light, and acidification as experimental perturbations. For all treatments, the delivery *schedule* rather than overall quantity served as the perturbation. For example, all nutrient perturbation treatments received the same total amount of nutrients, but some treatments received them as pulses rather than as continuous input. We established a total of 52 experimental units divided into five treatments, several of which had multiple treatment levels (Table 1). For each treatment level, there were four replicate mesocosms, and all experimental units were established beginning 1 May. In the “constant environment” treatment (C) we added weekly total nitrogen and phosphorus inputs at a constant rate (i.e., constant drip) via peristaltic pumps to replace the estimated 35% loss of N and P per week. Two perturbation treatments involved varying the frequency of nutrient inputs in order to generate different degrees of environmental variability: simultaneous additions of nitrogen and phosphorus (N+P) and additions that alternated inputs of nitrogen and phosphorus (N|P). In the N+P and N|P treatments, we produced three treatment levels by

TABLE 1. Description of experimental perturbations and treatment levels with abbreviations.

Treatment	Abbreviation	Treatment levels
Constant input of nutrients	C	only one treatment level
Simultaneous additions of nitrogen and phosphorus	N+P	additions at frequency of 1, 2, and 3 weeks
Alternating additions of nitrogen and phosphorus	N P	additions at frequency of 1, 2, and 3 weeks
Exposure to light by removing mesocosm shade cloth	Lt	exposure at frequency of 1, 2, and 3 weeks
Added HCl solution to lower pH from 9.75 to 6 for 24 h	Ac	acid control (constant nutrients + NaCl), additions at frequency of 2 and 3 weeks

Note: There were four replicate mesocosms for each treatment level.

using addition frequencies of 7, 14, or 21 d. The size of each pulse was 35% of the target N and P levels and it was identical for each pulsed treatment. Therefore in the 7-d frequency treatment level, the entire weekly nutrient input was delivered as a pulse once a week. In the 14- and 21-d treatment levels, because the intended perturbation was nutrient delivery schedule rather than total nutrients, a constant drip was necessary to maintain the same average target weekly nutrient input as the other treatments. This schedule resulted in the same total nutrient input across all treatments (and levels); only the frequency of nutrient pulses varied. 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 variability due to weather fronts. The N|P treatment differed from the N+P treatment in that, for the N+P treatment, both nitrogen and phosphorus were added on each scheduled perturbation day (i.e., every 7, 14, or 21 d), while the N|P treatment alternated additions of nitrogen and phosphorus such that only one of the two elements was added on each date.

We also used light regime and acidification as perturbations (Table 1). Light perturbations were accomplished by alternating periods of shade and light at specified intervals. For example, mesocosms in the 1 week treatment were covered for 1 week, then exposed for 1 week. In our acidification treatments, we lowered the pH from a normal pH of ≈ 9.75 to a pH of 6 for a 24 h period at intervals of 2 or 3 weeks (Table 1). The reduction in pH was accomplished through the addition of 1.2N HCl solution and the return to normal pH was accomplished by adding a 6.3% NaOH solution. NaCl is a product of the reaction between HCl and NaOH, so to control for changes in salinity, a molar equivalent of NaCl was added to the “acid control” tanks. While the other three treatments (N+P, N|P and Lt) explicitly targeted phytoplankton, we expected that the acidification treatment would affect multiple trophic levels simultaneously. Pulses of light, pH, and

alternating N|P may not have exact analogs in nature, but they were included in the experimental design to test both the theoretical of the role of environmental variability and the generality of its effects for inducing compensatory dynamics.

Measurement and analysis

We sampled each mesocosm 32 times at even intervals every 4–5 d from 7 May through 24 September of 2002. On each sampling date, we collected 16 samples of 750 mL using a tube sampler made from 2-inch PVC pipe (5.08 cm diameter) designed to sample the entire water column. The 16 tube samples were spread evenly across the mesocosm and pooled in a single bucket from which we extracted a 300-mL sample for phytoplankton analysis. The remainder was filtered through 80- μ m mesh, handpicked to remove unwanted particulates (e.g., clumps of detritus, sand, etc.) and preserved in sucrose Lugols solution for microscopic enumeration in the lab. We estimated biomass by applying published length–mass regressions to abundance data.

We examined temporal stability of the zooplankton community using aggregate community measures. As a measure of aggregate variability, we used the coefficient of variation (CV) in total zooplankton biomass through time for each mesocosm (Cottingham et al. 2001). We analyzed these results by performing one-way ANOVA with planned contrasts; in particular, we planned to contrast response variables between constant and variable environments.

To examine the changes in species composition of zooplankton communities through time, we employed Principal Coordinates Analysis (PCoA) to reduce the dimensionality of the zooplankton community data set and to visualize the changes in the zooplankton community within each treatment. We performed a single PCoA on a Bray-Curtis dissimilarity matrix that included all experimental units and all points in our time series, thus allowing direct comparison between all perturbations and treatments on a common scale.

To investigate the mechanisms that contributed to differences in stability among treatments, we examined a metric of community synchrony combined with wavelet analysis (Keitt and Urban 2005, Keitt and Fischer 2006, Downing et al. 2008). Metrics of synchrony examine the

amount of negative covariance between species in a community using population time series and usually take the form of variance ratios (VR) comparing variance of the community aggregate to the summed variance of individual species (Frost et al. 1995, Loreau and de Mazancourt 2008). In this study, we elected to use a metric developed by Loreau and de Mazancourt (2008) because it is greatly improved over previously proposed VR-style metrics (e.g., Frost et al. 1995). The metric is less sensitive to community size effects compared to earlier VR metrics (though not immune; Bauer et al. 2014), and the resulting statistic is standardized between 0 and 1 as opposed to other versions of VRs. For the VR we employed, 0 indicates perfect compensatory fluctuations between species while 1 indicates perfect synchrony (Loreau and de Mazancourt 2008).

