

Biodiversity and ecosystem functioning in aquatic microbial systems: a new analysis of temporal variation and species richness-predictability relations

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Studies of microbial communities from aquatic ecosystems provide important insights into relations between various aspects of ecosystem functioning and changes in biodiversity. Aquatic microbial systems provide a valuable counterpoint to studies of terrestrial systems, because patterns reflect consequences of interactions occurring over many generations of community development, and are unlikely to represent artifacts of the initial conditions established in experimental communities. In this paper we re-analyse our previously published data to separate the contributions of temporal and spatial variation to overall variation in ecosystem functioning. A new analysis based on re-sampling confirms a negative relationship between richness and the variability of one ecosystem process, carbon dioxide flux. The negative relationship reflects high variation among communities of low species richness, rather than high temporal variation within communities of low richness. We also review the various transformations and summary statistics proposed as alternate measures of variability in ecosystem functioning, to point out that different measures are often appropriate for different kinds of data. Finally, we conclude that arguments about the cosmopolitan distribution of microbes do not preclude the existence of important relations between microbial species richness and ecosystem functioning.

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Studies of the relations between biodiversity and various aspects of ecosystem functioning have generated tremendous controversy within the ecological community (Grime 1998, Wardle et al. 2000, Loreau et al. 2001, Loreau et al. 2002). In part, this controversy reflects different interpretations of the results of experiments conducted in terrestrial systems, largely focussing on the ecosystem impacts of terrestrial plants with relatively slow population dynamics. Because even the longest of these studies contain data that correspond to only a few generations of plants (Tilman et al. 2001), there is some concern that observed relations between richness and

ecosystem functioning are driven by persistent effects of initial experimental conditions. This controversy has focussed on the potential impacts of the densities and relative abundances of species on ecosystem functioning (Huston 1997, Naeem 2000, Wardle et al. 2000, Loreau et al. 2001). These concerns do not apply equally to aquatic microbial systems, which have provided other insights into relations between richness and ecosystem functioning (McGrady-Steed et al. 1997, Naeem and Li 1997, McGrady-Steed and Morin 2000, Naeem et al. 2000). The short generation times of even eukaryotic microorganisms (~3–24 hrs) make it possible to

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assemble communities from small initial inocula of organisms, which then rapidly grow to maximum densities and species compositions set by system dynamics rather than initial experimental conditions (Petchey et al. 2002). These systems also make it possible to evaluate statistically significant explicit links between the population dynamics of component organisms and ecosystem dynamics (McGrady-Steed and Morin 2000).

Despite these advantages, other criticisms have been raised about the interpretation of some recent results from aquatic microbial systems. These criticisms involve (1) analyses that confound the sources of variation observed in ecosystem functioning (Loreau et al. 2001), (2) potential artifacts resulting from experimental designs (Fukami et al. 2001), (3) the choice of data transformations and summary statistics used to evaluate variation in ecosystem functioning (Cottingham et al. 2001), and (4) whether variation in microbial richness is likely to be meaningful in natural ecosystems (Finlay 2002). Here we reanalyse previously published data (McGrady-Steed et al. 1997) using resampling statistics to show that the fundamental relation between biodiversity and variation in ecosystem functioning is not a consequence of analytical artifacts.

Background

Overview of studies in aquatic microbial microcosms

Studies in microbial microcosms provided some of the first explorations of relations between biodiversity and ecosystem functioning in aquatic ecosystems. Other recent studies (Cardinale et al. 2002, Downing and Leibold 2002) have begun to explore similar dynamics involving larger, longer-lived, aquatic organisms. Some of the microbial studies are reviewed in detail elsewhere (Petchey et al. 2002), but a few of the important findings are reconsidered here. McGrady-Steed et al. (1997) and Naeem and Li (1997) both suggested that patterns of variation in ecosystem functioning, termed either ecosystem predictability or ecosystem reliability, depended on biodiversity, specifically the number of species, functional groups and trophic levels. McGrady-Steed et al. (1997) also described a non-linear effect of microbial richness on decomposition rates consistent with redundant effects of species on this process. In contrast, effects of richness on invasibility in the same study were complex, with invasion success depending more on the species composition of the community than on species richness. Other studies have explored effects of richness on population dynamics (McGrady-Steed and Morin 2000), responses to environmental change (Petchey et al. 1999), and complex interactions between producers and decomposers (Naeem et al. 2000). Increased richness results in reduced average densities of species, resulting in community-wide density compensation (McGrady-

