Species richness, environmental fluctuations, and temporal change in total community biomass

Owen L. Petchey, Tim Casey, Lin Jiang, P. Timon McPhearson and Jennifer Price

Theory and empirical results suggest that high biodiversity should often cause lower temporal variability in aggregate community properties such as total community biomass. We assembled microbial communities containing 2 to 8 species of competitors in aquatic microcosms and found that the temporal change in total community biomass was positively but insignificantly associated with diversity in a constant temperature environment. There was no evidence of any trend in variable temperature environments. Three non-exclusive mechanisms might explain the lack of a net stabilising effect of species richness on temporal change. (1) A direct destabilising effect of diversity on population level variances caused some populations to vary more when embedded in more diverse communities. (2) Similar responses of the different species to environmental variability might have limited any insurance effect of increased species richness. (3) Large differences in the population level variability of different species (i.e. unevenness) could weaken the relation between species richness and community level stability. These three mechanisms may outweigh the stabilising effects of increases in total community biomass with diversity, statistical averaging, and slightly more negative covariance in more diverse communities. Our experiment and analyses advocate for further experimental investigations of diversity-variability relations.

O. L. Petchey, T. Casey, L. Jiang, P. T. McPhearson and J. Price, Dept of Ecology, Evolution, and Natural Resources, Cook College, Rutgers Univ., New Brunswick, NJ 08901, USA (current address of OLP, Dept of Animal and Plant Sciences, Alfred Denny Building, Western Bank, Sheffield S10 2TN, U.K. [o.petchey@sheffield.ac.uk]).

Recent theory describes how diversity affects the temporal variability of aggregate community properties (Micheli et al. 1999), such as total community biomass (for reviews see Tilman 1999 and Cottingham et al. 2001). Empirical studies suggest lower temporal variability in more diverse communities that may result from a variety of mechanisms linking diversity and variability (McNaughton 1985, Tilman 1996, McGrady-Steed et al. 1997, Naeem and Li 1997). Here we present a novel experimental investigation of the relations between species richness and the temporal variability in total community biomass of aquatic microcosm communities in different environments. We use indirect evidence to distinguish, where possible,

between the mechanisms that may link species richness and temporal variability.

The temporal variability of a community property has been used as a measure of community stability (Tilman 1999). Mathematically, however, stability is an intrinsic property of a system, whereas observed levels of temporal variability in population, community, or ecosystem dynamics result from intrinsic and extrinsic factors (Lewontin 1969, Ives 1995). Indeed, temporal variability and stability (i.e. resilience) are monotonically related in the absence of environmental variability, but this equitability breaks down when environmental variables fluctuate through time (Taylor 1992, Horwood 1993). We measured temporal variability because:

(i) it is related to stability in a constant environment, (ii) diversity-variability relations are the focus of recent theory, and (iii) observed variability may be of greater practical interest than intrinsic stability. The temporal change in an aggregate community property, such as total community biomass, can be measured by the coefficient of variation in total biomass:

$$
\text{Temporal change} = \frac{\text{SD(Total biomass)}}{\text{Total biomass}}
$$

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

(1)

Here $\bar{B}_i = \sum_{t=1}^{n} B_{i,t}/n$ and $B_{i,t}$ is the biomass of the ith (or jth) of s species during the tth of n samples through time (Lehman and Tilman 2000). Equation 1, in conjunction with the mean-variance relations of population densities, can be used as a null model (Gotelli and Graves 1996) of effects of species richness on temporal change (Doak et al. 1998, Tilman et al. 1998). Equation 1 also provides a tool for investigating which of the three components of temporal change (total biomass, which is the sum of the biomass of each species; total variance, which is the sum of the temporal variance of each species; and total covariance, which is the sum of the temporal covariances between all pairs of species in a community) contribute stabilising and destabilising influences. Increasing total biomass with increasing diversity reduces temporal change; increasing total variance or total covariance with increasing diversity increases temporal change. The net effect of diversity on temporal change is determined by the relative strength of these stabilising and destabilising contributions. Equation 1 makes no attempt to and cannot identify the mechanisms (Table 1) that cause changes in total biomass, total variance, and total covariance as a result of changes in diversity. Total covariance, for example, can be negative due to inter-specific competition even when species respond to environmental fluctuations in a correlated fashion. Other methods such as direct experimental manipulation of the mechanism and multivariate autoregressive models (Ives 1995) are more appropriate for disentangling the mechanisms (e.g. species interactions and environmental variation) that cause changes in total variances and covariances with diversity.

We assembled microcosm communities that initially comprised two to eight competing ciliate and rotifer species to examine how diversity affects a range of community properties, including temporal change in total community biomass. We limited our study to competitive communities because theory about effects of species richness in competitive communities (Tilman

et al. 1997, Ives et al. 1999, Yachi and Loreau 1999, Hughes and Roughgarden 2000, Lehman and Tilman 2000, Nijs and Roy 2000) is arguably better developed than theory about effects of species richness in food-webs (May 1972, Naeem 1998, Rastetter et al. 1999, Ives et al. 2000). The generation times of the microbes in our experiment range from hours to days, so that our six week experiment included twenty to fifty generations and, therefore, long term population and community dynamics. Our data is appropriate for testing theory about long-term effects of diversity on variability (Yachi and Loreau 1999, Hughes and Roughgarden 2000). Microbial microcosms also allow direct manipulations of diversity and escape the interpretative difficulties associated with indirect manipulations of diversity (Dodd et al. 1994, Tilman 1996) and observational studies (Wardle et al. 1997). The different patterns of temperature fluctuations in our experiment, constant, fast, and slow fluctuations, tested whether results were affected by environmental variability. The biomass of each species in each community was estimated twice during the experiment. This allowed many more individual communities than if we recorded biomasses more often. Consequently we use the term temporal change rather than temporal variability. In addition, we cannot separate temporal change caused by stochastic fluctuations from temporal change caused by directional changes (Gaston and McArdle 1994).

