

Population and community variability in randomly fluctuating environments

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The prediction that environmental fluctuations may destabilise populations and yet stabilise aggregate community properties has remained largely untested. We examined population and community stability under constant and fluctuating temperatures in simple planktonic assemblages of differing algal richness. Temperature dependent resource competition produced a highly asymmetric community structure where algal community biomass was dominated by one species. For a given level of species richness, temperature fluctuations induced lower community covariance and thus stabilised community biomass. However, increasing algal species richness increased the variability of population abundance and growth rates, as well as population and community variability. Consumer dynamics were directly destabilised by environmental fluctuations. These results confirm recent theoretical studies suggesting a stabilising effect of environmental fluctuations at the community level. However, they also support the theoretical prediction that increasing species richness may be of limited value for community stability, most especially in asymmetric communities, when competition directly affects population variability.

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With the growing awareness of unprecedented rates of species loss and the concern of changes in climate variability (Hulme et al. 1999) there has been renewed focus upon the issue of population and community stability. Theory now suggests several means by which population fluctuations may stabilise aggregate community properties (reviewed by Cottingham et al. 2001). However, empirical tests of this theory are few. Here we report the results from an experiment that examined population and community stability in constant and randomly fluctuating environments at different levels of species richness in simple planktonic assemblages. Multiple definitions of stability exist in the literature (reviewed by Loreau et al. 2002), but here we focus on the temporal variability, or constancy, of populations and commu-

nities as a measured by the coefficient of variation (Micheli et al. 1999).

Population stability in a stochastic environment depends upon the sensitivity of population growth rates to environmental fluctuations; large changes in growth rate will tend to be translated into large fluctuations in density (Ives 1995a). The inclusion of other species introduces the possibility of direct and indirect effects on population variability; such interspecific effects may also be modulated by environmental variation (Ives 1995b). Strong competitive interactions tend to decrease population resilience with increasing species richness (Lehman and Tilman 2000). However, instability at the population level does not necessarily translate into instability at the community level.

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For a given trophic level, and a fixed number of species, the variability of an aggregate community process (total biomass) will be lower than the variability of its component species populations when they do not fluctuate in perfect synchrony. Because in general population fluctuations within any given community are not perfectly synchronous this stabilising effect is likely to be common (Doak et al. 1998), and its strength will depend to a great extent upon the degree of asynchrony in species fluctuations. Various effects may generate such asynchrony in particular differential species' responses to environmental fluctuations (McNaughton 1977). A substantial body of theory now supports the notion that such a buffering effect is enhanced by increasing species richness (Walker 1992, Ives et al. 1999, Yachi and Loreau 1999, Ives and Hughes 2002) because the addition of each new species increases the range of responses to the varying environment at the community level. Communities exhibiting such a stabilising dynamic will be characterised by uneven community rank abundance distribution at any one point in time, and changes in abundance ranking through time.

Whether such a buffering effect acts to stabilise the dynamics of a predator is thought to depend upon whether the predator is generalist or specialist (Pimm 1982). A generalist predator will be stabilised by the asynchrony in prey availability associated with the buffering effect. However, a predator specialising on a small subset of the available prey species will be expected to show increased variability associated with the fluctuating densities of its prey. In general, the stability of predator dynamics in response to increasing prey species richness is likely to depend upon changes in prey reliability, prey biomass and prey composition (Luckinbill 1979, Petchey 2000b).

Recently, several theoretical studies have identified general conditions for the existence of a positive diversity-stability relation (Tilman et al. 1998, Hughes and Roughgarden 2000). In a review and synthesis of recent theoretical results Ives and Hughes (2002) define two conditions necessary for a stabilising effect of increasing species richness. Firstly, the net effect of competition on the variability in population growth rates of component species should be independent of species number (that is variability in per capita growth rates should remain the same irrespective of the number of species in the community) and the strength of interspecific competition, and secondly, all species within the community should have approximately equal densities. Although these assumptions are not excessively unrealistic conditions under which the breakdown can be easily identified. For example, highly asymmetric competition may result in communities characterised by the relatively long-term dominance of one or a few species as opposed to communities of species with approximately

equal densities; a characteristic of natural communities that would seem to be the norm rather than the exception (Rahel 1990, Venrick 1990, Padisák 1992, Bengtsson 1994).

Previous experimental tests of population and community stability theory have either adopted inter-replicate measures of variability as a surrogate for temporal stability (Naeem and Li 1997), or have used only two samples to estimate temporal variability (Petchey et al. 2002), whilst field studies have examined temporal stability over relatively short temporal scales (Tilman 1996, Mulder et al. 2001, Pfisterer and Schmid 2002). None have directly measured multiple time series of population and community stability in controlled constant and fluctuating conditions. Here we report the results from an experiment that measured the temporal stability of a model planktonic community in which environmental fluctuations and species richness were controlled. The population dynamics of each algal species both in monoculture and in polyculture, and in the presence and absence of environmental fluctuations were recorded over a long period relative to their generation times. The factorial design allowed us to directly assess the relative importance of environmental variability and interspecific interactions for population and community stability. For a given level of species richness environmental fluctuations stabilised total algal biomass. Increasing algal species richness resulted in increased population and community variability. Thus a fluctuation induced buffering effect was counterbalanced by a destabilising effect of increasing species richness on population variability. Predator dynamics were destabilised by environmental fluctuations. We discuss our results in the light of current theory.

Methods

The experimental system

The experimental communities were assembled from a species pool consisting of the rotifer *Brachionus calyciflorus* and six algal species: four green algae – *Kirchneriella lunaris*, *Scenedesmus obliquus*, *Staurastrum polymorphum* and *Chlorella vulgaris*, and two diatoms – *Synedra acus* and *Asterionella formosa*.