Prior to calculating the VR, we wavelet transformed all time series. Wavelet analysis is a spectral technique that partitions the variability contained in a time series into variability associated with specific timescales (Keitt and Urban 2005). For example, variance associated with fluctuations on a 10-d fluctuation period can be separated from variance associated with 50-d periods. Variance at each scale is statistically independent from variance at other scales, thus the wavelet transformation combined with a VR allows timescale-specific evaluation of community dynamics because the VR can be calculated specifically at each timescale since it preserves both frequency based information (i.e., timescales) as well as an estimation of actual temporal dynamics. In other words, it converts data in the response \times time domain to data in the response \times time \times frequency domain (Keitt and Fischer 2006, Downing et al. 2008). Wavelet transformations were performed using the Morlet wavelet with six octaves and four voices, implemented using the cwt function in the Rwave package of the R environment (R Development Core Team 2011). Since the Morlet is complex valued, we examined results based on both real and imaginary parts and found little difference. To reduce wrap-around and end effects, we zero-padded our

time series and did not evaluate observations from extreme frequencies (the two smallest and five largest frequencies). We calculated the VR at each of 17 remaining timescales to examine how asynchrony varied with timescale (Keitt and Fischer 2006). We used one-way ANOVA to evaluate treatment differences at those scales of interest identified graphically.

Evaluation of mechanisms responsible for compensatory dynamics

For each of the three classes of mechanisms that lead to compensatory dynamics, we made predictions for our four perturbation experiments based on expectations from theory (Table 2). We compared these predictions to our empirically generated results to evaluate possible mechanisms. We also performed several analyses that were targeted at alternative explanations for any observed community temporal stability (Downing et al. 2014). In particular, we were interested in three alternative classes of mechanisms: (1) stability through decreased population variance, (2) insurance (McNaughton 1977) or statistical averaging effects (Doak et al. 1998), and (3) dominant species (Steiner 2005) or selection effects (Wardle 1999). The test for the first mechanism is simply an examination of population variances across treatments. Both insurance and statistical averaging effects are predicated on increased diversity, so only if differences in diversity across treatments existed would we expect those effects, and dominant species effects are the result of a single dominant taxon that has low population variance. We also conducted Second Stage Analysis (SSA; Clarke et al. 2006) as part of our evaluation of which mechanisms were likely responsible for producing compensatory dynamics. SSA is a technique that directly evaluates the congruence between time series by comparing dissimilarity structures among groups in designed studies (Clarke et al. 2006). In our case, to evaluate the possibility of fluctuation-independent mechanisms, we

TABLE 2. Characteristics of the three major mechanisms for generating compensatory dynamics in competitive communities and the ways in which data from our experiments can address each.

Compensatory mechanism	Characteristics of mechanism	Predictions for our experiment
Fluctuation independent	Direct response to environment differs between species (Ives et al. 1999, Loreau and de Mazancourt 2008)	Correlation structure between species should change with both type and schedule of perturbation.
Fluctuation dependent: endogenous	Competition for resources. Cycles produced by nonlinearities in consumer–resource interactions or by interactions between resources (Abrams 2006).	Larger differences between perturbation and control for perturbations involving resources (N+P, N P, Lt) vs. not involving resources (Ac).
Fluctuation dependent: exogenous	Temporal autocorrelation in environmental variability generally reduces compensatory dynamics, especially autocorrelation over longer timescales (Gonzalez and De Feo 2007).	Compensatory dynamics should be less apparent in treatments with longer intervals between perturbations (controls > 1 week > 2 week > 3 week).

Note: Treatment abbreviations and explanations are in Table 1.

compared the congruence in correlation structures among true replicates (for example, N+P vs. N+P; 1 week vs. 1 week) to the congruence for comparisons across treatments for both perturbation type and perturbation schedule (for example, N+P vs. N|P; 1 week vs. 2 weeks).

RESULTS

In all treatments, there was a similar overall temporal trajectory of the zooplankton community based on PCoA (PCoA Axis 1 = 32% variance, PCoA Axis 2 = 20% of variance; Fig. 2). During the first 25 d of the experiment, communities shifted rapidly from assemblages dominated by copepods to assemblages dominated by cladocerans, in particular *Scapholebris*, *Daphnia*, and *Bosmina*. During this period, they also increased in detectable taxon richness. Over the next 4 weeks, there was an increase in relative abundance of *Ceriodaphnia*, *Simocephalus*, Calanoids, and copepod nauplii (Fig. 2), but despite shifts in relative dominance, richness did not change appreciably for the last three-quarters of the experiment (Supplementary Materials, Appendix S2: Fig S1). There were notable differences in the assemblage time series among specific perturbation treatments. In particular, several perturbation treatments varied less at the end of the experiment relative to the constant environment. This result was most obvious in the 1-week and 3-week pulse treatments of the N+P, N|P, and the Lt perturbation experiments. There were also clear differences in the time series of Ac perturbation treatments when compared to other perturbation types (Fig. 2).

Regardless of perturbation type or frequency, taxon richness followed a similar temporal trend throughout the experiment (Supplementary Materials, Appendix S2: Fig S1). Richness increased from around seven detectable taxa immediately post inoculation, to ≈ 12 taxa by 40 d. Taxon richness fluctuated around an average ≈ 12 taxa per sample throughout the remaining 100 d of the experiment and any differences among perturbation treatments were idiosyncratic with no consistent differences between perturbation type or frequency. Results were very similar with other common diversity indices (Table 3).