Regardless of the mechanisms that cause changes in total biomass, total variance and total covariance, eq. 1 provides a null model for comparison with our results. We determined how each of these three components of temporal change (eq. 1) related to diversity in each of three environments. In the constant environment the total variance and covariance result only from inter-specific interactions, whereas in the variable environments total variance and covariance result from both inter-specific interactions and environmental fluctuations. We used additional analyses to identify, where possible, the mechanisms that might be responsible for effects of diversity on each of these three components of temporal change (Table 1). The null model represented by eq. 1 was unable to account for our positive trend between temporal change and species richness in the constant environment. A model of the experiment was consistent with a direct destabilising effect of diversity on population level stability, that is absent from eq. 1, causing the results in our experiment.

Materials and methods

Experimental design

We used a two-way factorial design with diversity (initially 2, 4, 6, or 8 species) and temperature regime (one constant temperature, two fast temperature fluctu-

ations, and two slow temperature fluctuations) as treatments. There were 16 different communities; four at each of the four diversity levels. Selection of species combinations followed established practice for manipulations of diversity within a single trophic level (Allison 1999), except that we chose to have as many species as possible represented across the two species communities. We did not replicate identical communities in the same environment because we were most interested in the effects of diversity. The 16 different communities experienced either of the five different temperature regimes, making a total of 80 microcosms. Eight of these were contaminated by non-treatment species during the experiment and were excluded from all analyses. The constant temperature microcosms remained at 22°C, while the fast (average rate of change, $\bar{x} \pm 1$

SD $= 6.9 \pm 4.7$°C 12 h^{-1} and 6.7 ± 5.0°C 12 h^{-1}) and slow (1.7 ± 1.3°C 12 h^{-1} and 2.1 ± 1.9°C 12 h^{-1}) patterns of temperature fluctuations varied between 12°C and 32°C. This 20°C range of temperatures falls within the range seen in natural ecosystems in our area of New Jersey, USA. The fast and slow fluctuations were white and reddened time series of temperature fluctuations (Halley 1996, Kaitala et al. 1997) very similar to the temperature series in Fig. 1 of Petchey (2000a).

Community assembly

We assembled and maintained each of the 80 microbial communities in a 250 ml Pyrex screw-capped bottle

Table 1. The mechanisms that can generate and/or modify relations between the three statistical components of temporal stability and diversity (eq. 1). References are for theoretical studies that show how that component can vary with diversity and thereby influence temporal stability.

| Component of temporal stability		Proposed mechanism by which species richness affects the component	Influence of increased species richness on temporal stability	References
(1) Total biomass	(a)	Selection effects: total biomass is influenced by the greater probability that any particular species is included in a more diverse community. (This effect is more important when species differ more.)	• Stabilising if large species dominate (total biomass increases with increasing diversity) • Destabilising if small species dominate (total biomass decreases with increasing diversity)	(Tilman et al. 1997, Tilman 1999, Loreau 2000, Loreau and Hector 2001)
	(b)	Resource use complementarity: total biomass increases with increasing species richness because of a greater range of resources exploited	• Stabilising	(Chapin et al. 2000, Petchey 2000c, Loreau and Hector 2001)
(2) Total variance	(a)	Statistical averaging (portfolio effect): statistical effect of adding the biomass fluctuations of a number of species together to get variation in total biomass	• Stabilising if log(mean)-log(variance) relation has slope of greater than 1 • Destabilising if log(mean)-log(variance) relation has slope of less than 1	(Doak et al. 1998, Tilman et al. 1998)
	(b)	Changes in population level variability: individual populations may become more or less variable with increasing diversity independent of the mean-variance relation in 2(a)	• Stabilising if species become less variable with increasing diversity • Destabilising if species become more variable with increasing diversity	(This study; Petchey 2000b)
	(c)	Uneven population level variability: a very variable species might determine community level variability regardless of all other species' presence or absence	• Neutral for the average relation, but adds scatter and weakens any relation	(Cottingham et al. 2001)
(3) Total covariance	(a)	Inter-specific interactions: interactions between populations can affect whether biomasses fluctuate in synchrony or out of synchrony	• Competitive interactions contribute to asynchronous dynamics and reduce temporal change in total biomass	(Lehman and Tilman 2000) (But see McCann et al. 1998, Ives et al. 1999)
	(b)	Responses to environmental fluctuations (insurance hypothesis): a greater range of responses to environmental change in more diverse communities ensures future functioning	• Stabilising if different species respond differently to environmental change (neutral otherwise)	(McNaughton 1977, Walker 1995, Ives et al. 1999, Walker et al. 1999, Yachi and Loreau 1999)
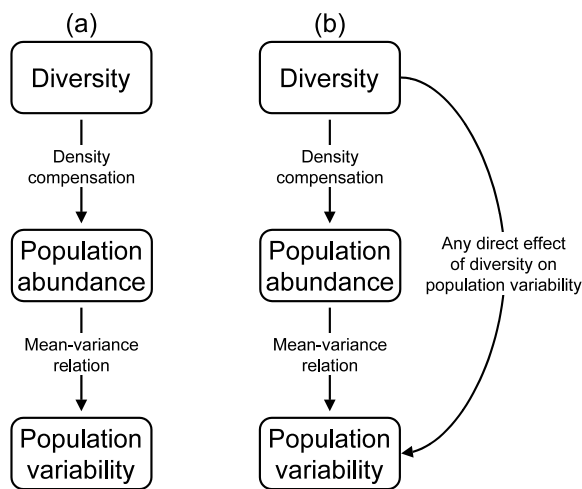
Fig. 1. Model frameworks for effects of diversity on population abundance and population variability. (a) Corresponds to Doak et al. (1998) and Tilman et al. (1998) where diversity affects population variability via density compensation and the mean-variance relation. (b) Corresponds to a framework which better fits the empirical data present here.