Assemblages of varying diversity (see below) were maintained in 100 ml screw top bottles in 80 ml of sterile artificial medium COMBO animate (Kilham et al. 1998; absolute concentrations of Si, P and N were 100, 50 and 1000 $\mu\text{mol l}^{-1}$ respectively), under semi-continuous culture (dilution = 0.05 day^{-1} , with sterile medium). This dilution represented an experimentally imposed density-independent mortality rate for all organisms within the assemblage. In order to ensure the long term persistence of all species once a week, and on the same day, a 100 μl of each algal species (green algal

species: ≈ 104 cells; diatom species: ≈ 103 cells) was added to each microcosm. The microcosms were manually shaken twice a day to ensure algal cell suspension. The specific light and temperature conditions adopted during the experiment are given below.

Environmental fluctuations

Random environmental variability possesses two important statistical properties, a long term correlation structure, and increasing variance through time (Pelletier 2002), that should be incorporated into any 'null' model of environmental fluctuations (Halley 1996). Here we adopted a $1/f$ model (Halley 1996) and constructed two series of random temperature fluctuations following the spectral mimicry method described by Cohen et al. (1999). A $1/f$ series can be approximated by the following trigonometric function:

$$\text{temperature}(t) = \sum_{f=1}^{n/2} \frac{1}{f^\gamma} \sin\left(\frac{2\pi ft}{n} + \theta_f\right) \quad (1)$$

Where n is the length of the series, f the frequency (units of cycles per 12 hr), t is the time (units of 12 hr), γ determines the relation between amplitude and frequency and θ_f is a uniform deviate $[0, 2\pi]$ which adds random phase to each sine wave. This experiment employed two temperature series, F1 and F2 (Fig. 1), with $n = 128$ and $\gamma = 1$, a maximum of 27.5°C , a minimum of 11.5°C , a mean of 20°C and a variance of 19.75. These two matching series had an almost identical Fourier spectrum.

Experimental design and sampling

Replicate microcosms were randomly assigned, in a constrained two-way factorial design, to an algal diversity (1, 3, and 6 algal species with *B. calyciflorus* introduced into each diversity level) and temperature treatment (two realisations of $\gamma = 1$ and one constant temperature series with the same mean). All levels were replicated four times making a total of 120 microcosms (10 species combinations \times 3 fluctuation types \times 4 replicates). We thus had monocultures of every algal species, three three-species combinations (1. *A. formosa* + *S. polymorphum* + *K. lunaris*, 2. *S. polymorphum* + *C. vulgaris* + *S. acus*, and 3. *S. acus* + *A. formosa* + *S. obliquus*) and the full six species community, and as a result were able to examine the effect of constant and fluctuating temperatures upon population and community stability with increasing species richness; although the limited number of species combinations precludes a general discussion regarding diversity effects per se.

Following algal inoculation all microcosms were maintained in the same temperature (20°C) and light

($50 \mu\text{mol m}^{-2}\text{s}^{-1}$, 12 hr: 12 hr photoperiod) controlled incubator for 21 days. This period allowed the microcosms to attain steady-state with the imposed dilution regime. On the 22nd day 20 *B. calyciflorus* individuals (0.25 ml^{-1}) were introduced into each microcosm. On the same day the 80 microcosms were then randomly distributed amongst four temperature controlled water baths ($50 \mu\text{mol m}^{-2}\text{s}^{-1}$ on a 12 hr: 12 hr photoperiod). The four baths were divided into two groups, A and B. Group A baths that produced temperature fluctuation series 1, and group B temperature fluctuation series 2. The 40 replicates assigned to the constant temperature conditions were maintained in the original incubator. The fluctuation treatments were then initiated, with a change in temperature every twelve hours according to the temperature series assigned to the water bath. This represented a total of 128 changes in temperature and an experiment length of 64 days.

Algal counts were performed microscopically with the use of a Malassez haemocytometer which has a reliable lower detection limit of 3×10^3 cells per ml. The biomass ($\text{mm}^3\text{ml}^{-1}$) of each species in each replicate was estimated by multiplying the estimated abundance by the average cell volume of 12 cells. Cell volume was calculated from the critical linear dimensions converted to volume using equations that approximate cell shapes (Wetzel and Likens 1991, cell volume was checked periodically throughout the experiment and was not observed to change). Rotifer densities were estimated with the use of stereomicroscope from counts of the number of individuals obtained in the 8 ml dilution recovered every two days.

Data analyses

The effect of species richness (three levels) and environmental fluctuations (three levels) on total algal community biomass, summed community variance, and summed community covariance was evaluated by ANOVA. The effect of species richness and environmental fluctuations upon the mean biomass (log-transformed), coefficient of variation (CV), and the standard deviation in per capita growth rates (σ_p) at the species level was evaluated by a separate ANOVA for each species. Unplanned comparisons were conducted using Bonferroni t-tests and specific treatments were compared using a minimum significant difference (MSD) ($\alpha = 0.01$). The standard deviation in per capita algal growth, scaled by the mean number of cells, was calculated from per capita growth rates estimated as $rt = \log_2 N_{t+1} - \log_2 N_t$. For a given level of species richness the difference between σ_p in the constant and fluctuating temperature treatments is a direct estimate of the variation in per capita growth rates due to environmental fluctuations.

There are a variety of ways of calculating community variability. Here we adopt the coefficient of variation (CV) estimated as $1/ST$ (Lehman and Tilman 2000) where,

$$\frac{1}{S_T} = \frac{\sqrt{\sum_{i=1}^s \text{Var}(B_i) + \sum_{i=1}^s \sum_{j \neq i}^s \text{Cov}(B_i, B_j)}}{\sum_{i=1}^s \bar{B}_i} \quad (2)$$

Here $\bar{B}_i = \frac{1}{n} \sum_{t=1}^n B_i$ and B_i is the biomass of the i th (or j th) of s species over n samples through time. All analyses were conducted in SAS (v8.02).

Results

Extremely good control of temperature was attained (Fig. 1), and recorded temperatures rarely differed from those required by more than $\pm 0.1^\circ\text{C}$. The slope γ of the spectral density of the two temperature fluctuation series recorded in the baths was 1.05 ± 0.09 and 0.95 ± 0.11 (± 1 se).