For three of our four types of perturbations, temporal stability of total zooplankton biomass was higher in communities subject to environmental variation relative to controls (Fig. 3). Linear contrasts of constant vs. variable environments revealed significantly greater stability in the variable environments for the N+P ($t_{12} = 2.48$; $P = 0.029$), N|P ($t_{12} = 2.52$; $P = 0.027$), and Lt ($t_{12} = 2.30$;

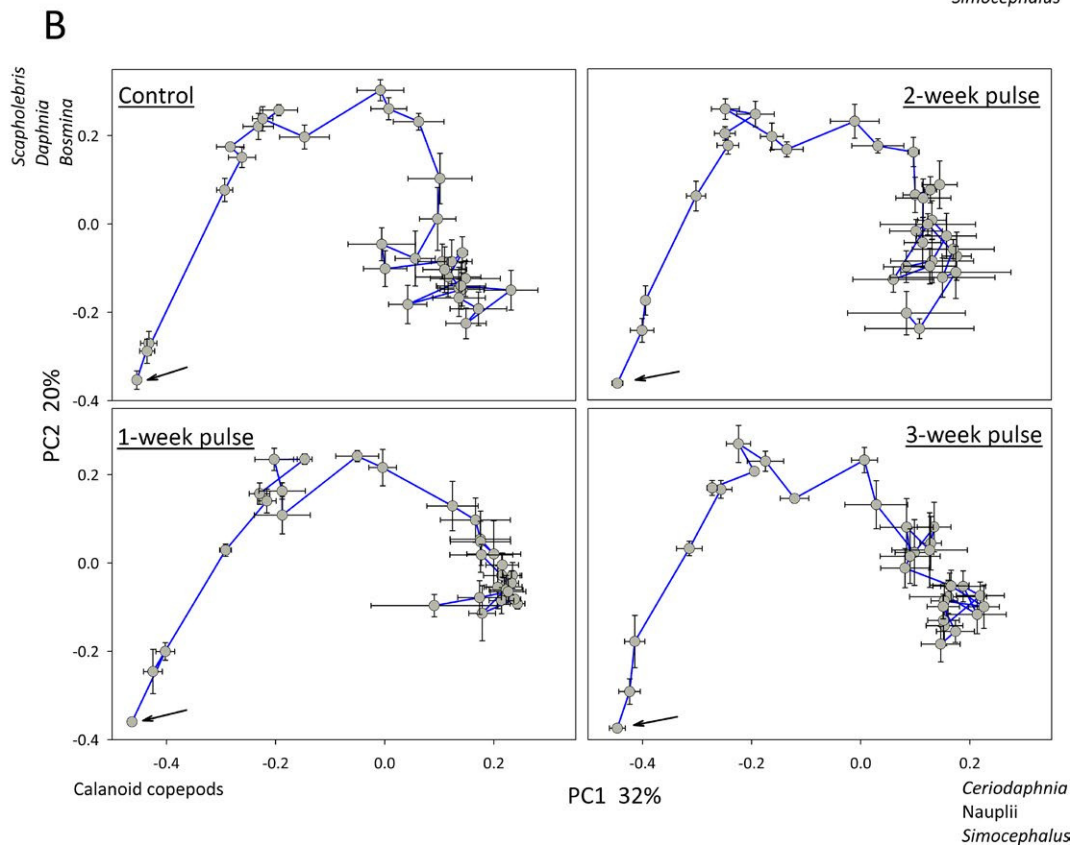
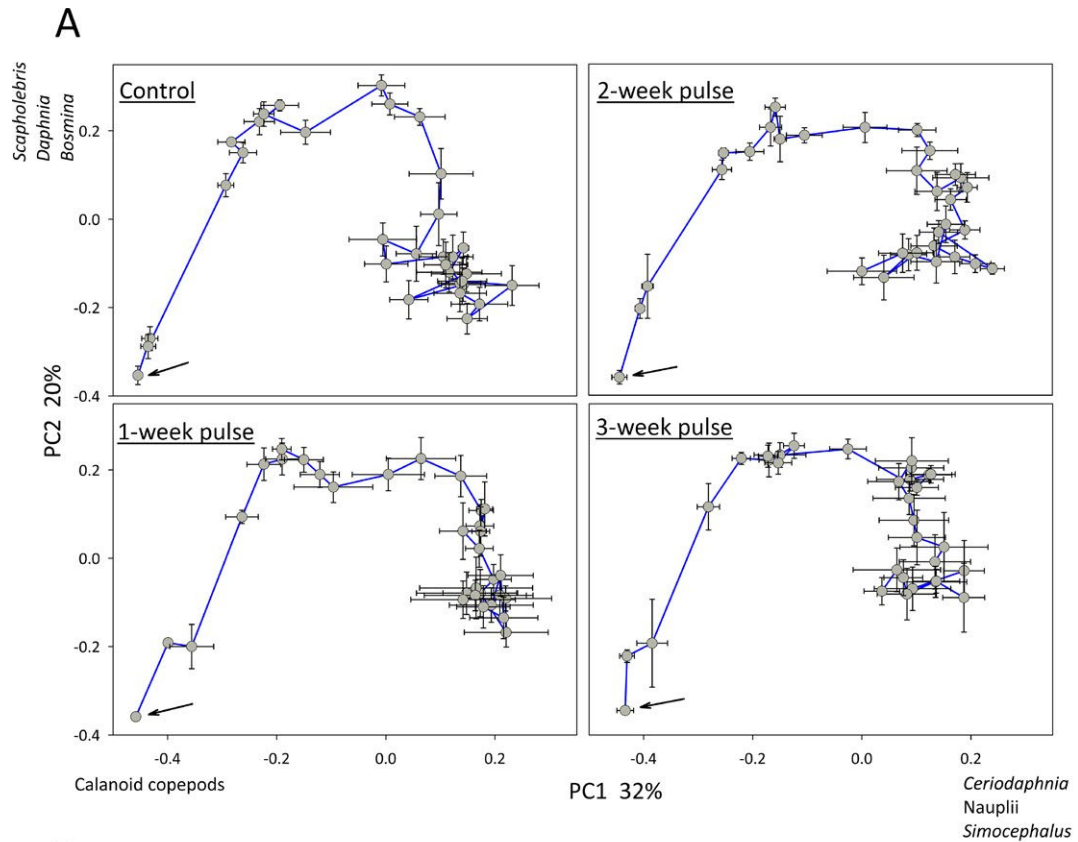
$P = 0.040$) experiments. Experimental perturbations by acidification (Ac) produced no differences between treatments ($t_9 = 0.17$; $P = 0.87$).