containing 100 ml of soil-water medium and six sterile wheat seeds. Soil-water medium was a sterilised mixture of 0.55 g Carolina Biological Supply protozoan pellet, 2.5 g of soil (from the Rutgers Display Garden pond, New Brunswick, NJ) and 1.5 l of well water. Sterile soil-water nutrient medium was inoculated first with bacteria (*Bacillus cereus*, *Bacillus subtilis* and *Serratia marcescens*) and then with different numbers and combinations of species, chosen from a pool of ten bacterivorous ciliates and rotifers, four days before the experiment started (Table 2). The ten bacterivorous protists and rotifers were obtained by either isolating the species from the Rutgers University Display Garden pond or obtaining the species from Carolina Biological Supply company (Burlington, NC, USA). The species were grown in soil-water medium stock cultures for many generations before the experiment. Adding a mixed culture of microflagellates and bacteria from all of the stock cultures to all the experimental microcosms standardised initial conditions. We removed 7 ml of medium each week and replaced this with 7 ml of soil-water medium with bacteria added within the previous 24 h. Our design does not control initial community biomass across treatments, though this must have little effect on the results because of the many generations of growth that occurred during the experiment (e.g. initial biomass was in the order of 1×10^{-4} mg per ml, whereas biomass during the experiment ranged from 10^{-2} to 10^{0} mg per ml).

Community monitoring

We measured the population density of each species during the 2nd and 6th week of the experiment. The population density of each species was estimated by counting the number of individuals in appropriately diluted drops of media using a dissecting or compound microscope. We calculated species biomass by multiplying the abundance of a species by the average cell mass of ten individuals of a species. Cell mass was calculated from the linear dimensions converted to mass using equations that approximate cell shapes (Wetzel and Likens 1991).

Analyses

Statistical tests were analyses of covariance (ANCOVA) with mean realised species richness as a continuous explanatory variable and environment (constant, fast, or slow fluctuating) as a categorical explanatory variable. Mean realised richness was the average number of species observed over the two sampling points. We grouped both fast and both slow fluctuating treatments into slow and fast fluctuating environments in accordance we previous analyses of such treatments (Petchey 2000a). The response variable in the ANCOVAs was either: temporal change in total community biomass (see eq. 1); log of total community biomass

Table 2. The species compositions of the different communities and mean cell masses of the different species. Species sharing the same initial diversity and letter (a, b, c, or d) were present in the same community.

Species	Cell mass (mg)	Initial diversity			
		2	4	6	8
Tillina sp.	4.4×10^{-2}	b	c	ad	abcd
Rotaria sp.	4.3×10^{-4}	d	ad	bc	acd
Monostyla sp.	2.2×10^{-4}	d	ac	abcd	abcd
Paramecium sp.	2.0×10^{-4}		bcd	ad	abcd
Colpoda sp.	2.4×10^{-5}	c	ab	abdc	abcd
Tetrahymena thermophila	2.0×10^{-5}	a	b	b	bd
Colpdium sp.	1.3×10^{-5}	c	d	cd	c
Loxocephalus sp.	5.7×10^{-6}	a	cd	abc	abd
Uronema sp.	7.2×10^{-7}		b	bd	abcd
Loxodes sp.	4.9×10^{-7}	b	a	ac	abc

$(\log_{10}(\Sigma^s_{i=1} \bar{B}_i))$; log of total variance $(\log_{10}(\Sigma^s_i \text{Var}(B_i)))$; total covariance $(\Sigma^s_i \Sigma^s_{i \neq j} \text{Cov}(B_i, B_j))$; mean population biomass $(\bar{B}_i)$; or population coefficient of variation $(\text{CV}(B_i))$. We log-transformed total biomass and total variance to better meet ANCOVA assumptions and used CV (as opposed to the generally more appropriate $\text{SD}(\log(n))$) to measure population stability because of the zeros in the data (Gaston and McArdle 1994). Spearman rank correlation was used to verify the conclusions of the ANCOVA for the relationships between temporal change in total community biomass and realised species richness in each environment separately. The log(population mean, $\bar{B}_i$)-log(population variance, $\text{Var}(B_i)$) relationship was fit using a separate linear regression for each species.