Following their introduction it became apparent that the rotifers were only able to maintain growth within the microcosms containing *Chlorella* and/or *Scenedesmus*, and within 7–10 days the extinction of *B. calyciflorus* had been confirmed from all other monocultures and the single three-species combination not containing these two algae; suggesting a more specialised feeding behaviour than had been expected. Therefore the dynamics of *Chlorella* and *Scenedesmus* also reflect the effects of predation, whilst the dynamics of *B. calyciflorus* reflect the interaction between temperature fluctuations and prey variability.

Single species algal biomass

The temporal mean biomass of each species differed substantially in monoculture (Fig. 1). *Staurastrum* and *Kirchneriella* exhibited the greatest yields followed in descending order by *Chlorella*, *Scenedesmus* and *Synechococcus* and *Asterionella* (Table 1, 2, and all analyses hereafter). Average species yield of four of the six species declined as the number of species in the community increased (monoculture > 3 species > 6 species: Table 2). *Scenedesmus* was the only species with yields unaffected by growth in polyculture.

Total community biomass

Mean total algal biomass increased with increasing species richness ($F_{2,108} = 9.31$, $P = 0.0002$). However,

none of the replicate three or six species communities had a greater temporal mean biomass than the best monoculture (i.e. *Staurastrum*, Table 1).

Mean total algal biomass did not differ between the fluctuation treatments ($F_{2,108} = 0.02$, ns), and there was no significant interaction between the fluctuation and richness treatments (fluctuation \times richness: $F_{4,108} = 0.97$, ns).

Single-species variability

Differences in the CV of up to 40% were observed amongst species, both in monoculture and polyculture. Increasing species richness increased the CV of all species, except *Scenedesmus* (Table 2). The CV of *Staurastrum* and *Scenedesmus* declined significantly from constant to fluctuating temperatures (Table 2), whereas the CV of the other 4 species was not significantly affected by the fluctuating temperatures. None of the species exhibited a fluctuation \times richness interaction.

The σ_p increased with algal diversity for five of the six species although the main effect of diversity was not significant for *Scenedesmus*. In general, temperature fluctuations had no effect on the σ_p of the monocultures, whilst σ_p increased markedly and consistently from constant to fluctuating temperatures in the 3 species communities. The 6 species communities were characterised by substantial differences amongst species in the response of σ_p from constant to fluctuating temperatures (Fig. 3, Table 2). A significant diversity \times fluctuation interaction upon σ_p was observed for all species (Fig. 3, Table 2), except *Chlorella*, for which there was a significant main effect of the diversity and fluctuation treatments. The strong diversity \times fluctuation interaction for five of the six species reflects how the response of σ_p to the temperature fluctuations depended upon the diversity of the community within which it was embedded.

Algal community variability

Increasing species richness did not significantly affect the CV of community biomass ($F_{2,111} = 2.43$, $P = 0.09$), although inspection of Fig. 2 indicates that increasing species richness tended to increase community variability. Closer analysis of the components of Eq. 2 confirmed that the summed covariance of the six species communities was substantially greater (93.5%) than that of the three species communities ($F_{1,42} = 234.4$, $P < 0.001$). There was no significant difference in the summed variance between three and six species communities ($F_{1,42} = 1.15$, ns).

The CV of total community biomass was 24% (F1) and 14% (F2) lower under fluctuating than constant