For three of our four perturbation types, VR analysis demonstrated significantly decreased synchrony in Variable environments compared to Constant environments at several temporal scales (Fig. 4). Not surprisingly, the three perturbations that resulted in decreased synchrony in variable environments were the same three perturbations that produced higher stability in variable environments (N+P, N|P, Lt). The strongest indications of decreased synchrony were at oscillation periods of ≈ 42 –72 d where there were highly significant differences (< 0.01) between perturbation treatments in the N+P and N|P experiments, and significant differences ($0.01 < P < 0.05$) in the Lt experiment. There were also indications of decreased synchrony in pulsed environments at oscillation periods of ≈ 18 –25 d in the N+P, N|P, and Lt experiments, but the magnitude of differences between perturbation treatments was smaller. There were no differences in perturbation treatments at any timescale in the Ac experiment.

Phytoplankton also had clear responses to the perturbation treatments in three of the four experiments: N+P, N|P, and Lt (Table 4). Interestingly, while the effects of the manipulation on total algal biomass only manifested as a change in response through time with no treatment effects, the biomass of edible phytoplankton showed strong responses to the perturbation treatment, either as a direct effect or as an interaction. However, the direction of effect differed among treatments, with the control producing higher biomass in the Lt experiment, but with the 3-week and 2-week perturbations producing higher biomass in the N|P and N+P, respectively (Table 5).

We performed several analyses that allowed us to examine alternative mechanisms that could be responsible for compensatory dynamics. For decreased population variance, there were no mesocosms in which there was significantly lower population variance in perturbation treatments. For statistical averaging/insurance effects, taxon richness followed a very similar trajectory across both treatments and across the four perturbation types and thus could not generate difference among treatments (Supplementary Materials Appendix S2: Fig S1). Dominant species/sampling effects: in our experiment, some taxa were more abundant than others in our mesocosms as would be expected, but the most abundant taxon changed through time, and no taxon ever completely swamped all other taxa. The results of the SSA clearly indicated that perturbation types produced larger differences in the

FIG. 2. Principal Coordinates Analysis showing temporal trajectories of zooplankton community composition in each treatment during the 144-d experiment: (A) simultaneous pulses of nitrogen and phosphorus, (B) alternating pulses of nitrogen and phosphorus, (C) light pulses, and (D) acid pulses. Each point represents the bivariate average of four mesocosms (\pm SE). Black arrows indicate the beginning of the experiment. Taxa names below/beside each axis indicate taxa that weighted heavily on each axis.



