

REPORT

Connectivity, scale-dependence, and the productivity–diversity relationship

Jonathan M. Chase and Wade A. Ryberg
Department of Biology,
Washington University in St
Louis, Campus Box 1137, One
Brookings Drive, St Louis, MO,
USA
Correspondence: E-mail:
waryberg@artsci.wustl.edu

Abstract

We surveyed freshwater ponds (localities) nested within watersheds (regions) to evaluate the relationship between productivity and animal species richness at different spatial scales. In watersheds where the ponds were relatively distant from one another (likely reducing the level of interpond dispersal of many organisms), we found a scale-dependent productivity–diversity relationship; at local scales (among ponds), diversity was a hump-shaped function of productivity, whereas at regional scales (among watersheds), diversity monotonically increased with productivity. Furthermore, this relationship emerged because there was a strong relationship between productivity and pond-to-pond species compositional differences. Alternatively, in watersheds where ponds were relatively close together (likely leading to higher rates of dispersal of many organisms), we found no scale-dependence; diversity was a hump-shaped function of productivity at both local and regional scales. Here, the relationship between species compositional dissimilarity and productivity was much weaker. We conclude that whether or not scale-dependence is observed in productivity–diversity relationships will depend, at least in part, on the degree of connectivity among localities within regions.

Keywords

Beta-diversity, connectivity, diversity, monotonic, productivity, scale-dependence, species richness, unimodal.

Ecology Letters (2004) 7: 676–683

INTRODUCTION

The relationship between the primary productivity (the rate of net photosynthetic production per unit area) of a given area and the number of species that live in that area provides a compelling characteristic of environments that can be used to help understand the controls on biodiversity. Despite decades of research, the form of the relationship between primary productivity and biodiversity, as well as the underlying mechanisms creating this relationship, remain unclear (see reviews by Waide *et al.* 1999; Mittelbach *et al.* 2001). Some factors attributed to variation observed in productivity–diversity relationships include the influence of disturbance (Wilson & Tilman 2002), consumers (Worm *et al.* 2002), niche specialisation (Kassen *et al.* 2000), resource heterogeneity (Weitz & Rothman 2003), and community history (Fukami & Morin 2003; Weitz & Rothman 2003). In addition, several authors have suggested that the spatial scale at which the data are collected could lead to variation in productivity–diversity patterns (Wright *et al.* 1993; Waide *et al.* 1999; Mittelbach *et al.* 2001);

relatively small, local-scale patterns are more often hump-shaped (diversity first rises and then declines with productivity), whereas relatively large, regional-scale patterns are more often monotonically increasing.

Here we argue that the presence of scale-dependence in the productivity–diversity relationship will depend on the connectance, or rates of dispersal among localities. This is because connectance often strongly influences the degree of compositional dissimilarity (β -diversity) among localities. Specifically, several theoretical models show that higher dispersal rates or increased connectivity among localities can homogenize species composition among localities, decreasing community dissimilarity (β -diversity) (Hastings & Gavrillets 1999; Amarasekare 2000; Mouquet & Loreau 2002, 2003). Empirical surveys (Harrison & Quinn 1989; Harrison 1997, 1999; Chase 2003a) and experiments (Forbes & Chase 2002; Kneitel & Miller 2003) support this relationship in a variety of ecosystems. Thus, we predict that the presence of scale-dependence in the productivity–diversity relationship will depend on the degree of connectance among localities. Specifically, we predict that when

connectivity is low, dissimilarity (β -diversity) should be high. If there is also a strong relationship between productivity and dissimilarity, then different productivity–diversity relationships will be generated at different scales of study (as was found in Chase & Leibold 2002). Alternatively, we predict that when connectivity is high, dissimilarity (β -diversity) should be low weakening the relationship between productivity and dissimilarity and diminishing the effects of scale on the productivity–diversity relationship. Under these conditions, scale-dependant patterns should not emerge.