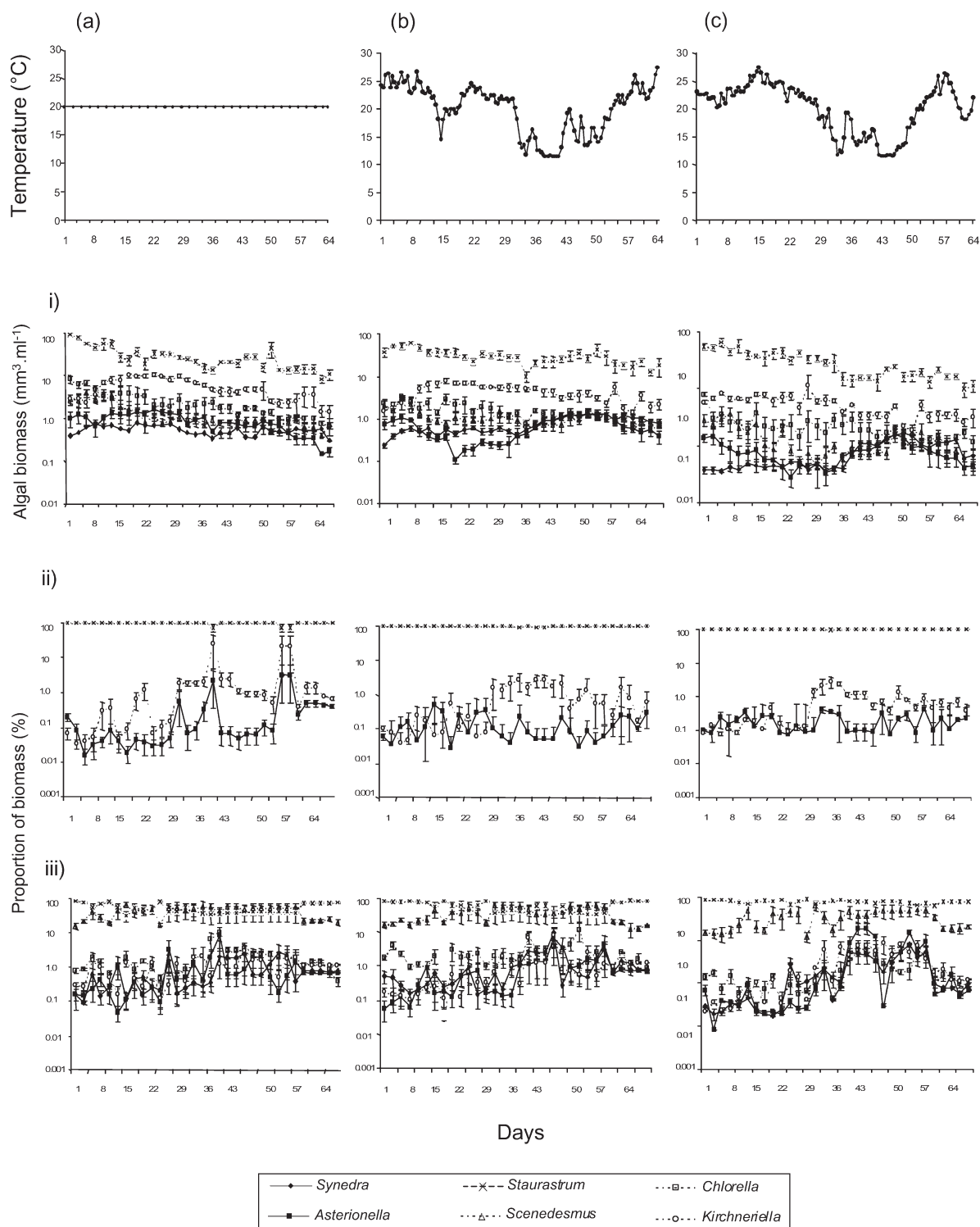


Fig. 1. Temperature series for (a) constant temperature in the incubator, (b) F1 and (c) F2 recorded from the water baths with the corresponding mean biomass dynamics (± 1 se) of all species in monocultures (i). Mean biomass dynamics (± 1 se) of all monocultures ($\times 10^3$), (ii) for one three species community (percent biomass), and (iii) the six species communities (percent biomass), from the (a) constant, (b) F1 and (c) F2 temperature treatments.

Table 1. The mean \pm 1 s.e.m for the coefficient of variation (CV), the standard deviation of per capita growth rates (cp), and mean biomass (ln-transformed, $\text{mm}^3 \text{ ml}^{-1}$) for all algal species in monoculture, and community CV (Eq. 2) and biomass for the polycultures in both constant and fluctuation treatments.

	CV biomass			σ_p			Mean biomass		
	Constant	Fluctuating 1	Fluctuating 2	Constant	Fluctuating 1	Fluctuating 2	Constant	Fluctuating 1	Fluctuating 2
<i>Synedra</i>	0.49 \pm 0.09	0.47 \pm 0.06	0.61 \pm 0.05	0.07 \pm 0.007	0.06 \pm 0.004	0.06 \pm 0.009	19.96 \pm 0.11	20.29 \pm 0.07	20.23 \pm 0.12
<i>Asterionella</i>	0.71 \pm 0.06	0.47 \pm 0.16	0.73 \pm 0.03	0.09 \pm 0.01	0.11 \pm 0.006	0.12 \pm 0.01	20.28 \pm 0.10	19.98 \pm 0.14	20.16 \pm 0.04
<i>Staurastrum</i>	0.74 \pm 0.05	0.55 \pm 0.05	0.65 \pm 0.03	0.09 \pm 0.007	0.09 \pm 0.004	0.08 \pm 0.007	23.83 \pm 0.06	23.92 \pm 0.18	23.88 \pm 0.04
<i>Scenedesmus</i>	0.88 \pm 0.07	0.59 \pm 0.04	0.84 \pm 0.10	0.08 \pm 0.01	0.09 \pm 0.005	0.12 \pm 0.01	20.56 \pm 0.24	20.61 \pm 0.22	20.63 \pm 0.20
<i>Chlorella</i>	0.86 \pm 0.05	0.56 \pm 0.06	0.86 \pm 0.15	0.06 \pm 0.01	0.09 \pm 0.006	0.09 \pm 0.01	21.24 \pm 0.24	20.94 \pm 0.14	21.14 \pm 0.36
<i>Kirchneriella</i>	0.65 \pm 0.09	0.54 \pm 0.03	0.56 \pm 0.09	0.08 \pm 0.02	0.08 \pm 0.003	0.08 \pm 0.03	22.12 \pm 0.19	21.98 \pm 0.17	22.24 \pm 0.05
<i>Synedra</i>	1.01 \pm 0.18	0.62 \pm 0.07	0.68 \pm 0.04	0.06 \pm 0.003	0.24 \pm 0.05	0.21 \pm 0.01	17.58 \pm 0.02	17.90 \pm 0.14	17.86 \pm 0.02
<i>Staurastrum</i>	0.72 \pm 0.05	0.65 \pm 0.03	0.66 \pm 0.03	0.05 \pm 0.006	0.19 \pm 0.05	0.20 \pm 0.01	22.63 \pm 0.09	22.72 \pm 0.21	22.37 \pm 0.02
<i>Chlorella</i>	0.64 \pm 0.11	0.47 \pm 0.04	0.53 \pm 0.15	0.02 \pm 0.003	0.09 \pm 0.02	0.08 \pm 0.01	20.92 \pm 0.05	20.89 \pm 0.14	20.71 \pm 0.08
Community	0.74 \pm 0.05	0.64 \pm 0.07	0.72 \pm 0.04				23.10 \pm 0.26	22.79 \pm 0.27	22.27 \pm 0.08
<i>Asterionella</i>	1.02 \pm 0.09	1.15 \pm 0.07	0.72 \pm 0.17	0.05 \pm 0.003	0.20 \pm 0.03	0.20 \pm 0.04	17.01 \pm 0.04	17.28 \pm 0.05	17.24 \pm 0.16
<i>Staurastrum</i>	0.86 \pm 0.04	0.46 \pm 0.03	0.46 \pm 0.05	0.03 \pm 0.004	0.10 \pm 0.001	0.09 \pm 0.005	23.52 \pm 0.06	23.83 \pm 0.12	23.90 \pm 0.07
<i>Kirchneriella</i>	0.80 \pm 0.04	0.95 \pm 0.03	1.00 \pm 0.08	0.07 \pm 0.004	0.20 \pm 0.01	0.23 \pm 0.03	18.38 \pm 0.12	18.59 \pm 0.11	18.49 \pm 0.06
Community	0.89 \pm 0.05	0.46 \pm 0.03	0.46 \pm 0.04				23.45 \pm 0.31	23.84 \pm 0.11	23.91 \pm 0.07
<i>Synedra</i>	0.76 \pm 0.11	0.69 \pm 0.07	0.91 \pm 0.17	0.05 \pm 0.003	0.17 \pm 0.02	0.21 \pm 0.02	17.28 \pm 0.04	17.61 \pm 0.04	17.58 \pm 0.08
<i>Asterionella</i>	0.61 \pm 0.18	1.00 \pm 0.11	0.86 \pm 0.07	0.04 \pm 0.004	0.17 \pm 0.02	0.19 \pm 0.04	16.91 \pm 0.02	17.14 \pm 0.09	17.20 \pm 0.14
<i>Scenedesmus</i>	1.08 \pm 0.11	0.83 \pm 0.08	0.77 \pm 0.07	0.02 \pm 0.002	0.10 \pm 0.006	0.12 \pm 0.02	20.83 \pm 0.18	20.72 \pm 0.20	20.25 \pm 0.18
Community	1.08 \pm 0.11	0.82 \pm 0.08	0.74 \pm 0.06				21.12 \pm 0.37	20.78 \pm 0.21	20.36 \pm 0.17
<i>Synedra</i>	0.76 \pm 0.11	0.66 \pm 0.05	0.67 \pm 0.08	0.19 \pm 0.01	0.16 \pm 0.02	0.22 \pm 0.01	17.23 \pm 0.08	17.41 \pm 0.06	17.48 \pm 0.05
<i>Asterionella</i>	1.19 \pm 0.08	1.09 \pm 0.03	1.03 \pm 0.03	0.16 \pm 0.02	0.17 \pm 0.04	0.25 \pm 0.03	17.01 \pm 0.08	17.21 \pm 0.07	17.46 \pm 0.16
<i>Staurastrum</i>	1.04 \pm 0.06	0.78 \pm 0.07	0.85 \pm 0.08	0.19 \pm 0.02	0.12 \pm 0.02	0.19 \pm 0.02	22.21 \pm 0.03	22.33 \pm 0.04	22.38 \pm 0.05
<i>Scenedesmus</i>	0.93 \pm 0.06	0.72 \pm 0.05	0.58 \pm 0.09	0.08 \pm 0.008	0.09 \pm 0.006	0.07 \pm 0.008	20.77 \pm 0.08	20.74 \pm 0.06	20.81 \pm 0.08
<i>Chlorella</i>	0.99 \pm 0.12	1.19 \pm 0.15	1.13 \pm 0.16	0.17 \pm 0.02	0.20 \pm 0.02	0.18 \pm 0.02	17.53 \pm 0.14	17.86 \pm 0.05	17.68 \pm 0.17
<i>Kirchneriella</i>	0.83 \pm 0.10	0.79 \pm 0.17	0.72 \pm 0.06	0.23 \pm 0.01	0.15 \pm 0.03	0.24 \pm 0.02	17.68 \pm 0.07	17.58 \pm 0.06	17.91 \pm 0.07
Community	1.22 \pm 0.06	0.94 \pm 0.06	0.97 \pm 0.07				22.62 \pm 0.62	22.12 \pm 0.07	22.24 \pm 0.07