We used a model of the experiment to investigate potential causes of the diversity-variability trend in the constant environment. Two models (Fig. 1) recreated the experimental results, either with a direct destabilising effect of diversity on population level variability included or excluded. We limited the models to the constant environment because environmental fluctuations would be difficult to incorporate.

In both models we estimated the direct effect of diversity on population biomass using the equation $B_i(s) = a_i + b_i \times s$ where a_i and b_i are the estimates of the regression coefficients of the empirical relations between the biomass of species i and species richness. Negative values of b_i would indicate that the biomass of a species decreases as species richness increases, that is, density compensation. This equation predicts the biomass of each species in each environment at a given diversity level quite well (85% of the variance in empirical species biomasses in the constant environment is explained by this equation) mostly because it accounts for the considerable differences between the mean biomass of different species.

In the first model (Fig. 1a), we estimated the species level variance as a function of only mean biomass: $\text{Var}(B_i) = c_i \times B_i(s)^{z_i}$. Here, c_i and z_i are the intercept and the slope, respectively, of the linearised relation, $\text{Log}(\text{Var}(B_i)) = \text{Log}(c_i) + z_i \times \text{Log}(B_i(s))$, for species i. In this first model, diversity only has an indirect effect on species variances which is mediated through the direct effect of diversity on species biomasses.

In the second model (Fig. 1b), we included a direct effect of diversity on species variance by estimating the species variances using $\log(\text{Var}(B_i)) = \log(c_i) + z_i \times \log(B_i(s)) + d_i \times \log(s)$. Here, d_i represents the direct effect of diversity on species variance and, when estimated from the data, is positive for 5 out of the 10 species. We used these empirical relations to recreate the biomass and stability of each species in each experimental community (matching the species combinations in the actual communities) and used these values to calculate the expected community stability using eq. 1.
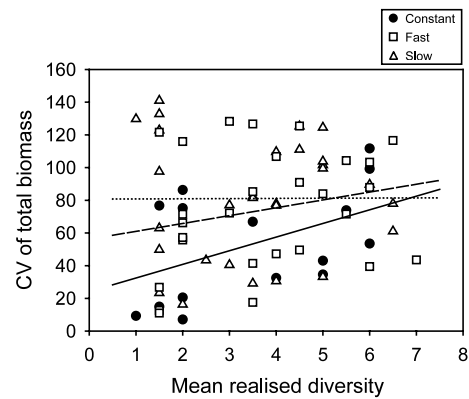

Fig. 2. The relations between temporal change in total community biomass and realised species richness. Filled circles indicate communities in the constant environment, unfilled squares represent communities in the fast fluctuating environment, and unfilled triangles indicate communities in the slow fluctuating environment. The lines show the best linear fit by ANCOVA (solid for constant temperature, dashed for fast environmental changes, and dotted for slow environmental fluctuations.

Results

There was no strong nor general relation between the temporal change in total community biomass and species richness. The temporal change in total community biomass was positively associated with diversity in the constant environment, although the relationship was not significant at $\alpha = 0.05$ (Fig. 2; overall effect of mean realised species richness in ANVOCA: $F_{1,66} = 3.06$, $p < 0.08$; Spearman for constant environment $r_s = 0.47$, $p < 0.08$; fast environment $r_s = 0.22$, $p < 0.25$; slow environment $r_s = 0.00$, $p < 1.0$). In the constant environment this indicates a weak destabilising effect of species richness on temporal change in total community biomass. Lack of evidence of a strong stabilising effect of species richness on total community biomass requires explanation, as does the slightly destabilising effect of species richness in the constant environment, because theory generally predicts a stabilising effect of increased species richness.

More variable environmental conditions tended to cause greater change in total community biomass at low level of species richness, though, again, the effect was not significant at $\alpha = 0.05$ (effect of environment in ANCOVA: $F_{2,66} = 2.5$, $p < 0.09$; interaction in ANCOVA: $F_{2,66} = 0.86$, $p = 0.43$). Total biomass changed more in the slowly fluctuating environment, changed least in the constant environment, and change in biomass was intermediate in the fast fluctuating environment. The gradients of the relationships in the different environments could result from measuring biomass at just two time points and thereby constraining the maximum value of temporal change to 141.2.

Total biomass

The total community biomass increased with increasing diversity (ANCOVA: $F_{1,66} = 27.1$, $p < 0.0001$) and was unaffected by the pattern of environmental fluctuations (Fig. 3a; ANCOVA: environment $F_{2,66} = 1.2$, $p = 0.32$; interaction $F_{2,66} = 0.7$, $p = 0.52$). Our data was insufficient to apply tests that can distinguish between the different mechanisms that cause positive biomass-diversity relations (Table 2; Hector 1998, Loreau 1998, Emmerson and Raffaelli 2000, Loreau and Hector 2001). Five low diversity communities with conspicuously high total biomass (Fig. 3a), were, however, all of the same composition (*Tillina + Loxodes*; and differed by the environment they experienced), indicating that composition can explain some aspects of the relation between total biomass and diversity (Hooper and Vitousek 1997, Tilman 1997). Large differences among species biomass (Fig. 4) suggest that selection effects (Table 1, mechanism 1a) might partially explain total biomass. Irrespective of the mechanism responsible, greater total biomass in more speciose communities will contribute towards less temporal change in more speciose communities in our experiment. Therefore changes in total biomass cannot account for the slightly greater temporal change in more diverse communities in the constant environment.