The plant and animal data presented in Chase & Leibold (2002) were surveyed from a series of watersheds that contained distantly connected ponds. These watersheds were chosen specifically in order to minimise variation due to factors other than productivity. Thus, the ponds used in the study were rather distant from one another to minimise the confounding influence of connectivity. However, at the time of the study (and Chase 2003a), the lead author (JMC) had not considered the potential importance of connectivity *per se* in altering the scale-dependent productivity–diversity relationship. In the current study, we test the validity of our hypothesis that the patterns of scale-dependence of the productivity–diversity relationship depend on the degree of connectance among localities within regions by using data on animal richness and composition that was collected contemporaneously with the data in Chase & Leibold (2002). These latter data were collected using identical methodology, but for reasons other than measuring the scale-dependence of the productivity–diversity relationship. Specifically, they were collected to examine the influence of connectance on local and regional diversity (Chase 2003a), the relationship between productivity and the abundance of trophic levels (Chase 2003b), and a variety of other patterns (J. M. Chase unpublished). Thus, we are able to compare data from communities that were closer together, and likely experiencing a high level of connectivity with data from communities that were more isolated. Nevertheless, we note at the outset that these data are patterns, and cannot definitely test among the mechanisms leading to those patterns.

METHODS

Invertebrate sampling

From May to August of 1996, 1997 and 1998, we collected presence/absence data for benthic invertebrates (e.g. Amphipoda and Mollusca), benthic and free-swimming insects (primarily Coleoptera, Diptera, Hemiptera and Odonata), amphibians (larval Anura, larval and adult Caudata), and small fishes (primarily Cyprinidae, Umbridae and Gasterosteridae) from 60 ponds (also marshes and swamps) (chosen

from a larger survey; for specific criteria for selection, see below) in southwestern Michigan, MI, USA (Kalamazoo, Calhoun, and Barry Counties). We did not survey planktonic organisms (e.g. Cladoceran and Copepod zooplankton) in this study, although Leibold (1999) found similar variation in zooplankton diversity in many of the same ponds included in this survey. We also did not survey habitats that contained large fish, such as sunfishes (Family Centrarchidae), which are indicative of lake ecosystems. Because species presence/absence can vary temporally within and among seasons, we sampled all ponds early (May–June) and late (July–August) in all years. We classified a taxon as present if it was found in a pond in any sampling date over the course of the survey.

We sampled each pond using a 0.1 m \times 0.1 m wide D-net with 1 mm mesh. After every sweep, we dumped the specimens into a white enamel pan and identified them visually. In cases where specimens were unknown to the observer, or when multiple coexisting species were too similar to identify to the species level in the field, we collected and preserved voucher specimens in 70% ethanol and transported them back to the laboratory for more detailed identification. All identifications were facilitated using the keys in Peckarsky *et al.* (1990), Thorp & Covich (1991), and Merritt & Cummins (1996). We ignored terrestrial and semi-terrestrial species found on the surface or on emergent plants. Sweeps were alternated between the surface, the water column, and the benthos, and were spread throughout the pond (e.g. different depths and locations) so as to sample all of the possible heterogeneity and microhabitats within the ponds. We continued D-net sweeps in a pond until no new species were observed in ten sweeps. We identified approximately 50% of all individuals collected to species, 25% to genus, and 10% to family. The remaining 15% of individuals were midges of the family Chironomidae (Diptera), which we sorted into broad morphological categories.

Measuring productivity and abiotic variables

In each pond, we estimated *in situ* primary productivity by measuring periphytic algal accrual in 0.05 m² cubical plastic tubs (modified from Clesceri *et al.* 1998). Each tub was covered by 0.33 mm mesh to exclude most grazers from the interior of the tub. This mesh blocked out approximately 10% of the available light, but did not significantly reduce algal growth in a controlled experiment performed in the absence of grazers (J. M. Chase unpublished data). Tubes were suspended approximately 2 cm below the surface of each pond by attaching them to bamboo stakes, and were placed in each pond for 15-day staggered between mid-June and late-July 1998. After the 15-day growth period, algae were scraped off of the inside of the tub, dried, and burned

in a muffle furnace to calculate ash-free dry matter (an index of the amount of organic matter present) (see also Chase & Leibold 2002; Chase 2003a,b).