Table 2. The results of ANOVA on the effects of temperature fluctuations (F), and algal species richness (R) on the coefficient of variation of biomass (CV), and on the standard deviation of per capita growth rate (σ_p). ns indicates $P > 0.01$. Unplanned comparisons between levels of algal richness were conducted using Bonferroni t-tests ($\alpha = 0.01$).

	CV				σ_p				Biomass			
	Fluctuation	Richness	R \times F		Fluctuation	Richness	R \times F		Fluctuation	Richness	R \times F	
<i>Synedra</i>	$F_{2,36} = 1.63$ ns	$F_{2,36} = 7.5$ $P = 0.002$ $1 < 3 = 6$	$F_{4,36} = 0.73$ ns		$F_{2,36} = 8.04$ $P = 0.001$	$F_{2,36} = 31.1$ $P < 0.0001$ $1 < 3 < 6$	$F_{4,36} = 10.45$ $P < 0.0001$		$F_{2,36} = 9.23$ $P = 0.0006$	$F_{2,36} = 802.5$ $P < 0.001$ $1 > 3 > 6$	$F_{4,36} = 0.23$ ns	
<i>Asterionella</i>	$F_{2,36} = 0.22$ ns	$F_{2,36} = 13.0$ $P < 0.0001$ $1 < 3 < 6$	$F_{4,36} = 2.75$ ns		$F_{2,36} = 13.38$ $P < 0.0001$	$F_{2,36} = 10.6$ $P = 0.0002$ $1 = 3 < 6$	$F_{4,36} = 5.38$ $P = 0.002$		$F_{2,36} = 4.2$ ns	$F_{2,36} = 1114.7$ $P < 0.0001$ $1 > 3 = 6$	$F_{4,36} = 4.0$ $P = 0.009$	
<i>Staurastrum</i>	$F_{2,36} = 14.29$ ns	$F_{2,36} = 20.5$ $P < 0.0001$ $1 = 3 < 6$	$F_{4,36} = 0.56$ ns		$F_{2,36} = 1.69$ ns	$F_{2,36} = 8.5$ $P = 0.001$ $1 = 3 < 6$	$F_{4,36} = 4.8$ $P = 0.003$		$F_{2,36} = 0.25$ ns	$F_{2,36} = 26.7$ $P < 0.0001$ $1 > 3 > 6$	$F_{4,36} = 0.05$ ns	
<i>Scenedesmus</i>	$F_{2,24} = 8.85$ ns	$F_{2,24} = 2.9$ ns	$F_{4,24} = 1.84$ ns		$F_{2,24} = 8.88$ $P = 0.001$	$F_{2,24} = 1.7$ ns	$F_{4,36} = 5.43$ $P = 0.003$		$F_{2,24} = 0.85$ ns	$F_{2,24} = 1.2$ ns	$F_{4,24} = 1.57$ ns	
<i>Chlorella</i>	$F_{2,24} = 0.61$ ns	$F_{2,24} = 16.2$ $P < 0.0001$ $1 = 3 < 6$	$F_{4,24} = 1.28$ ns		$F_{2,24} = 5.05$ $P = 0.014$	$F_{2,24} = 45.9$ $P < 0.0001$ $1 = 3 < 6$	$F_{4,36} = 0.86$ ns		$F_{2,24} = 0.08$ ns	$F_{2,24} = 329.1$ $P < 0.0001$ $1 = 3 > 6$	$F_{4,24} = 0.92$ ns	
<i>Kirchneriella</i>	$F_{2,24} = 0.00$ ns	$F_{2,24} = 10.2$ $P < 0.0006$ $1 = 3 < 6$	$F_{4,24} = 1.12$ ns		$F_{2,24} = 5.99$ $P = 0.008$	$F_{2,24} = 32.6$ $P < 0.0001$ $1 < 3 = 6$	$F_{4,36} = 9.43$ $P < 0.0001$		$F_{2,24} = 2.08$ ns	$F_{2,24} = 1333.2$ $P < 0.0001$ $1 > 3 > 6$	$F_{4,24} = 1.30$ ns	