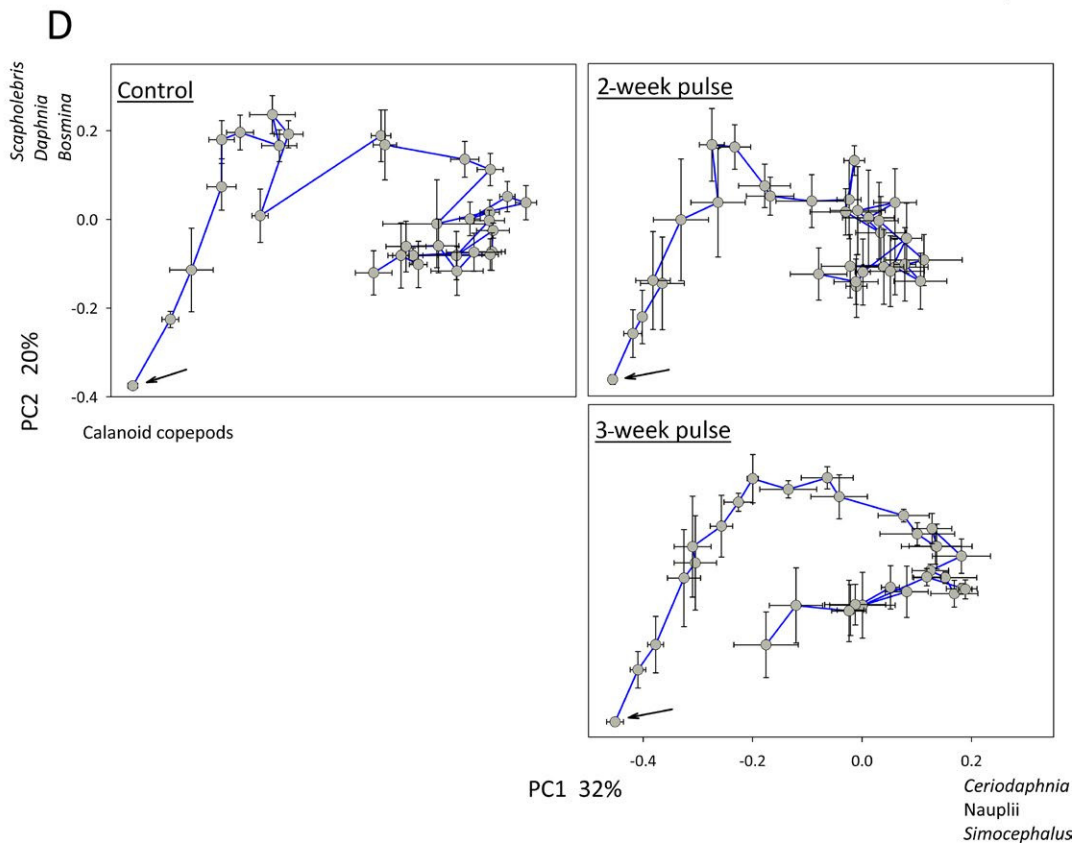
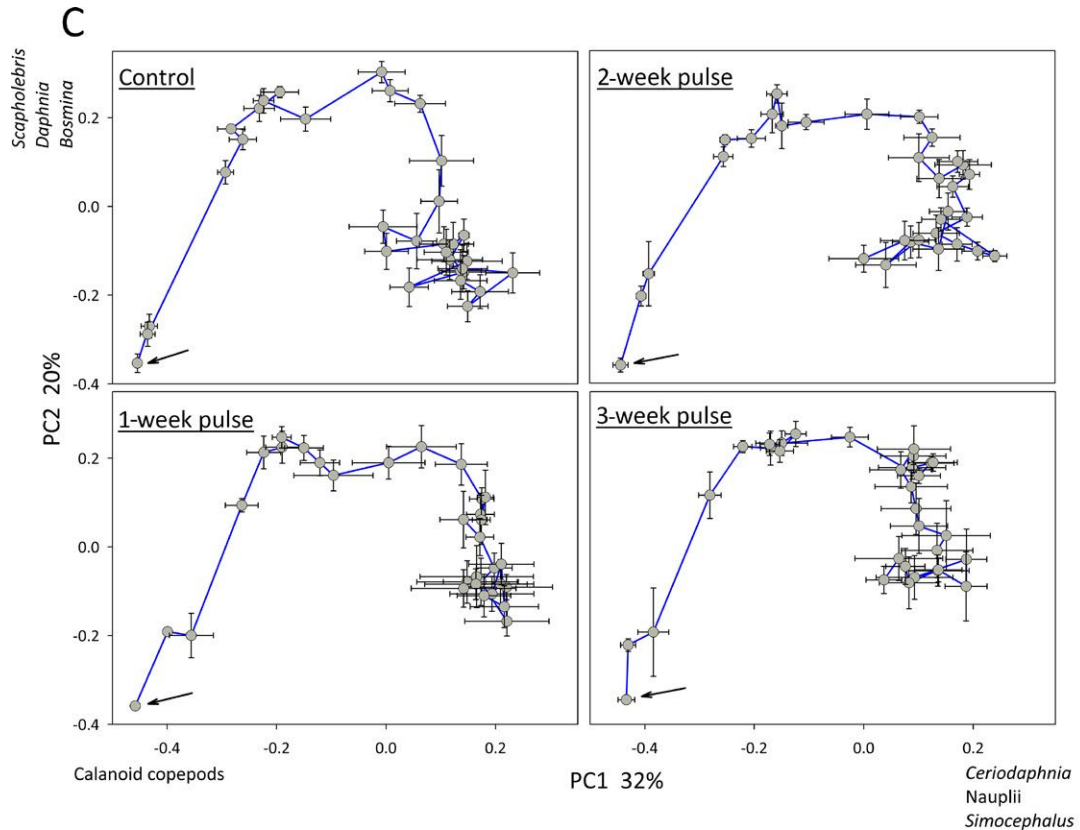


FIG. 2B Continued

TABLE 3. Correlations between biomass of zooplankton taxa and Principal Coordinates axes.

Taxon	PCoA axis 1	PCoA axis 2
<i>Ceriodaphnia</i>	0.77	0.22
<i>Scapholebris</i>	-0.063	-0.77
<i>Daphnia</i>	0.060	-0.64
<i>Cydorus</i>	0.45	-0.31
<i>Bosmina</i>	0.019	-0.67
<i>Alona</i>	0.49	-0.045
Calanoid Copepods	-0.15	-0.13
Cyclopoid Copepods	0.34	-0.035
Copepodites	0.35	-0.053
Nauplii	0.66	0.026
<i>Simocephalus</i>	0.52	-0.037
<i>Diaphanasoma</i>	0.38	0.18