In addition to estimating primary productivity in each pond, we also measured a variety of abiotic variables that might influence productivity (total nitrogen [TN], total phosphorus [TP], light) or species composition (dissolved O₂, pH, conductivity). We found very little variation in the latter abiotic factors, and no relationships with patterns of species composition or diversity, and so we do not discuss them further here. We did, however, find correlations between TN and TP (correlation: $r = 0.65$), and between both TN and TP and productivity (correlations: $r = 0.43$ and $r = 0.68$, respectively). Thus, as in other freshwater systems (e.g. Schindler 1978; Leibold 1999), variation in primary productivity among these ponds, and its subsequent relationship with species diversity, appears to be influenced by variation in nutrient inputs (mainly Phosphorus). Although we did not specifically consider factors that lead to the variation in nutrient loading in these ecosystems, they most likely included variation in geology of the surrounding soils, as well as variation in nutrient runoff from human activities (Kalff 2001).

Delimitation of local and regional communities

From a broader survey, we selected 60 ponds that occurred within watersheds. We defined individual ponds as the local scale and three adjacent local ponds nested within a watershed as the regional scale. Ponds within watersheds varied in both primary productivity (a continuous variable) and the degree of connectivity (either near or far apart). We took care so that each of the watersheds we selected had ponds that were similar in their primary productivity ($\pm 5 \text{ mg cm}^{-2}$ per 15-day) so that we could reasonably discuss productivity at both the pond and watershed scale. In each watershed, we chose three adjacent ponds for our analyses to standardise the surface area of each locality (range: 200–600 m²) and region (all three ponds range 750–1200 m²). This does not mean that each watershed only had three ponds, as they often had more. However, we made sure that the ponds in each region, but not included in this investigation, were within the range of productivity of sampled ponds within each watershed (productivity was measured in the same way as the focal ponds, see above). Furthermore, we chose wetland regions so that they were similar in their overall area of pond surface water (900–2000 m²) (including both surveyed and unsurveyed ponds).

We defined local species richness as the number of species found during any sampling period within a single pond and regional richness as the number of species found within the three-pond region during any sampling period. Finally, we calculated inter-pond dissimilarity in species

composition within each three-pond region as an index of β -diversity. We used species presence/absence data to calculate dissimilarity as $1 - C$, where C is Jaccard's index of community similarity (C). $C = j/(a + b - j)$; a and b are the number of species in each community, and j is the number of species that are present in both communities. Dissimilarity ranges from 1 when no species are shared between two communities to 0 when all species are shared. We averaged dissimilarity estimates from each pairwise comparison of ponds within a three-pond region to estimate regional dissimilarity.

Distance of separation as a surrogate for connectivity

For the less connected regions, we used the data from Chase & Leibold (2002) (see also Chase 2003a) on 10 watershed regions where the average distance among the three ponds within each region was large (300–600 m). As a comparison, we chose 10 watershed regions that were sampled contemporaneously and in an identical manner, and were otherwise similar in their area and range of productivities, but where the average distance among all of the ponds within each region was much smaller (10–150 m). One possibility that could occur when choosing watersheds where ponds differ in their proximity is that those ponds that are closer together could also be more similar in their environmental conditions than ponds that are farther apart. However, in all of the surveyed watersheds, we took care to choose ponds so that variation among ponds within a watershed was relatively small and standardised among the variables of interest (productivity and proximity). Furthermore, we found that there were no significant differences in the variances of productivity estimates and a variety of abiotic variables (dissolved O₂, pH, conductivity, TN, TP) among watersheds that varied in proximity (Bartlett's Chi-squared: all $P > 0.2$).