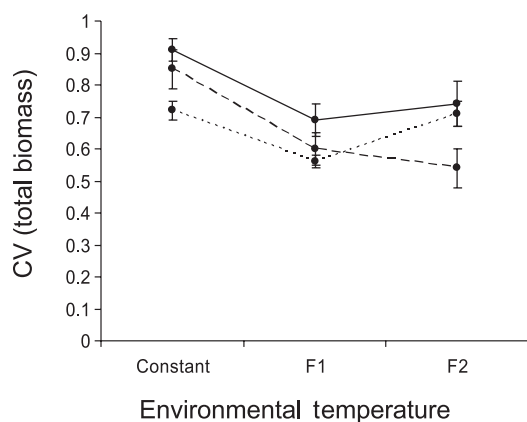


Fig. 2. Species richness \times environment interaction upon the CV of total algal community biomass. Solid line = 6 species communities, large dashes = 3 species, and, small dashes = monocultures (error bars = ± 1 se). F1 and F2 correspond to the two fluctuation treatments.

temperatures (Fig. 2; $F_{2,111} = 12.51$, $P < 0.001$). A significant interaction between the fluctuation and richness treatments ($F_{4,111} = 3.06$, $P = 0.02$) reflects the significant increase in monoculture variability from series F1 to F2, not apparent in the 3 and 6 species communities.

The CV of three and six species communities was lower under fluctuating than constant temperatures (three species F1 = 0.54 and F2 = 0.60 vs C = 0.85; six

species: F1 = 0.69 and F2 = 0.74 vs C = 0.91; MSD = 0.09), although there was no difference between fluctuation treatments (Fig. 2). The summed covariance of three and six species communities was respectively 92% and 57% lower under fluctuating than constant temperatures ($F_{2,42} = 19.02$, $P < 0.001$). A significant diversity \times fluctuation interaction indicated a differential response of the three ($F_2 < F_1 = \text{constant}$) and six ($F_1 = F_2 < \text{constant}$) species communities to the F2 fluctuation treatments ($F_{2,42} = 17.53$, $P < 0.001$). There was no significant difference in the summed variance between constant and fluctuating temperatures ($F_{2,42} = 1.59$, ns), nor any significant diversity \times fluctuation interaction ($F_{4,42} = 0.41$, ns).

Consumer dynamics

Mean rotifer density declined by $\approx 50\%$ with each increase in the level of algal species richness (Fig. 4a; $F_{2,51} = 11.9$, $P < 0.001$), whilst temperature fluctuations induced $\approx 70\%$ declines in mean rotifer density (C = 15 ml^{-1} , F1 = 4.1 ml^{-1} , F2 = 2.41 ml^{-1} ; $F_{2,51} = 21.5$, $P < 0.001$), there was no significant difference between the two fluctuation treatments. The diversity \times fluctuation interaction was not significant ($F_{4,51} = 1.5$, $P = 0.21$).

The CV of rotifer densities varied significantly in response to the fluctuation treatment ($F_{2,51} = 5.78$,