Steed and Morin 2000), without changing the variation in population dynamics noted in studies of different systems (Tilman 1996). A three-fold increase in richness did not substantially alter the responses of different microbial communities to strong simulated environmental warming (Petchey et al. 1999). Instead, communities consistently lost species from higher trophic levels in response to warming, leading to increased primary production in warmed systems as a result of the interruption of top-down effects caused by warming-induced extinctions. In the study by Naeem et al. (2000), interactions between producer (algae) and decomposer (bacteria) richness were complex, suggesting that overall productivity depended on the specific carbon compounds produced by algae and the differing abilities of bacteria to utilize those substrates. Of all these studies, only those suggesting reduced temporal variation in ecosystem processes in more diverse systems have engendered much controversy (McCann 2000, Cottingham et al. 2001, Fukami et al. 2001). We review the controversy and suggest a possible resolution below.

McGrady-Steed et al. (1997) described a negative relation between total variation in CO₂ flux and biodiversity in a series of microcosms (Fig. 1). This result has been questioned because the analysis described variation among replicate communities over six successive weeks of observation as well as variation among different replicates in each sampling interval (Loreau et al. 2001), an approach that combines sources of both temporal and spatial variation. While this analysis described the total range of variation observed during the experiment (McGrady-Steed et al. 1997), it

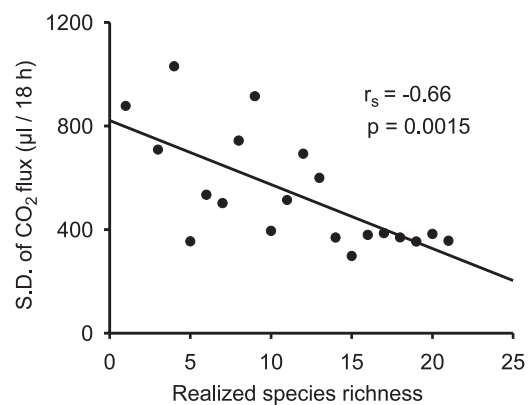


Fig. 1. Example of a negative relation between species richness and variability in ecosystem functioning based on data reported in McGrady-Steed et al. (1997). This analysis used data from only a single species composition at each initial level of species richness, but it represents only one of 64 ways that treatments could be selected to create a richness gradient. The pattern is based on measures of CO₂ flux in replicate communities at six points (weeks) over time, and combines temporal variation within replicates and spatial variation among replicates.

did not separate temporal variation within replicate communities, a measure of dynamic stability, from variation among replicate communities (individual microcosms) at a single point in time. Variation among replicates could be caused either by a tendency for different microcosms to have different compositions associated with differences in functioning, or by microcosms to exhibit similar temporal patterns of variation that are temporally “out of phase”.

The pattern of variation in ecosystem functioning reported by Naeem and Li (1997) was generally similar to that described by McGrady-Steed et al. (1997). Although a different response variable (the abundance of algae as a proxy of primary production) and a different measure of biodiversity (the number of species per functional group) was used, Naeem and Li (1997) found a similar negative relationship between variability in functioning and biodiversity. This result has been challenged on the grounds that the way the richness gradient was constructed confounds similarity among replicates in species composition with changes in biodiversity (Naeem and Li 1998, Wardle 1998, Fukami et al. 2001). This is a consequence of using one of several possible designs to explore relations between richness and functioning.

Experimental designs

Three kinds of experimental designs have been used. We call the approach adopted by Naeem and Li (1997) an unreplicated combinatorial design (Table 1A), an ap-

proach that had been advocated to ensure that any effects of richness on the average value of an ecosystem process were not confounded with changes in species composition (Allison 1999, Hector et al. 1999, Tilman 1999). In this design, replicates of a given richness level contain the same number of species, but typically have different species compositions selected at random from a larger species pool. This design overcomes the criticism of confounding richness with species composition, leveled at earlier designs that we term replicated nested design.

Replicated nested designs create a richness gradient by using lower richness systems with species compositions that are nested sub-sets of higher richness systems (Table 1B). Such a design faithfully mimics a particular sequence of species losses from high richness systems (Naeem et al. 1994). Each composition is typically replicated multiple times. However, because some species are only present in higher richness treatments, it is difficult to establish whether any observed differences in ecosystem functioning are caused by changes in the number of species per se, or by the impacts of particular species. Replicated nested designs are not subject to the critique of low compositional similarity among low richness treatments (Fukami et al. 2001).