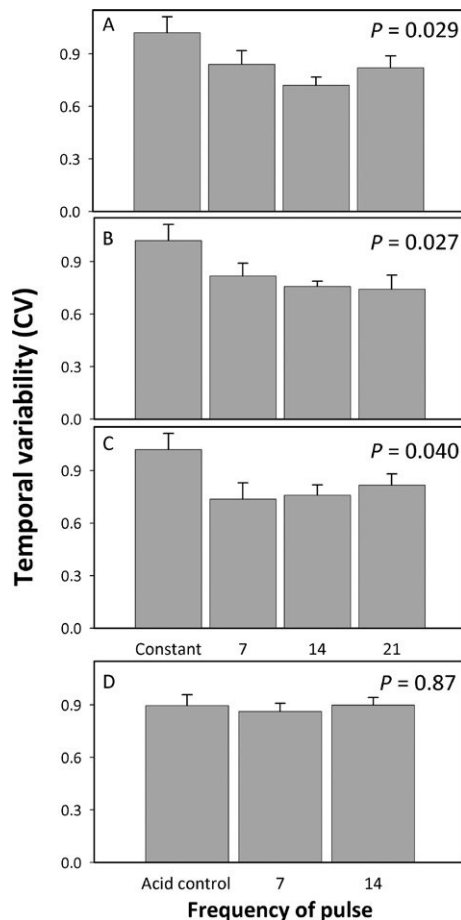


FIG. 3. Temporal variability in total zooplankton density (measured as the coefficient of variation through time \pm SE) in four experimental perturbations: (A) simultaneous pulses of nitrogen and phosphorus, (B) alternating pulses of nitrogen and phosphorus, (C) light pulses created by removing shade cloth covering the mesocosms, and (D) acid pulses. Probabilities in each panel are the results of planned linear contrasts comparing the constant environment to the three fluctuating environments.

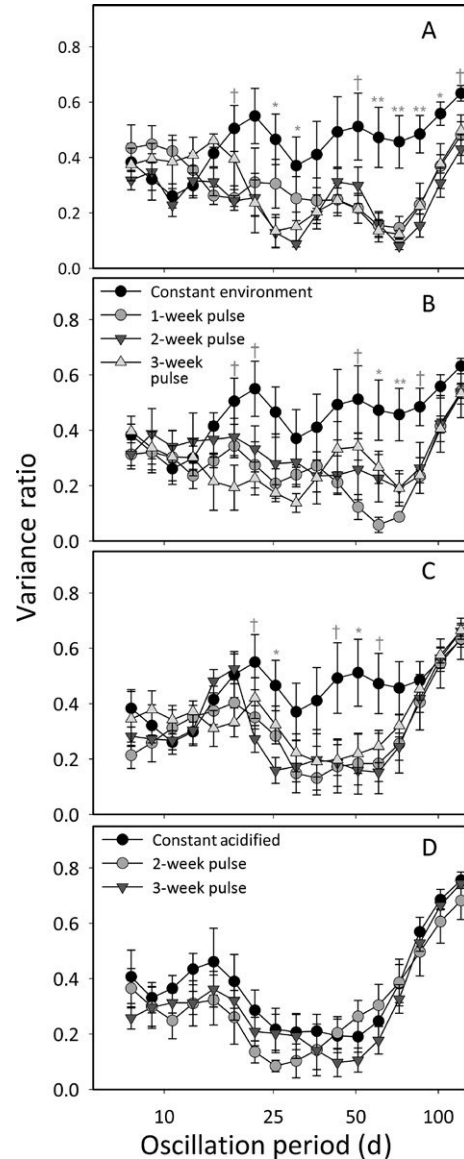


FIG. 4. Variance ratios (VR) of zooplankton communities across a range of frequencies (measured as period or days/cycle) after time series were decomposed by temporal scale. The period axis is pictured on a logarithmic scale to maximize clarity of results the axis. Each panel represents a different perturbation: (A) simultaneous pulses of nitrogen and phosphorus, (B) alternating pulses of nitrogen and phosphorus, (C) light pulses, and (D) acid pulses. The legend in panel B applies to panels A, B, and C. Error bars represent one standard error of the mean. The variance ratio gives an indication of the amount of synchrony in community dynamics with one being perfect synchrony between all species and 0 being complete asynchrony or compensation. † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$ from one-way ANOVA at individual timescales.

correlation structure than perturbation schedule, contrary to the prediction that both type and schedule should have strong effects. Details and results of this analysis are found in Supplementary Materials (Appendix S1: Tables S1–S4).

TABLE 4. Effect of experimental perturbations on phytoplankton biomass based on pigment concentrations.

Experiment and response	Treatment	Time	Treatment \times Time	Trend
N+P				
Total algae	0.25	<0.001	0.53	C > NP2 > NP1 > NP3
Total edible	0.039	<0.001	0.15	N+P2 > C > N+P1 > N+P3
N P				
Total algae	0.17	0.030	0.85	N P3 > N P1 > C > N P2
Total edible	0.18	<0.001	0.010	N P3 > C > N P1 > N P2
Lt				
Total algae	0.13	0.0021	0.48	C > L2 > L3 > L1
Total edible	0.44	<0.001	0.046	C > L2 > L1 > L3
Ac				
Total algae	0.13	0.088	0.36	A3 > AC > A2
Total edible	0.28	0.0041	0.98	A2 > A3 > AC

15 Note: Effects are from a general linear repeated measures model with treatment (perturbation frequency) and time as factors.

TABLE 5. Correlation between average population variance and the variance ratio (Loreau and de Mazancourt 2008).

Experiment	<i>r</i>	<i>P</i> (df)
N+P	-0.61	0.012 (14)
N P	-0.46	0.077 (14)
Lt	-0.40	0.12 (14)
Pooled	-0.51	0.00081 (38)

Note: *r* = Pearson's Correlation coefficient, df = degrees of freedom for test of significant correlation.