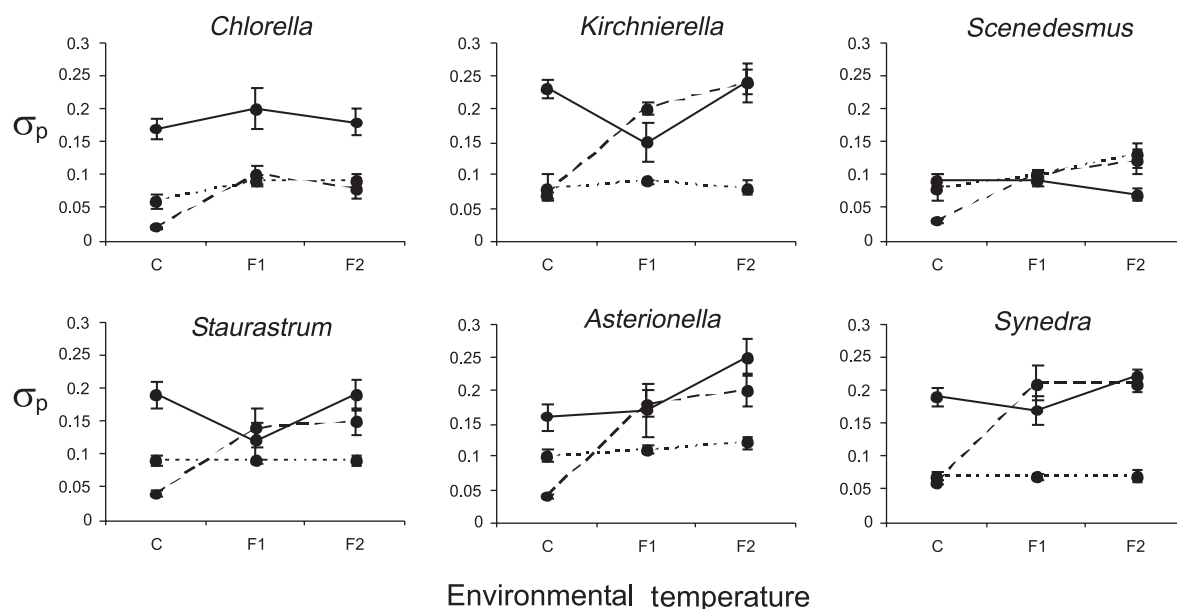


Fig. 3. Species richness \times environment interaction upon standard deviation of per capita growth rate (σ_p) for each algal species (error bars = ± 1 se). C = constant, F1 and F2 = the two fluctuation treatments. Solid line = 6 species communities, large dashes = 3 species, and, small dashes = monocultures. Statistics reported in the text were conducted upon the log-transformed data. Three species: *Synedra*: MSD = 0.04; *Asterionella*: MSD = 0.04; *Staurastrum*: MSD = 0.04; *Scenedesmus*: MSD = 0.03; *Chlorella*: MSD = 0.03; *Kirchneriella*: MSD = 0.04. Six species: *Synedra*: MSD = 0.04; *Asterionella*: MSD = 0.04; *Staurastrum*: MSD = 0.04; *Scenedesmus*: MSD = 0.03; *Chlorella*: MSD = 0.03; *Kirchneriella*: MSD = 0.04.

$P < 0.005$), and were $\approx 30\%$ more variable under fluctuating temperatures than constant temperatures (Fig. 4b); there was no significant difference between the two fluctuation treatments. The CV of rotifer densities did not differ significantly with algal species richness ($F_{2,51} = 1.94$, $P = 0.15$), and there was no significant diversity \times fluctuation interaction ($F_{4,51} = 1.62$, $P = 0.18$).

Discussion

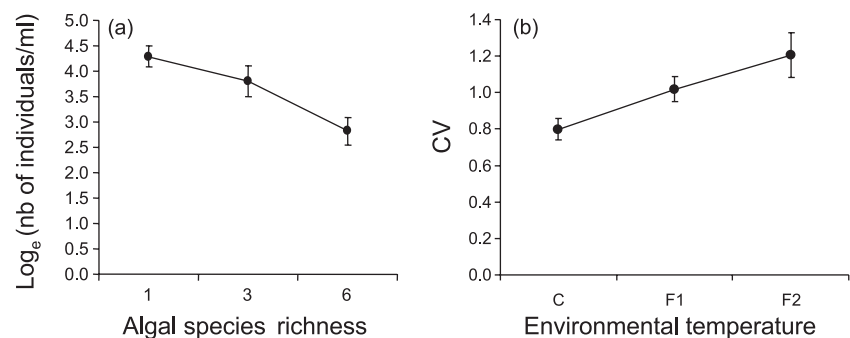
Algal variability

The results of this experiment demonstrate how population and community variability derive from the combined influence of interspecific interactions and environmental fluctuations. In comparison to the constant treatment, temperature fluctuations had no effect on the σ_p of any the species monocultures. The CV of the dominant species *Staurastrum* and *Scenedesmus* declined slightly, but there was no effect of temperature variation on the CV of the remaining four species. The absence of any effect of the reddened temperature fluctuations on these two measures of population variability was unexpected. Previous experiments using ciliate protozoa have established significant destabilizing effects of temperature fluctuations (Luckinbill and Fenton 1978, Petchey 2000b, Gonzalez and Holt 2002, Laakso et al. 2003). In polyculture, however, temperature fluctuations had marked effects on the σ_p of each species, as indicated by the significant diversity \times fluctuation interactions (Fig. 3, Table 2); this effect was not reflected in the CV of population densities. This result suggests that species interactions are important because the growth response of each species to the temperature fluctuations depended not only on the direct effect of the temperature fluctuations, but also on the indirect effects acting through changes in the abundances of the other species in the community (Ives 1995b).

At the community level, total community variability of both the three and six species assemblages was lower under fluctuating temperatures (Fig. 2). Given that there was no effect of the fluctuation treatment upon mean community biomass, or community variance, this latter effect can only be explained by the significant fluctuation induced reductions in community covariance (Eq. 2). This is in contrast to the result reported by Petchey et al. (2002) where no stabilising effect of temperature fluctuations was observed in bacterivorous microbial communities. The stabilising effect we observed here was generated by the temperature-dependent resource competition (Tilman et al. 1986). The periods when the temperature fluctuations descended below 15°C were characterised by an increase in the biomass of the diatom species (Fig. 1). These data support the suggestion that environmental fluctuations may play a role in stabilising community variability. However, as predicted by theory the extent of this buffering effect was limited by the strong and persistent asymmetry in species biomass (Ives and Hughes 2002).