A third kind of approach that can evaluate relations between biodiversity and variation in ecosystem functioning uses what we call a replicated combinatorial design. This approach combines the features of replicated nested and unreplicated combinatorial designs, so that there are several different species combinations within each richness level, each of which is replicated

Table 1. A. Example of a nested replicated design, analogous to the one described by Naeem et al. (1994). For simplicity, the richness gradient is assembled from three species, indicated by the letters A, B, and C, and there are three replicates of each level of diversity = species richness. Richness is effectively altered by deleting or adding the same species from all replicates at a given richness level. B. Example of an unreplicated combinatorial design, analogous to the one described by Naeem and Li (1997) or Tilman et al. (1996). C. Example of a replicated combinatorial design, analogous to the ones described by McGrady-Steed et al. (1997) and Hector et al. (1999). Richness is altered by selecting species at random from a species pool, to yield more than one species composition at each level of richness, each of which is replicated multiple times. Only two of the nine possible richness gradients are shown.

Species richness	Composition of replicates	% Similarity of replicates			
A. Nested replicated design.					
1	[A], [A], [A]	100			
2	[A+B], [A+B], [A+B]	100			
3	[A+B+C], [A+B+C], [A+B+C]	100			
B. Unreplicated combinatorial design.					
1	[A], [B], [C]	0			
2	[A+B], [B+C], [A+C]	50			
3	[A+B+C], [A+B+C], [A+B+C]	100			
C. Replicated combinatorial design.					
Species richness	Composition 1	% similarity	Species richness	Composition n	% similarity
1	[A], [A], [A]	100	... 1	[C], [C], [C]	100
2	[A+B], [A+B], [A+B]	100	... 2	[B+C], [B+C], [B+C]	100
3	[A+B+C], [A+B+C], [A+B+C]	100	... 3	[A+B+C], [A+B+C], [A+B+C]	100

multiple times (Table 1C). Logistical constraints sometimes restrict the use of alternate species compositions to lower levels of the richness gradient (McGrady-Steed et al. 1997), although in some cases there are alternate compositions across the entire richness gradient (Hector et al. 1999). Multi-trophic level systems impose other constraints, because food webs cannot generally be assembled at random from a larger species pool (Raffaelli et al. 2002). Replication of the different species combinations is crucial, since it allows estimation of variation in ecosystem functioning within levels of richness (e.g. among replicates of a specified composition) without confounding that variation with differences in species composition or percent similarity among replicates. Below, we suggest how this information can be re-sampled to establish patterns between richness and variation in ecosystem functioning using the many possible richness gradients that can be created by considering one composition at a time within each richness level.

Statistical methods

Temporal variation

We used the original data from McGrady-Steed et al. (1997) to estimate temporal variation in CO₂ flux within each experimental unit (i.e. in microbial microcosms). Temporal variation was calculated from six measures of CO₂ flux made for each microcosm at weekly intervals. Because CO₂ flux can take positive or negative values, and because the standard deviation and mean of this measure were not significantly correlated ($r_s = 0.35$, $p = 0.12$, $n = 21$), we did not log transform these data. Similarly, because the mean value of CO₂ flux was close to zero within richness levels, we did not use the coefficient of variation to describe variability, as suggested by Cottingham et al. (2001), since it would involve dividing the standard deviation of CO₂ flux by a very small value of fluctuating sign. Absence of a strong correlation between the variance and the mean (Doak et al. 1998 and Tilman et al. 1998 for a discussion of biodiversity-ecosystem functioning), negative values of some observations, and the uniformly small value of the mean within richness levels, suggest that the standard deviation of CO₂ flux is the more reliable measure of variation. Other approaches, such as Levene's test for relative variation (Schultz 1985) may also be valuable, but such more complex comparisons are beyond the immediate scope of this paper.

We explored relations between temporal variation in CO₂ flux and richness in two ways. First, we calculated the Spearman correlation between the standard deviation of CO₂ flux over time with the average value of species richness through time in each microcosm. This

tested for an overall effect of richness on temporal variation in ecosystem functioning. We used Spearman rank correlations as a conservative test in situations where the normality of data was questionable. We also tested for differences among the various treatments (species composition) in temporal variability, using an analysis of variance (ANOVA) of the values of temporal standard deviation in CO₂ flux estimated for replicates of the same initial composition. Here, every initially different species composition was treated as a different level of the factor being analysed, regardless of values of species richness in those different compositions.