Total variance

The total variance increased with increasing species richness (ANCOVA: $F_{1,66} = 39.6$, $p < 0.0001$) and contributes towards greater temporal change in more diverse communities (Fig. 3b). This effect was not, however, due to the absence of statistical averaging (Table 1, mechanism 2a). The slope of the mean-variance relation was significantly greater than one for all species (Fig. 3d), the necessary condition for statistical averaging (Table 1). The slopes of the mean-variance relationship in our experiment falls within the range for spatial variation found in natural populations (Downing 1986). There was also good evidence for density compensation: the density of every species tended to decrease with increasing species richness and this relation was significant for five species (Table 3). Environmental variability did not affect total variance (ANCOVA: environment $F_{2,66} = 2.7$, $p = 0.07$; interaction $F_{2,66} = 1.2$, $p = 0.30$). These empirical patterns match the theoretical conditions necessary for statistical averaging to cause less temporal change in more diverse communities (Doak et al. 1998, Tilman et al. 1998).

The population level variability of six of the nine species for which tests were possible showed a trend towards greater variability in more diverse communities, though only two trends were statistically significant at $\alpha = 0.05$ (Table 3). Whether these species-specific
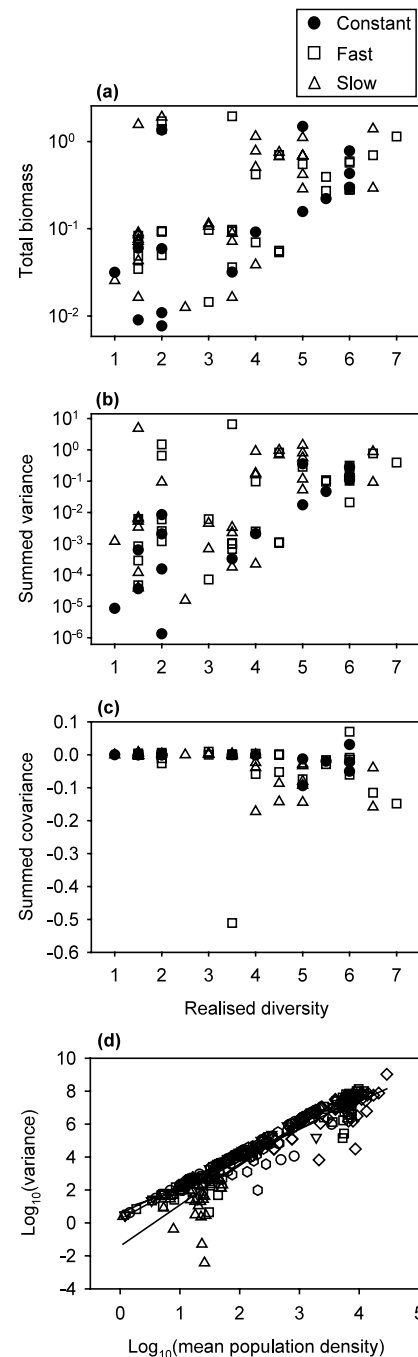

Fig. 3. The relations between diversity and (a,b, and c) the three components of temporal stability, and (d) the mean-variance scaling relation. (d) The species-specific mean-variance relationships had slopes ranging from 1.7 to 2.5. The unusual distribution of points results from a constraint placed on log(variance) when populations were present at one sampling time, but not observed at the other ($\log(\mathrm{Var}(0, x)) \propto 2 \log(x) + \mathrm{constant}$). Different symbols and regression lines are for different species in (d) but need not be readily distinguished. Values are plotted on log-scaled axis, rather than plotting logged-values on a linear scale. Summed covariance is, by definition, zero in a community with only one species.
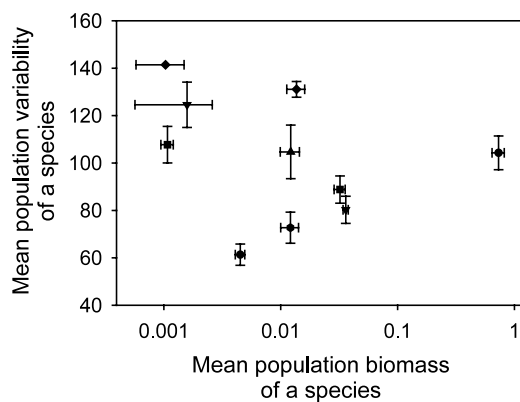
Fig. 4. The mean population biomass of each species plotted against the mean population level variability (CV) of the species across the entire experiment. Error bars are ± 1 SE.

patterns amount to a net stabilising or destabilising effect of diversity on temporal change in total community biomass depends on the slopes and intercepts of the species-specific relationships and distribution of species among communities. For example, a species that was strongly destabilized by increased species richness may not influence the overall pattern if it has low mean variability compared to all other species.

Mean population variability differed among species (Fig. 4). This unevenness in population level variability generally weakens relations between species richness and temporal change by adding scatter to the relation, especially at low diversities (Table 1, mechanism 2c).

Total covariance

The total covariance became slightly more negative as diversity increased (Fig. 3c) (ANCOVA: $F_{1,66} = 5.8$, $p < 0.05$) and therefore contributed a weak stabilising influence on temporal change in more diverse communities. More negative covariance can only result from

changes in competitive interactions along the species richness gradient in the constant environment. There was no significant effect of environment or significant interaction between realised richness and environment (ANCOVA: environment $F_{2,66} = 0.1$, $p = 0.89$; interaction $F_{2,66} = 0.4$, $p = 0.66$).