For this investigation, we assume that these differences in average distance among ponds translated directly into differences in the dispersal rates of the animals within those ponds. Unfortunately, we have no data to indicate how the variation among ponds from these two datasets, the less connected regions (300–600 m average distance of separation) and the more connected regions (10–150 m average distance of separation), actually varied in dispersal among the organisms of interest. Although a considerable amount of research has been done on dispersal among freshwater invertebrates, there are few general conclusions (Bohonak & Jenkins 2003). Certainly, many of the organisms in our surveys can either passively or actively disperse among ponds that are at relatively large distances from each other (e.g. adult dragonflies can travel large distances). Furthermore, the mechanisms of dispersal can be highly variable among different types of systems and among taxa; what might be 'close' for some species is certainly 'far'

for others. We do not intend to say that dispersal was not possible among the less connected regions, or that connectivity was the same for all species investigated. Instead, we suggest that on the whole, dispersal was likely to be much less frequent among habitats that are farther apart. This supposition seems to be supported in part by simple geometric expectations (e.g. ponds closer together have a higher probability of random encounters by dispersers) from some of the available evidence from freshwater systems (Bohonak & Jenkins 2003) and from the patterns of species diversity observed in these systems (Chase 2003a). Nevertheless, future analyses of these sorts of patterns would be well served to identify the rates of connectivity (dispersal) among localities directly, rather than to infer them from distances.

Statistical analyses

We compared the effects of primary productivity on dissimilarity using analysis of covariance (ANCOVA) with the categorical variable of connectance (low and high) as the covariate. We analysed species richness at local (average species richness across three adjacent ponds) and regional (cumulative species richness among three adjacent ponds) scales using linear and quadratic regression. We first determined whether the quadratic regression fit the data significantly better than a linear relationship using the likelihood ratio test (LRT; Box & Draper 1987). When a relationship had a significant quadratic term, we tested whether the peak of the relationship was interior, indicating a hump-shaped relationship using the test devised by Mitchell-Olds & Shaw (1987) (hereafter MOS-test). This test determines whether the estimated peak of the relationship (determined from the non-linear regression procedures) and its confidence intervals are significantly higher than the minimum of the independent variable measured (productivity in this case) and significantly lower than the maximum of the independent variable; this is done by comparing the estimate of the peak using t -tests (see Leibold 1999; Mittelbach *et al.* 2001; Chase & Leibold 2002 for similar usage of this test).

Because we only have $N = 10$ regions for both the more and less connected datasets, we only have 10 points for the regressions of regional richness. In order to compare this with the regressions of local richness, we took the average of local richness of the three ponds within the region so that the local richness values also had $N = 10$. With such a low sample size, the possibility of detecting a significant quadratic term using the LRT is very conservative. Furthermore, with low sample sizes, the estimate of the peak of the relationship using non-linear regression will generally have a large confidence interval. In order to be as liberal as possible in discovering patterns, we have chosen to

use $\alpha = 0.10$ as our critical value rather than the typical $\alpha = 0.05$ for both the LRT for the significance of the quadratic term and for the t -tests in the MOS-test for whether the relationship was hump-shaped or not (see also Mittelbach *et al.* 2001). Note also that in previous analyses (Chase & Leibold 2002; Chase 2003a), non-linear regressions of local diversity were calculated using each locality (pond) as an independent point ($N = 30$), giving more power to find strongly significant hump-shaped relationships.

All statistics were performed in SYSTAT[®] 10.2 (Evanston, IL, USA).