Variation among microcosms

The problem of reduced compositional similarity among low richness experimental units means that a simple ANOVA approach probably cannot be used to analyze variation in ecosystem functioning using either unreplicated or replicated combinatorial designs (Fukami et al. 2001). This problem does not arise in replicated nested designs, since all replicates within each richness level have an initial compositional similarity of 100%, although the attribution of causation to richness or species composition remains problematic. We argue that a reasonable way to evaluate the relationship between biodiversity and temporal variation in ecosystem functioning would involve sampling many different richness gradients, each having a particular species composition, replicated multiple times, at each richness level. We did this by re-sampling existing data using a simple algorithm. For each re-sampled richness gradient, the Spearman rank correlation between richness and the standard deviation of functioning was estimated. Then the frequency distribution of the correlation coefficients obtained from the many different re-sampled gradients was used to infer how often negative or positive relations between richness and variability in functioning were likely to occur.

Replicated combinatorial designs contain the information needed to simulate (by re-sampling) many different possible richness gradients. To do this, different richness gradients are re-sampled by using information from replicates of one composition per richness level at a time, evaluating the summary statistics of interest (here the rank correlation between the S.D. of CO₂ flux and richness), and repeating this process for all of the different possible combinations of initial compositions that can be used to create the gradients. For a richness gradient with S different levels of species richness with C different species combinations at each richness level, the number of possible gradients is C^S . In the case of our replicated partial combinatorial design (Table 2), where $C = 4$ over the 3 lowest richness levels, there were 64

Table 2. Species combinations used to create the species richness gradients (from McGrady-Steed et al. 1997). Letters a, b, c, and d indicate the species composition of up to four different communities within each level of species richness. Each species composition was replicated five times. Taxa in parentheses failed to become established. Letters in parentheses in the zero species treatment indicate organisms that contaminated microcosms originally containing only bacteria. Different richness gradients were sampled from this set of species richness treatments by using all possible combinations of species richness treatments, taken one at a time within each richness gradient. For example, one gradient would be (0a, 3a, 5a, 10a, 15a, 20a, 25a, 31a), a second could be (0a, 3b, 5c, 10d, 20a, 25a, 31a), and so on. Any two gradients can differ at most in the composition of three species richness treatments (3, 5, and 10) or 15 replicate microcosms.

Trophic position	Organism	Initial species richness treatment							
		0	3	5	10	15	20	25	31
Producers	<i>Ankistrodesmus</i> sp. 1	(a)	c		a,c	a	a	a	a
	<i>Chlamydomonas</i>	(a)	a,b	a-c	a-d	a	a	a	a
	Diatom sp.			c,d	b,d				
	<i>Euglena</i>					a	a	a	a
	<i>Netrium</i>					a	a		
	(<i>Phacus</i>)				a			a	a
	(<i>Peridinium</i>)				a		a	a	a
	<i>Scenedesmus</i>		d	a,d	b-d	a		a	a
	<i>Staurastrum</i>			b	b-d		a	a	a
	Herbivores	<i>Brachionus</i>		c		c	a		
<i>Frontonia</i>			d		a,d		a	a	a
Hypostome sp.			b	c	b		a	a	a
<i>Stentor</i> sp. 1				b	b		a	a	a
<i>Stylonychia</i>				a,d	c		a	a	a
Bacterivores		<i>Aspidisca</i>							a
	(<i>Amoeba</i>)							a	a
	(<i>Coleps</i>)							a	a
	<i>Colpidium</i>			c	a,c	a	a	a	a
	<i>Colpoda</i> small							a	a
	<i>Colpoda</i> large							a	a
	<i>Halteria</i>		a		d	a	a	a	a
	Gastrotrich sp.				a,d	a			a
	Microflagellates	(a)	a-d	a-d	a-d	a	a	a	a
	<i>Monostyla</i>			a	b		a	a	a
	<i>P. bursaria</i>				b		a	a	a
	<i>Paramecium</i> sp. 2			d	a,d	a		a	a
	<i>Rotaria</i>			b	c	a		a	a
	<i>Spirostomum</i>				d	a		a	a
Predators	Heliozoa sp.				b			a	a
	(<i>Oxytricha</i>)				a		a	a	a
	<i>Stentor</i> sp. 2				c	a	a	a	a
	(<i>Urostylela</i>)					a	a		a

possible ways to create richness gradients using one composition per level of richness (Table 2). This is enough to describe the frequency distribution for values of the rank correlation between richness and variation in ecosystem functioning (here CO₂ flux). We described this pattern in each of the six weeks of the experiment, which also removed any influence of temporal variation and instead focused only on variation among individual microcosms of initially similar composition and identical current species richness. For the reasons described earlier in the analysis of temporal variation, we used the standard deviation in CO₂ flux among replicates of identical species richness as a measure of variation in ecosystem functioning, and correlated this with observed values of species richness on the day of measurement, using the Spearman rank correlation coefficient (r_s) as the summary statistic. We then used the frequency distribution of the 64 values of r_s to make inferences about how likely a negative relation between species richness and variation in functioning would be over a range of possible richness gradients.