Negative covariance in variable environments could result from changes in the competitive interactions or a greater range of species responses to environmental fluctuations in more diverse communities (Table 1, mechanism 3a). This highlights the limitations using the total covariance (and total variance) for examining relations between temporal change and species richness in variable environments. Nevertheless, greater negative covariance contributes toward lower temporal change in more diverse communities.

The model of dynamics in the constant environment

The model showed that excluding all possible direct effects of diversity on species variances results in a negative trend between diversity and the temporal change in total biomass (slope $= -1.31$; $p = 0.63$) and explains 47% of the variance in the experimental change in total biomass. Including direct effects of diversity on population level variability recreates the data more accurately (predicted slope $= 8.8$; $p = 0.07$; observed slope $= 8.4$; $p = 0.07$) and explains 76% of the observed variance in change in total biomass.

Discussion

Here we present evidence for little or no relation between the number of competitive species in microbial microcosm communities and the temporal change in total community biomass. In constant environmental conditions there was a trend towards greater change in

Table 3. Effects of environmental variability and species richness on mean population density and population variability (CV) of each species. ANCOVA tested for effects of richness, environmental variation and their interaction. The symbols *, **, and *** indicate $p < 0.05$, $p < 0.01$, and $p < 0.001$ respectively; ns indicates $p > 0.05$.

Species	Effect on mean population density				Effect on population variability			
	Error df	Environment	Richness	Interaction	Error df	Environment	Richness	Interaction
Colpidium	13	*	** (negative)	ns	5	*	ns (negative)	*
Colpoda	8	*	ns (negative)	*	2	*	ns (positive)	*
Loxocephalus	35	ns	ns (negative)	ns	34	ns	** (positive)	ns
Loxodes	29	*	*** (negative)	ns	29	ns	ns (positive)	ns
Monostyla	43	*	** (negative)	ns	43	ns	ns (negative)	ns
Paramecium	34	ns	** (negative)	ns	34	ns	ns (positive)	ns
Rotaria	25	ns	ns (negative)	ns	25	ns	* (negative)	ns
T. thremophila	3	ns	ns (negative)	ns	0	Insufficient data		
Tillina	29	ns	*** (negative)	ns	13	ns	ns (positive)	ns
Uronema	23	ns	ns (negative)	ns	12	ns	* (positive)	ns

total biomass in more diverse communities. Three non-exclusive explanations could account for this apparent contradiction with frequent theoretical predictions of a stabilising effect of diversity on aggregate community properties. First, a direct effect of diversity on population level variability (Table 1, mechanism 2b) is consistent with results in the constant environment. This direct effect of diversity on population level stability is absent from recent models (Doak et al. 1998, Tilman et al. 1998). Second, theory predicts stabilising effects of diversity only when species differ in their responses to environmental change (Ives et al. 1999). Our species may not differ much in their response to environmental change, though we do not know their temperature optima. And third, the differences in population variability that we observed among the species tend to weaken relations between diversity and the variability of aggregate properties. We also found evidence for community wide density compensation and a strong positive relation between species richness and total community biomass. Our results are not necessarily at odds with theory, in particular they may not contradict the insurance hypothesis, and advocate for a more detailed and mechanistically oriented investigation of the determinants of temporal change in microbial microcosms and other communities.

Relating our result to other empirical results

Results from previous experimental manipulations of diversity (see Table 2 of Cottingham et al. (2001)) and observational studies (McNaughton 1985) provide equivocal evidence for a general negative relation between diversity and the temporal variability of aggregate community and ecosystem properties. Several differences between studies might explain the contrasting results.

First, there are differences in how variability was measured in different studies. Naeem and Li (1997) and McGrady-Steed et al. (1997) included variability among replicates (spatial variability), and variability among communities at each diversity level in their measure of variability, whereas we used a purely temporal measure of variability. Including variability among replicates could be important if stabilising/destabilising mechanisms influence spatial and temporal variability differently. Including variability among different communities at each diversity level may influence diversity-variability relations because different high diversity communities share more species in common than do different low diversity communities. This might predict lower biomass differences between high diversity communities than low diversity communities (Fukami et al. 2001). McGrady-Steed et al. (1997) show, however, that variability decreases even when calculated for one community at each diversity level.

Different variability metrics are used in different studies (Cottingham et al. 2001) and the metric of choice can affect the variability estimate (Gaston and McArdle 1994). Furthermore, we only measured biomasses twice, whereas other studies measured biomass more frequently. It is possible that this could affect the exact form of the diversity-variability relation, but it also seems unlikely that this alone could cause opposing diversity-variability relations. Further experiments and analyses of published experiments should assess potential differences between spatial and temporal stability, employ a standard measure of variability, and sample more than twice during an experiment.

Second, the design of diversity manipulations can influence interpretation of results (Huston 1997, Wardle 1998, Allison 1999). We selected species randomly, within some minor constraints, in order to experimentally remove effects of composition on variability. We did not replicate communities with the same species composition because we were primarily interested in how diversity affects community properties. Other experiments have used different diversity manipulations ranging from completely random selection of species (Symstad et al. 1998, Hector et al. 1999) to non-random selections of species due to biological constraints (McGrady-Steed et al. 1997). We reduced the potential bias caused by selecting a subset of all possible communities (we used 20 out of a possible 510) by assembling as many different combinations as possible (at a cost of few samples through time). (In hindsight, we might have profited more by assembled many more communities and at the expense of no environmental variability treatment.) We cannot be sure, however, that a different subset of the 510 possible communities might have produced a completely different diversity-variability relation. At present we know of no method for predicting or measuring the potential for bias caused by selecting a subset of all possible communities.