RESULTS

Dissimilarity in community composition was positively correlated with primary productivity in both the high- and low-connectance watersheds (high-connectivity regression: $n = 10$, $r^2 = 0.69$, $P < 0.005$; low-connectivity regression $n = 10$, $r^2 = 0.78$, $P < 0.001$); however, the slope values differed significantly depending on the categorical value of connectivity (low or high) (ANCOVA: MS = 0.33, $F_{1,16} = 22.15$, $P < 0.001$; Fig. 1). Three-pond regions with lower average inter-pond distances had much shallower productivity–dissimilarity slopes (slope = 0.0027) than regions with higher average inter-pond distances (slope = 0.012).

In the less connected regions, the relationship between local richness and productivity (Fig. 2a) was better fit by a quadratic regression ($r^2 = 0.42$, $F_{1,7} = 3.89$) than the linear regression ($r^2 = 0.03$, $F_{1,8} = 4.69$) (LRT; $P < 0.09$). Furthermore, the MOS-test showed that the estimated peak of the relationship was significantly higher than the minimum, and greater than the maximum of the independent (productivity) values (t -tests: $P < 0.05$). That is, in less

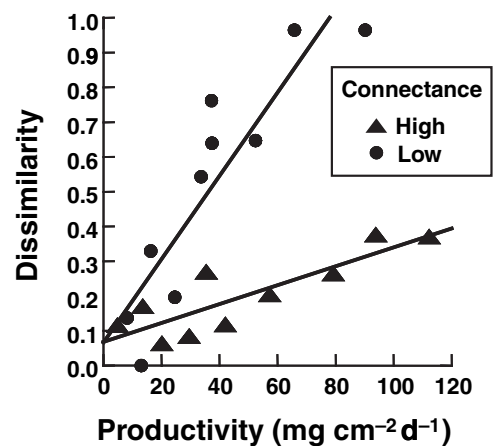


Figure 1 The relationship between primary productivity ($\text{mg cm}^{-2} \text{day}^{-1}$) and regional dissimilarity in ponds with high (triangles) and low (circles) connectance.

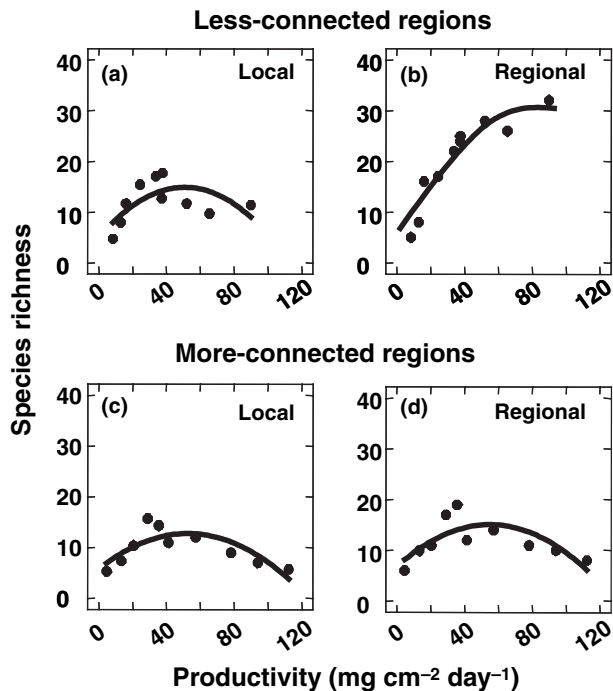


Figure 2 The relationship between primary productivity ($\text{mg cm}^{-2} \text{day}^{-1}$) and local and regional species richness in less and more connected systems. (a) Average local richness in unconnected regions, (b) regional richness in unconnected regions, (c) average local richness in more connected regions, (d) regional richness in more connected regions.

connected regions, the relationship between productivity and species richness at local scales was hump-shaped. In addition, in less connected regions, the relationship between regional richness and productivity (Fig. 2b) was better fit by a quadratic regression ($r^2 = 0.93$, $F_{1,7} = 5.35$) than the linear regression ($r^2 = 0.78$, $F_{1,8} = 13.90$) (LRT; $P < 0.07$). However, this relationship failed the MOS-test (t -tests: $P > 0.15$), indicating that it was not hump-shaped. Thus, in less connected (more distant) regions, there was scale-dependence in the shape of the relationship between productivity and species richness; it was hump-shaped at local scales and asymptotically increasing at regional scales (see also Chase & Leibold 2002; Chase 2003a).