The procedure used the following simple algorithm. 1) Microcosms assigned to a particular richness gradient were sorted into classes having the same value of observed species richness. 2) The standard deviation of CO₂ flux was estimated for microcosms within each level of observed species richness. Where a level of species richness contained only a single observation, it was dropped from the analysis, since the standard deviation could not be calculated. 3) The rank correlation between the standard deviation of CO₂ flux and species richness was then described by estimating Spearman's correlation coefficient over all levels of richness. 4) Steps 1-3 were repeated for each of the 64 distinct richness gradients, to describe the distribution of correlations that might be observed. Each richness gradient was assembled so that replicates within each initial level of species richness corresponded to a single species composition. 5) The entire process was repeated for data from each week of the six-week study, to remove any contribution of temporal variation from the observed variation among microcosms.

Results

Temporal variation in ecosystem functioning

A plot of the relation between the standard deviation of CO₂ flux within each microcosm over time against the average value of eukaryotic species richness within each microcosm revealed no obvious trends (Fig. 1, $r_s = -0.10$, $P = 0.35$, $n = 85$). However, an ANOVA for the effects of different initial species richness treatments on the standard deviation of CO₂ flux indicated that some initial species compositions were more variable than others ($F_{16,68} = 4.94$, $P < 0.0001$). Plotting the average species richness of each treatment against the average standard deviation of CO₂ flux reveals that the differences are not a simple linear function of species richness (Fig. 2, $r_s = -0.19$, $P = 0.47$, $n = 17$). From this analysis we conclude that temporal variation in ecosystem functioning was an unlikely source of the negative relation between total variation in CO₂ flux and species richness reported by McGrady-Steed et al. (1997).

Variation among microcosms in ecosystem functioning

The distribution of values of Spearman correlation coefficients between the standard deviation of CO₂ flux within groups of replicates with the same species richness

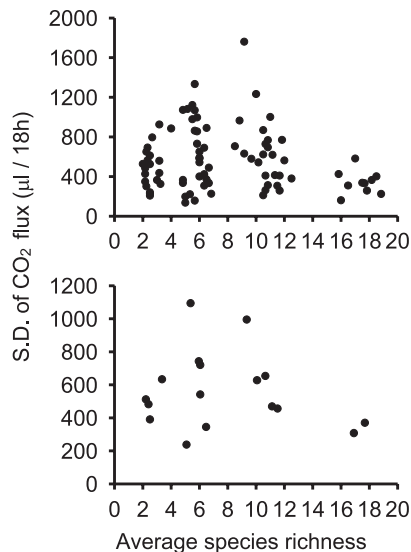


Fig. 2. Patterns of temporal variation within communities of different species richness. Top panel: each point corresponds to a single replicate community (microcosm). Species richness is the average over time in each microcosm. Bottom panel: each point corresponds to an average across replicates within treatments corresponding to different initial species compositions. Species richness is the average across replicates for values measured over time.