Third, and we consider most likely, biological differences between experiments might cause a direct destabilising effect of diversity on population level stability in our experiment that was absent, or much weaker in studies that found stabilising effects of species richness. We used communities containing only competitors and their resource, bacteria. In contrast, other studies have manipulated diversity across several trophic levels simultaneously (Naeem et al. 1994, McGrady-Steed et al. 1997, Naeem and Li 1997), manipulated diversity indirectly (Tilman 1996), and manipulated diversity within a pre-existing community (Tilman 1996). Including only competitors in communities may reduce the variation in species responses to environmental variability and thereby weaken or prevent any insurance effect (Walker 1992, 1995, Ives et al. 1999). Including species that range greatly in their population level variability (Fig. 4) would also weaken any diversity-variability relation.

Relating our result to theory

Equation 1 has been combined with mean-variance scaling relations to predict (Doak et al. 1998, Tilman et al. 1998, Tilman 1999) and investigate (Tilman 1996, 1999) relations between diversity and the stability of aggregate community properties. This is a phenomenological and statistically based framework for understanding and predicting diversity-stability relations. This model does not included direct effects of diversity on population level stability, rather, it assumes only an indirect effect of diversity on population stability that is mediated through effects of diversity on population size (Doak et al. 1998, Tilman et al. 1998, Tilman 1999). The mean-variance scaling relation modulates this indirect effect of diversity on population variance (Tilman et al. 1998). This model therefore assumes that population level stability is determined only by population density, and does not depend on the size or structure of the surrounding community. The direct effect of diversity on population variance (Fig. 1b) that we observed in our experiment allows community properties to affect population level variance directly and independently of population density. Including such a direct effect was sufficient to recreate the positive diversity-variability trend in the constant environment. We cannot identify the mechanism(s) that might be responsible for the apparent direct effect of diversity on population level stability, though it seems unlikely that none occur in real ecological communities.

In general, eq. 1 and mean-variance scaling may assume the absence of many other biological mechanisms that link diversity with the mean, variance, and covariance. An alternate approach is to employ mechanistic and biologically based models to explain and predict diversity-stability relations (Ives et al. 1999, Hughes and Roughgarden 2000, Ives et al. 2000). Such models do not explicitly specify mean-variance relations or mean-diversity relations, rather, these relations result from inter-specific interactions between populations and the pattern of species responses to environmental change. Explanations of empirical diversity-stability relations within this biologically based framework can be accomplished using autoregressive models that isolate effects of species interactions and responses to environmental fluctuations (Ives et al. 1999). The more mechanistic basis of biologically motivated models are preferable if we seek a mechanistic explanation of diversity-stability relations.

In conclusion, we found that diversity has stabilising and destabilising influences on the temporal stability of total community biomass. Stabilising mechanisms were statistical averaging, increasing total biomass with increasing diversity, and weakly decreasing negative covariance with increasing diversity. A direct destabilising effect of diversity on species variability, however, was strong enough to overwhelm any stabilising influences of diversity and result in slightly positive diversity-variability relation in the constant environment.

References

Allison, G. W. 1999. The implications of experimental design for biodiversity manipulations. – Am. Nat. 153: 26–45.

Chapin, F. S., Zavelata, E. S., Eviner, V. T. et al. 2000. Consequences of changing biodiversity. – Nature 405: 234–242.

Cottingham, K. L., Brown, B. L. and Lennon, J. T. 2001. Biodiversity may regulate the temporal variability of ecological systems. – Ecol. Lett. 4: 72–85.

Doak, D. F., Bigger, D., Harding, E. K. et al. 1998. The statistical inevitability of stability-diversity relationships in community ecology. – Am. Nat. 151: 264–276.

Dodd, M. E., Silvertown, J., McConway, K. et al. 1994. Stability in the plant communities of the Park Grass experiment: the relationships between species richness, soil pH and biomass variability. – Philos. Trans. R. Soc. Lond. B Biol. Sci. 346: 185–193.

Downing, J. A. 1986. Spatial heterogeneity: evolved behavior or mathematical artifact? – Nature 323: 255–257.

Emmerson, M. C. and Raffaelli, D. G. 2000. Detecting the effects of diversity on measures of ecosystem function: experimental design, null models and empirical observations. – Oikos 91: 195–203.

Fukami, T., Naeem, S. and Wardle, D. A. 2001. On similarity among local communities in biodiversity experiments. – Oikos 95: 340–348.

Gaston, K. J. and McArdle, B. H. 1994. The temporal variability of animal abundances: measures, methods and patterns. – Philos. Trans. R. Soc. Lond. B Biol. Sci. 345: 335–358.

Gotelli, N. J. and Graves, G. R. 1996. Null models in ecology. – Smithsonian Institution.

Halley, J. M. 1996. Ecology, evolution and 1/f-noise. – Trends Ecol. Evol. 11: 33–37.