The expectation of the insurance hypothesis of an enhanced buffering effect with increasing species richness was not observed here (Fig. 2). Theory identifies two factors important for interpreting these results (Ives and Hughes 2002). Increasing species richness may preclude a positive diversity-stability relation if competition or any other effect acts: 1) to unevenly reduce mean population densities and, 2) to increase the variability of per capita growth rates (Hughes and Roughgarden 2000, Ives and Hughes 2002). The experimental results obtained here pertain to these two effects and can be understood through an explication of temperature dependent resource competition likely to be operating in these model systems. Diatoms and green algae are known to compete strongly for phosphorous (P) and show clear temperature dependent, resource trade-offs for this and others nutrients (silicon, Si). Previous work has established that diatoms are competitively dominant at high Si:P ratios and low temperatures ($< 15^\circ\text{C}$), and that green algae are dominant at low Si:P ratios and high

Fig. 4. (a) The effect of algal species richness upon mean rotifer density; (b) the effect of temperature fluctuations upon the coefficient of variation (CV) of rotifer density (error bars = ± 1 se). C = constant, F1 and F2 = the two fluctuation treatments.



temperature ($> 15^{\circ}\text{C}$, Tilman et al. 1986). In this study the communities were cultured at a mean temperature of 20°C using the standard COMBO medium (Kilham et al. 1998), which has a low Si:P ratio of 2. Although, under monoculture, these conditions favour the growth of green algae, diatom growth was not negligible (green algae 10^5 – 10^6 ml^{-1} , diatoms 10^4 ml^{-1}). However, growth in polyculture revealed the greater competitive ability of the green algae, under these particular resource and temperature conditions, and explains their strong numerical and biomass dominance (Fig. 1). The competitive interactions in these communities therefore not only reduced mean species densities but did so in a highly asymmetrical fashion (i.e. the strong biomass dominance of *Staurastrum*). Secondly, increasing species richness increased the variability of the per capita growth rates of all species (Fig. 3) except *Scenedesmus* (the principal prey species of *B. calyciflorus*). Thus the two key factors identified by Ives and Hughes (2002) that may act to suppress an enhanced buffering effect with increasing species richness were observed in this experiment. This second aspect is important for understanding the destabilizing effect of diversity in this experiment. As Ives and Hughes (2002) stress, a species rich community will not be more stable than a species poor community if the variability in per capita growth rates are greater in the former. Although we clearly have a limited number of levels of diversity, and only one six species combination, to our knowledge this is the first clear experimental demonstration of such a direct destabilising effect of diversity upon the variability of population growth rates.

Yachi and Loreau (1999) present results from a model that explicitly addresses the effect of a highly uneven biomass distribution upon community stability, and therefore implicitly incorporates strong competitive asymmetries. They demonstrate a stabilising effect of increasing species richness as species dominance changes through time. But as the authors point out, their basic model is not directly relevant when dominance is unchanging through time, as was the case in this experiment. However, they discuss unpublished results from a model of constant dominance and state that “species with a consistently low productivity have no contribution to insurance effects, whatever their species richness” (Yachi and Loreau 1999). Under this scenario community variability will be directly determined by the variability of the dominant and no insurance effects will be apparent. From the results obtained here we can now add that the effects of competition, or any other effect, that increases population variability (especially of the dominant, in this case *Staurastrum*) with increasing species richness may increase community variability (Tilman et al. 1998) and produce a negative diversity-stability relation.

The generality of our results will depend upon how typical the dynamics observed in this experiment are of

natural systems. Clearly these microcosms are simplified ‘model’ systems (Lawton 1995) and were designed to test recent theory; much like many models they do not accurately represent any particular field system; for example, the semi-continuous resource renewal rate makes this system donor-controlled which approximates some natural systems better than others. However, the general features of the population and community dynamics presented here can be compared to those observed in the field. Aquatic communities often present highly asymmetric species-biomass distributions (Padišák 1992), and phytoplankton dynamics are typically reported to be influenced by physical variables (Sephton and Harris 1984). Terrestrial communities are also typified by highly asymmetric biomass distributions and many of the best studied natural communities are characterised by the long-term (with respect to generation time) dominance of one or a few species (Kempton and Taylor 1979, Rahel 1990, Bengtsson 1994). Very little data exists that could be used to confirm the generality of the positive relation we observe between species richness and the variability of per capita population growth rates. This sort of data is hard won because one needs to estimate the variability in population growth rates in the presence and absence of interspecific interactions (our monoculture vs polyculture comparison). Furthermore, one cannot use the relation between variance in population biomass and the number of species (Tilman 1996, McGrady-Steed and Morin 2000) as a surrogate because this relation is affected by competition (compare CV and σ_p results presented here). Given the critical nature of this effect for community stability (Ives and Hughes 2002) further empirical studies addressing the indirect effects of species richness on variability in per capita population growth rates are needed.

Rotifer dynamics

The dynamics of *B. calyciflorus* were in theory directly affected both by the dynamics of its prey and the stochastic fluctuations in its environment (Ives 1995a, Ives et al. 2000). We were able to assess this by comparing the CV and mean density of *B. calyciflorus* across the available range of fluctuation and algal richness combinations.

The significant reduction in mean rotifer density with increasing algal diversity reflected the reduced availability of *Scenedesmus* and *Chlorella* in polyculture. *Scenedesmus* was the only algal species for which σ_p did not increase from monoculture to polyculture suggesting a strong control of its dynamics by the rotifer. The destabilising effect of increasing algal richness upon *Chlorella* (the other prey species) was not translated into increases in the CV of rotifer densities. Furthermore,

these two prey species covaried positively throughout the experiment, so any potentially stabilising effect associated with prey switching (Luckinbill 1979, Petchey 2000a) could not operate here.

Fluctuating temperatures increased the CV of rotifer densities by ~50% compared with the constant temperature treatment. Again this was likely to be a direct effect of temperature upon rotifer growth as *B. calyciflorus* is known to exhibit population oscillations of increasing amplitude with increasing temperature (Halbach 1979). Thus it seems that the major changes in the dynamics of *B. calyciflorus* were principally determined by the direct effect of variable temperature upon population growth rates, the dynamics of its prey being of secondary importance here.

Conclusion

We have described results from an experimental model system that demonstrate a stabilising effect of environmental fluctuations at the community level. However, this effect was not enhanced by increasing species richness. Two theoretical conditions that explain this result were met; 1) a highly asymmetric community structure and, 2) increasing variability of per capita population growth rates with increasing diversity. Our results thus provide the first direct test of recent theory, and identify conditions that may preclude the generality of a positive diversity-stability relation.

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