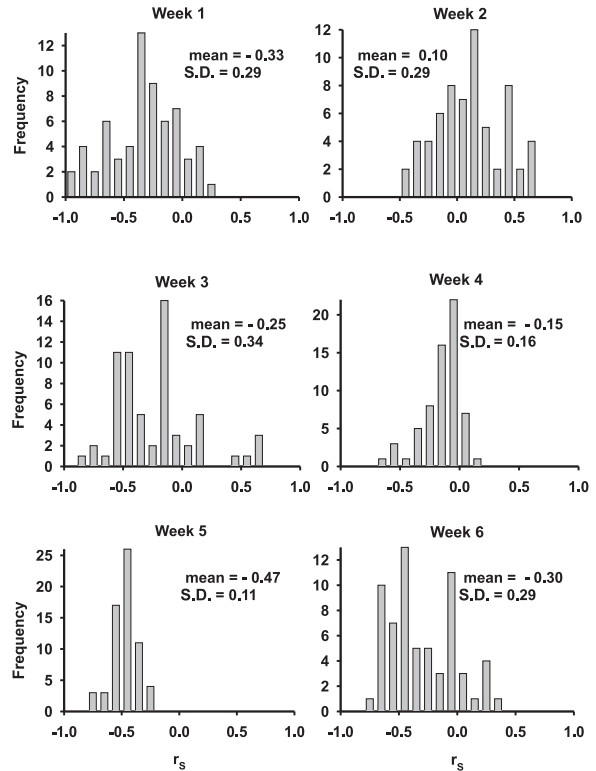


Fig. 3. Frequency distributions for Spearman rank correlations between the standard deviation of CO₂ flux within levels of realized species richness and the value of species in a replicate at the time of measurement. Each correlation coefficient corresponds to a different combination of treatments used to create a richness gradient, so that each level of initial richness is represented by a single species composition replicated multiple times. This analysis shows patterns of variation among communities at six different points (weeks) in time, so the variation does not include temporal variation, only variation among communities with the same species richness.

and those values of species richness shows that for four of the six sampling weeks, values of the correlations were predominantly negative (Fig. 3). On the other weeks, patterns were less distinct. This pattern suggests that most of the variation related to species richness was among microcosms of identical richness within time periods.

Discussion

Sources of ecosystem variation along replicated richness gradients

Our analysis confirms that low richness systems are more variable in one aspect of ecosystem functioning, the flux of CO₂ in aquatic microbial microcosms. Our analysis also shows that this pattern is not simply caused by an increase in temporal variation in CO₂ flux within

low richness systems. Although species composition did affect temporal variability, there was no simple relation between species richness and temporal variability of CO₂ flux within experimental units. Instead, the main link between increased variation and reduced richness apparently resulted from differences among microcosms having the same species richness at the same point in time. This is the pattern of variation that was captured by evaluating the correlations between the standard deviation of CO₂ flux and the species richness within each week of the experiment.

While the cause of the negative relation between variability in CO₂ flux and species richness remains speculative, we suspect that systems with a small number of species distributed across several trophic levels are more likely to lose entire functional groups by chance. Consequently, if rates of ecosystem processes depend on species richness, systems of low richness are more likely to display large differences in functioning (Petchey et al. 1999). Random loss of entire functional groups, such as consumers or primary producers, within a low richness system could determine whether that system is a source or sink for CO₂. For example, if low richness communities tended to be dominated either by algae or consumers, large differences in CO₂ flux could result. In contrast, more diverse communities might be less likely to be dominated by either of these functional groups.

The analytical solution that we propose for evaluating effects of richness on the variability of ecosystem processes requires a larger number of replicate experimental units than might be employed in unreplicated combinatorial designs. This increase in effort is needed only for questions related to the variability of processes or attributes. For questions related to average responses, the kinds of designs described in Table 1B are quite adequate. Obviously, if responses to perturbations are of interest, as in Petchey et al. (1999), Pfisterer and Schmid (2002), and Worm et al. (2002), then even larger designs with both more factors and more replicates are required. Such designs will realistically involve trade-offs in the number of richness levels against the total number of experimental units used.

Data transformations and measures of variability

Some authors have suggested that data used to evaluate effects of richness on variability should be logarithmically transformed to minimize the risk of artifacts arising from the frequently observed correlations between the means and variances of variables (Cottingham et al. 2001). While this precaution is clearly important in many cases, it is unnecessary for variables where the mean and variance do not show significant positive correlations (McGrady-Steed et al. 1997). Log transformations are

also impractical for variables like fluxes that take on positive and negative values, since the logarithms of negative numbers are undefined. While it might seem tempting to simply add a constant to transform such variables into all positive values, the choice of the transformation will strongly affect measures of variability, as McArdle et al. (1990) have shown. In such situations, use of the standard deviation of untransformed values remains the best option to express variability. In situations where responses can only take on positive values (population sizes, biomass, productivity) and where the variance is likely to be positively correlated with the mean, logarithmic transformations are advisable.

Cottingham et al. (2001) also suggested that some measures of variability are preferable to others. In particular, for untransformed data, they argued that the coefficient of variation is preferable to the standard deviation. Again, this suggestion makes good sense when applied to data that take on only positive values, and where the variance is likely to increase with the mean (McArdle et al. 1990). However, with our data on CO₂ flux, one problem is that means may be relatively small and fluctuate around zero (Fig. 2 in McGrady-Steed et al. 1997), in which case the standard deviation is being standardised by division with a small number of fluctuating sign. For this reason, we would argue that in such cases the coefficient of variation should not be automatically chosen as the measure of variability.