Hector, A. 1998. The effect of diversity on productivity: detecting the role of species complementarity. – Oikos 82: 597–599.

Hector, A., Schmid, B., Beierkuhnlein, C. et al. 1999. Plant diversity and productivity experiments in European grassland. – Science 286: 1123–1127.

Hooper, D. U. and Vitousek, P. M. 1997. The effects of plant composition and diversity on ecosystem processes. – Science 277: 1302–1305.

Horwood, J. W. 1993. Population variance and deterministic stability analysis. – J. Anim. Ecol. 62: 588–591.

Hughes, J. B. and Roughgarden, J. 2000. Species diversity and biomass stability. – Am. Nat. 155: 618–627.

Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. – Oecologia 110: 449–460.

Ives, A. R. 1995. Predicting the response of populations to environmental change. – Ecology 76: 926–941.

Ives, A. R., Gross, K. and Klug, J. L. 1999. Stability and variability in competitive ecosystems. – Science 286: 542–544.

Ives, A. R., Klug, J. L. and Gross, K. 2000. Stability and species richness in complex communities. – Ecol. Lett. 3: 399–411.

Kaitala, V., Lundberg, P., Ripa, J. and Ylikarjula, J. 1997. Red, blue and green: dyeing population dynamics. – Ann. Zool. Fenn. 34: 217–228.

Lehman, C. L. and Tilman, D. 2000. Biodiversity, stability, and productivity in competitive communities. – Am. Nat. 156: 534–552.

Lewontin, R. C. 1969. The meaning of stability. – In: Woodwell, G. and Smith, H. (eds), Brookhaven symposia in biology. Diversity and stability in ecological systems. Brookhaven National Laboratory, pp. 13–23.

Loreau, M. 1998. Separating sampling and other effects in biodiversity experiments. – Oikos 82: 600–602.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. – Oikos 91: 3–17.

Loreau, M. and Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. – Nature 412: 72–76.

May, R. M. 1972. Will a large complex system be stable? – Nature 238: 413–414.

McCann, K., Hastings, A. and Huxel, G. R. 1998. Weak trophic interactions and the balance of nature. – Nature 395: 794–798.

McGrady-Steed, J., Harris, P. M. and Morin, P. J. 1997. Biodiversity regulates ecosystem predictability. – Nature 390: 162–165.

McNaughton, S. J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. – Am. Nat. 111: 515–525.

McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. – Ecol. Monogr. 55: 259–294.

Micheli, F., Cottingham, K. L., Bascompte, J. et al. 1999. The dual nature of community variability. – Oikos 85: 161–169.

Naeem, S. 1998. Species redundancy and ecosystem reliability. – Conserv. Biol. 12: 39–45.

Naeem, S. and Li, S. 1997. Biodiversity enhances ecosystem reliability. – Nature 390: 507–509.

Naeem, S., Thompson, L. J., Lawler, S. P. et al. 1994. Declining biodiversity can alter the performance of ecosystems. – Nature 368: 734–737.

Nijs, I. and Roy, J. 2000. How important are species richness, species evenness and interspecific differences to productivity? A mathematical model. – Oikos 88: 57–66.

Petchey, O. L. 2000a. Environmental colour affects aspects of single-species population dynamics. – Proc. R. Soc. Lond. B Biol. Sci. 267: 747–754.

Petchey, O. L. 2000b. Prey diversity, prey composition, and predator population stability in experimental microcosms. – J. Anim. Ecol. 69: 874–882.

Petchey, O. L. 2000c. Species diversity, species extinction, and ecosystem function. – Am. Nat. 155: 696–702.

Rastetter, E. B., Gough, L., Hartley, A. E. et al. 1999. A revised assessment of species redundancy and ecosystem reliability. – Conserv. Biol. 13: 440–443.

Symstad, A. J., Tilman, D., Willson, J. and Knops, J. M. H. 1998. Species loss and ecosystem functioning: effects of species identity and community composition. – Oikos 81: 389–397.

Taylor, A. D. 1992. Deterministic stability analysis can predict the dynamics of some stochastic population models. – J. Anim. Ecol. 61: 241–248.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. – Ecology 77: 350–363.

Tilman, D. 1997. Distinguishing between the effects of species diversity and species composition. – Oikos 80: 185.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. – Ecology 80: 1455–1474.

Tilman, D., Lehman, C. L. and Thomson, K. T. 1997. Plant diversity and ecosystem productivity: theoretical considerations. – Proc. Natl. Acad. Sci. USA 94: 1857–1861.

Tilman, D., Lehman, C. L. and Bristow, C. E. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? – Am. Nat. 151: 277–282.

Walker, B. 1995. Conserving biological diversity through ecosystem resilience. – Conserv. Biol. 9: 747–752.

Walker, B., Kinzig, A. and Langridge, J. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. – Ecosystems 2: 95–113.

Walker, B. H. 1992. Biodiversity and ecological redundancy. – Conserv. Biol. 6: 18–23.

Wardle, D. A. 1998. A more reliable design for biodiversity study. – Nature 394: 30.

Wardle, D. A., Zackrisson, O., Hörnberg, G. and Gallet, C. 1997. The influence of island area on ecosystem properties. – Science 277: 1296–1299.

Wetzel, R. G. and Likens, G. E. 1991. Limnological analyses. – Springer-Verlag.

Yachi, S. and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. – Proc. Natl. Acad. Sci. USA 96: 1463–1468.