DISCUSSION

In three of our four experiments, environmental variability led to stabilization of an aggregate community property, community biomass. This result may seem unusual since perturbations often result in increased temporal variability in populations, as was the case in this study. However, this increased population variability can actually result in stabilization of aggregate community properties when these increased population fluctuations lead to increased negative covariance between taxa and thus compensatory dynamics (Fig. 1, Gonzalez and Loreau 2009). For the same three perturbation experiments in which environmental variability led to greater stability in community biomass, the communities in variable environments had VRs that were significantly lower than the VRs of communities in constant environments (Fig. 4). These lower VRs indicated significantly greater compensatory variation in variable environments. At no timescales did the constant environment produce a significantly lower VR than any of the variable environment treatments for any of our experimental perturbations. For the N+P, N|P, and Lt perturbations, the strongest indications of compensatory dynamics occurred at oscillation periods approximately between 50 and 100 d. The literal interpretation of this result is that populations tended to negatively covary when population

time series were viewed at 50–100 d temporal scales. It should be understood that these temporal scales are not interpreted with literal exactness, i.e., oscillations of exactly 50 or 100 d, but are rather approximate cyclic periods. This fuzziness in timescale is expected with wavelet analysis since wavelets convert information in the *time* domain to information in a *time \times frequency* domain, resulting in a necessary tradeoff between localization in either domain due to the uncertainty principle (Grinsted et al. 2004).

An additional result that suggested compensatory dynamics as the stabilizing mechanism was a negative correlation between average population variance and the VR for the three perturbation experiments in which we saw stabilization in variable environments (). This result suggested that compensatory dynamics were actually encouraged by increases in population variance. In fact, perturbation treatments were often *more* stable than unperturbed controls, clearly demonstrating that it is the cross-species pattern in variance within a community that leads to increased or decreased variance in response to a disturbance. Other experimental studies have produced evidence demonstrating similar effects of environmental variability in a variety of systems (Gonzalez and Descamps-Julien 2004, Downing et al. 2008, Hector et al. 2010) and at least one previous study has shown that compensatory dynamics could be induced by increasing stress in experimental rock pool systems (Romanuk et al. 2010).

While mechanisms other than compensatory fluctuations can produce stabilizing effects on aggregate properties, in the case of our study, other mechanisms can be eliminated based on a closer examination of our results. Community variability could conceivably decrease if the variability of individual populations within the community decreased, but we did not detect such an effect and, in fact, the general trend was for population variance to be higher in variable environments. We can also eliminate statistical averaging and insurance effects as

producing decreased aggregate variability in this experiment since both of these mechanisms are predicated on increases in diversity within communities and, in the current study, diversity was effectively held constant in our experiments. We can also eliminate dominant species (Steiner et al. 2005) or sampling effects (Wardle 1999). In the case of dominant species or selection effects, a single stable species makes up the majority of abundance or biomass in a community, and thus confers aggregate stability on the community by its numerical dominance. In our experiment, some taxa were more abundant than others as would be expected. However, the identity of dominant species changed through time during the experiment and furthermore, the general trajectory of compositional change was similar across treatments and perturbation types (Fig. 2), therefore differences in dominance cannot explain differences in stability.

In our study, comparing community temporal trajectories across perturbation types and across treatments provides additional insight into the dynamics of communities in our mesocosms (Fig. 2). First, there are several characteristics of the community time series that demonstrate the effectiveness of our experimental mesocosms for understanding how community dynamics influence stability. The starting composition of all communities was highly similar, and the overall temporal trajectory generally followed a stereotyped pattern regardless of the particular perturbation or treatment. Additionally, there was high consistency among replicate mesocosms as indicated by error bars in Fig. 2, particularly at the beginning of the experiment. These trajectories also provide some indirect evidence of compensatory dynamics. Diversity did not differ among treatments nor perturbations and community change followed very similar general trajectories (Fig. 2), suggesting that differences in community stability were generated by modest changes in relative abundance rather than large changes in community composition driven by explosive population dynamics or the addition/deletion of taxa. Stabilization through such fluctuations are the hallmark of compensatory dynamics whether driven by competition between species (Frost et al. 1995) or by differential responses to environmental variation (Ives et al. 1999, Gonzalez and Loreau 2009).

The acidification perturbation did not produce results consistent with the other three perturbation experiments. There was no indication that community biomass was stabilized in fluctuating environments and no evidence of differences in degree of synchrony between treatments. Why did the Ac perturbation produce different results? Based on our knowledge of this system, there are two possible explanations. First, while the other three perturbations targeted primary producers, the acidification perturbation did not. Since several theoretical mechanisms for compensatory dynamics are based on the interactions between consumers and resources (Chesson 2000, Abrams 2006, Gonzalez and Loreau 2009), perturbations directly targeting producers like the N+P, N|P, Lt perturbations would be more likely to induce compensatory

dynamics compared to the Ac perturbation. Supporting this explanation is that, when compared to other treatments, zooplankton abundances for the three acidification treatments were among the lowest of the 13 total treatments. Second, the acidification perturbation was probably the least reflective of natural perturbations of the four types, and therefore perhaps most likely to produce novel responses.