The significance of biodiversity in microbial assemblages

Some ecologists have argued that relations between biodiversity and ecosystem functioning have little meaning for microorganisms (Finlay et al. 1997, Finlay 2002, Finlay and Fenchel 2002), based on the belief that most microbes have cosmopolitan distributions. The logic is that if all species can potentially occur everywhere, then richness is uniformly high, natural microbial systems are maximally redundant, and meaningful departures from maximal richness and normal functioning are unlikely. The evidence used to support this argument is that a large fraction of described species can be found in a small number of intensively studied sites and similar sets of species can sometimes be found in widely separated locations (Finlay 2002). While some species appear to be widely distributed, the frequency distribution of geographic range sizes for the full set of described species is far from clear. Others contest the assertion of ubiquity (Foissner 1999, Coleman 2002), arguing that cryptic species complexes, incomplete descriptions of extant species, and fragmentary data on geographic distributions make the cosmopolitan distribution of protists illusory at best. Biogeochemical processes driven by

microbes are often localized within very small patches, and consequently there is a greater likelihood that local diversity will vary in ways that affect processes. Global redundancy only implies local functional uniformity if microbial distributions are spatially homogeneous or scale invariant, which seems unlikely.

For a few well-studied genera, like the ciliate *Tetrahymena* (Elliot 1973, Nanney and McCoy 1976), it is quite clear that different species have different geographic distributions. Many of these species were once lumped within a single morphospecies, *Tetrahymena pyriformis* (Ehrenberg). However, molecular methods have resolved this single morphospecies into several sexually reproducing species as well as a number of asexual lineages (Nanney and McCoy 1976). Other surveys suggest that patterns of species richness of other protists are not consistent with cosmopolitan distributions (Hillebrand et al. 2001). Until we know much more about the geographical distribution of protists as a group, assertions about their ubiquity seem premature.

The range of microbial richness examined in recent studies (McGrady-Steed et al. 1997, Naeem and Li 1997, Petchey et al. 1999, McGrady-Steed and Morin 2000, Naeem et al. 2000) is small compared to the richness of some natural systems (Finlay and Fenchel 1999), but it is large relative to others, such as polar lakes (Parker et al. 1982, Bell and Laybourn-Parry 1999). This suggests that comparisons of ecosystem functioning along gradients of microbial richness can potentially provide insights into natural systems, while also serving as useful models of other systems that are less amenable to experimentation. Experimental studies of small-scale microbial systems provide opportunities for understanding the long-term consequences of biodiversity in systems that develop over many generations of the interacting organisms (Petchey et al. 2002). When conducted over a large number generations, such studies should display patterns reflecting the long-term impact of biodiversity on species interactions and ecosystem processes, rather than revealing transient effects of initial species densities that complicate studies of longer-lived organisms. This makes aquatic microbial systems a powerful model system for experimental studies of biodiversity and ecosystem functioning, as well as for studies of other problems where it is crucial to link population dynamics to properties of communities and ecosystems.

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References

- Allison, G. W. 1999. The implications of experimental design for biodiversity manipulations. – *Am. Nat.* 153: 26–45.
- Bell, E. A. and Laybourn-Parry, J. 1999. Annual plankton dynamics in an Antarctic saline lake. – *Freshwat. Biol.* 41: 507–519.
- Cardinale, B. J., Palmer, M. A. and Collins, S. L. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. – *Nature* 415: 426–429.
- Coleman, A. W. 2002. Microbial eukaryote species. – *Science* 297: 337.
- Cottingham, K. L., Brown, B. L. and Lennon, J. T. 2001. Biodiversity may regulate the 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.
- Downing, A. L. and Leibold, M. A. 2002. Ecosystem consequences of species richness and composition in pond food webs. – *Nature* 416: 837–841.
- Elliot, A. M. 1973. Life cycle and distribution of *Tetrahymena*. – In: Elliot, A. M. (ed.), *Biology of Tetrahymena*. Hutchinson, & Ross, Inc, Dowden, pp. 259–286.
- Finlay, B. J. 2002. Global dispersal of free-living microbial eukaryote species. – *Science* 296: 1061–1063.
- Finlay, B. J. and Fenchel, T. 1999. Divergent perspectives on protist species richness. – *Protist* 150: 229–233.
- Finlay, B. J. and Fenchel, T. 2002. Microbial eukaryote species. – *Science* 297: 337.
- Finlay, B. J., Maberly, S. C. and Cooper, J. L. 1997. Microbial diversity and ecosystem function. – *Oikos* 80: 209–213.
- Foissner, W. 1999. Protist diversity: estimates of the near-imponderable. – *Protist* 150: 363–368.
- Fukami, T., Naeem, S. and Wardle, D. A. 2001. On similarity among local communities in biodiversity experiments. – *Oikos* 95: 340–348.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. – *J. Ecol.* 86: 902–910.
- Hector, A., Schmid, B., Beierkuhnlein, C. et al. 1999. Plant diversity and productivity experiments in European grasslands. – *Science* 286: 1123–1127.
- Hillebrand, H., Watermann, F., Karez, R. et al. 2001. Differences in species richness patterns between unicellular and multicellular organisms. – *Oecologia* 126: 114–124.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. – *Oecologia* 110: 449–460.
- Loreau, M., Naeem, S., Inchausti, P. et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. – *Science* 294: 804–808.
- Loreau, M., Naeem, S. and Inchausti, P. (eds) 2002. *Biodiversity and ecosystem functioning: synthesis and perspectives*. – Oxford Univ. Press.
- McArdle, B. H., Gaston, K. J. and Lawton, J. H. 1990. Variation in the size of animal populations: patterns, problems and artefacts. – *J. Anim. Ecol.* 59: 439–454.
- McCann, K. S. 2000. The diversity-stability debate. – *Nature* 405: 228–233.
- McGrady-Steed, J. and Morin, P. J. 2000. Biodiversity, density compensation and the dynamics of populations and functional groups. – *Ecology* 81: 361–373.
- McGrady-Steed, J., Harris, P. M. and Morin, P. J. 1997. Biodiversity regulates ecosystem predictability. – *Nature* 390: 162–165.