Downing et al. (2008) described early results from this experiment that were roughly equivalent to the N+P perturbation portion of the experiment described here. Despite several changes in analytical methodology, our results in the two studies are almost completely equivalent with one major exception: in Downing et al. (2008), we found significantly higher synchrony in pulsed environments compared to the control at short temporal scales (period ≈ 1 d) and we did not report a similar result in the current study. There are at least two possible explanations for this discrepancy. First, in 2008, we employed a variance ratio proposed by Frost et al. (1995) and in the current work, we use the asynchrony metric of Loreau and de Mazancourt (2008). The Loreau and de Mazancourt metric differs in several ways, but perhaps most importantly, it is distributed between 0 and 1. In contrast, the Frost et al. metric is bounded by a 0 minimum but bounded at the upper limit only by properties of the data, thus frequently resulting in a highly asymmetrical distribution of VRs (Loreau and de Mazancourt 2008). As a result, synchrony is overemphasized with the Frost et al. metric. Second, the actual pattern of results are quite similar despite differences in statistical results (compare Fig. 4A to Fig. 4 in Downing et al. 2008). The statistical results differ because in 2008 we averaged across the three pulsed treatments for simplicity of presentation. Additionally the linear contrast (1 week + 2 week + 3 week vs. $3 \times$ control) produced a statistically significant response that we did not find in the current study despite the results being largely congruent because pooling variance in the linear contrast increases statistical power.

Our results join a relatively small collection of experimental demonstrations of a reduction in variability of an aggregate community property to levels below those of unperturbed controls in response to a perturbation. Simple plankton microcosm communities demonstrated similar dynamics in response to temperature variability (Gonzalez and Descamps-Julien 2004), as did grassland communities in response to plowing disturbance (Grman et al. 2010). In each of the previous examples, investigators also concluded that compensatory variation was the most likely explanation for the measured result.

Evaluating the mechanisms producing compensatory dynamics

Comparing our results to theoretical expectations (Table 2), we concluded that the most likely mechanistic explanation for compensatory dynamics in our set of experiments was fluctuation-dependent endogenous

cycles. Based on theory, the specific prediction for our experiments for this mechanism was that perturbations involving algal resources—N+P, N|P, Lt—would be more likely to produce compensatory cycles than a perturbation that directly affected primary consumers like our Ac perturbation (Table 2). Our results exactly matched that prediction. Additionally, direct analysis of the response of phytoplankton to the experimental treatments showed that while there were no effects on total phytoplankton biomass, there were strong effects of treatments on edible phytoplankton in the N+P, N|P, and Lt experiments. This direct response of edible plankton suggests exactly the type of consumer-resource interactions that are expected to drive fluctuation-dependent endogenous cycles. It is also likely that the simplified environment of our mesocosms relative to natural systems allowed us to detect dynamics that may be considerably more difficult to detect in natural systems with considerably greater spatial and temporal heterogeneity. Nevertheless, studies in natural systems (e.g., Vasseur et al. 2005, Vasseur and Gaedke 2007) indicate the presence of similarly complex patterns of synchrony-compensation.

On the other hand, predictions for the other two mechanisms, fluctuation-independent and fluctuation-dependent exogenous cycles, did not closely match our results. Results poorly supported the prediction for fluctuation-dependent exogenous cycles that stronger compensatory dynamics should occur with uncorrelated environmental variation and diminish with autocorrelated variation, particularly at longer periods. In none of the experiments did the control treatment show any evidence of compensatory dynamics. Additionally, for the three perturbation types that showed strong compensatory signals, two types (N+P and Lt) showed no strong differences between 1-, 2-, and 3-week perturbation frequencies. The N|P perturbation did somewhat reflect the predicted response with significantly stronger compensatory dynamics in the 1-0week perturbation treatment, though the three perturbation schedules were still more similar to one another than to the controls, counter to predictions (Fig. 3). With regard to fluctuation-independent mechanisms, our results did not match the prediction that differences in correlation structure between perturbation types should be much greater than differences among perturbation frequencies.

Scale dependence and community dynamics

Our experiment revealed that compensatory dynamics were clearly detectable only when population time series were decomposed into multiple temporal scales using spectral transformation, adding to a growing body of work that clearly demonstrates the utility of considering multiple temporal scales when investigating temporal dynamics (e.g., Vasseur et al. 2005, 2014, Keitt and Fischer 2006, Vasseur and Gaedke 2007, Downing et al. 2008, Keitt 2008). Dynamics of natural populations are driven by a wide range of processes including

environmental variation, interactions with other species, and species' own vital rates. Each of these processes is capable of producing a characteristic temporal signal in a population time series (Ives 1995) and distinguishing between the sources of signals can be extremely difficult when multiple signals of differing periodicity are overlain into a single time series, possibly with interactive effects (Keitt 2008). In both our previous work with this system (Downing et al. 2008) and in our current study, compensatory dynamics occur within a limited range of temporal scales, and as such, can be masked by synchronous dynamics at other scales (Keitt and Fischer 2006, Downing et al. 2008).

The masking effect of multiple drivers in population time series may also explain why previous attempts to search for compensatory dynamics by searching for negative covariances between species in typical community data sets have concluded that compensatory dynamics are rare in natural systems (e.g., Houlahan et al. 2008). The possible explanation is elegantly described by Gonzalez and Loreau (2009): "Environmental variation (biotic and abiotic) is multidimensional and represents a mixed set of forces that will rarely directly translate the negative covariation in species responses to the environment into the realized multispecies dynamics." On the other hand, a recent examination of compensatory dynamics using appropriate spectral techniques concluded that compensatory dynamics seemed rare, though the analysis focused primarily on longer timescales (Vasseur et al. 2014). Based on our current and previous results, we suggest that compensatory dynamics may be common in nature, but are rarely revealed through analysis of raw data from natural systems. However, despite difficulty of detection, our work suggests that these dynamics can have a strong stabilizing effect on aggregate community properties. Effective study will likely require targeted data collected from experiments, or observationally at appropriate timescales and analyzed with appropriate methodologies, of which spectral transformations may be among the most currently useful.

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