- Naeem, S. 2000. Reply to Wardle et al. – *Bull. Ecol. Soc. Am.* 81: 241–246.
- Naeem, S. and Li., S. 1997. Biodiversity enhances ecosystem reliability. – *Nature* 390: 507–509.
- Naeem, S. and Li., S. 1998. Reply: a more reliable design for biodiversity study? – *Nature* 390: 30.
- Naeem, S., Thompson, L. J., Lawler, S. P. et al. 1994. Declining biodiversity can alter the performance of ecosystems. – *Nature* 368: 734–737.
- Naeem, S., Hahn, D. R. and Schuurman, G. 2000. Producer-decomposer co-dependency influences biodiversity effects. – *Nature* 403: 762–764.
- Nanney, D. L. and McCoy, J. W. 1976. Characterization of the species of the *Tetrahymena pyriformis* complex. – *Trans. Am. Micros. Soc.* 85: 664–682.
- Parker, B. C., Simmons, G. M., Seaburg, K. G. et al. 1982. Comparative ecology of plankton communities in seven Antarctic oasis lakes. – *J. Plankt. Res.* 4: 271–286.
- Petchey, O. L., McPhearson, P. T., Casey, T. M. et al. 1999. Environmental warming alters food web structure and ecosystem function. – *Nature* 402: 69–72.
- Petchey, O. L., Morin, P. J., Hulot, F. et al. 2002. Contributions of aquatic model systems to our understanding of biodiversity and ecosystem functioning. – In: Loreau, M., Inchausti, P. and Naeem, S. (eds), *Biodiversity and ecosystem functioning*. Oxford Univ. Press, pp. 127–138.
- Pfisterer, A. B. and Schmid, B. 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. – *Nature* 416: 84–86.
- Raffaelli, D., van der Putten, W. H., Persson, L. et al. 2002. Multi-trophic dynamics and ecosystem processes. – In: Loreau, M., Inchausti, P. and Naeem, S. (eds), *Biodiversity and ecosystem functioning*. Oxford Univ. Press, pp. 147–154.
- Schultz, B. B. 1985. Levene's test for relative variation. – *Syst. Zool.* 34: 449–456.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. – *Ecology* 77: 350–363.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. – *Ecology* 80: 1455–1474.
- Tilman, D., Wedin, D. and Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. – *Nature* 379: 718–720.
- Tilman, D., Lehman, C. L. and Bristow, C. E. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? – *Am. Nat.* 151: 277–282.
- Tilman, D., Reich, P. B., Knops, J. et al. 2001. Diversity and productivity in a long-term grassland experiment. – *Science* 294: 843–845.
- Wardle, D. A. 1998. A more reliable design for biodiversity study? – *Nature* 394: 30.
- Wardle, D. A., Huston, M. A., Grime, J. P. et al. 2000. Biodiversity and ecosystem function: an issue in ecology. – *Bull. Ecol. Soc. Am.* 80: 235–239.
- Worm, B., Lotze, H. K., Hillebrand, H. et al. 2002. Consumer versus resource control of species diversity and ecosystem functioning. – *Nature* 417: 848–851.