In more connected regions, the relationship between local richness and productivity (Fig. 2c) was better fit by a quadratic regression ($r^2 = 0.63$, $F_{1,7} = 4.30$) than the linear regression ($r^2 = 0.07$, $F_{1,8} = 8.15$) (LRT; $P < 0.08$), and the MOS-test showed that the relationship was significantly hump-shaped (t -tests: $P < 0.05$). Similarly, in more connected regions, the relationship between regional richness and productivity (Fig. 2d) was better fit by a quadratic regression ($r^2 = 0.55$, $F_{1,7} = 4.83$) than a linear regression ($r^2 = 0.02$, $F_{1,8} = 10.65$) (LRT; $P < 0.07$), and again the MOS-test showed that this relationship was significantly

hump-shaped (t -tests: $P < 0.05$). Thus, in more connected (closer) regions, there was no scale-dependence in the shape of the productivity–diversity relationship; it was significantly hump-shaped at both spatial scales.

DISCUSSION

There is increasing recognition that in order to understand patterns and variation in local and regional diversity relationships, compositional variation from site-to-site must be explicitly considered (Loreau 2000, Veech *et al.* 2002). In order for a scale-dependent relationship of species diversity to exist along some environmental gradient (productivity in this case), there also has to be a relationship between compositional dissimilarity among localities (i.e. β -diversity) and that environmental factor. This is a very simple truism that results from the relationship between regional diversity, local diversity, and site-to-site compositional dissimilarity [e.g. regional diversity (γ) = local diversity (α) + dissimilarity (β); Loreau 2000, Veech *et al.* 2002]. For example, there was scale-dependence in the productivity–diversity relationship we observed among ponds that are relatively isolated from one another (Figs 2a,b) (see also Chase & Leibold 2002; Chase 2003a); local richness declined while regional richness increased over the same range of increasing productivity. This result can only be explained by a strong increase in the dissimilarity among local pond communities at high levels of productivity, as we saw for the distantly connected ponds in Fig. 1.

Although evidence for scale-dependent productivity–diversity relationships continues to accrue (Waide *et al.* 1999; Mittelbach *et al.* 2001; Chase & Leibold 2002), in some cases, no such scale-dependence is observed (Mittelbach *et al.* 2001, Cox *et al.* unpublished work, Chalcraft *et al.* unpublished work). Indeed, from our surveys of pond regions that were more closely aligned (and presumably more connected), but surveyed contemporaneously with those that were more distant (discussed above), we found no evidence for scale-dependent productivity–diversity relationships (Figs 2c,d). This lack of scale-dependence was despite the fact that in the more closely aligned ponds, there was still a positive relationship between pond-to-pond compositional dissimilarity and the primary productivity of those watershed regions (Fig. 1). In this case, the strength (slope) of the relationship between compositional dissimilarity and primary productivity was rather shallow, and thus not strong enough to create fundamentally different productivity–diversity relationships at the different spatial scales.

We note that there is not likely to be an absolute criterion that determines the degree of slope needed for the relationship between productivity and dissimilarity in order for the productivity–diversity pattern to emerge as

scale-dependent. For example, the calculation of dissimilarity among localities can give similar values whether the difference among communities is due to species composition being nested among localities (i.e. the species in a community with the lowest richness is a subset of the species in the community with the highest richness) or if there is simple replacement among species among localities. However, whether localities within a region have variation in community composition that is nested or replaced can have very different consequences for patterns of local and regional richness.

Chase & Leibold (2002) argued that three possible mechanisms could create increased compositional dissimilarity with productivity, leading to scale-dependent productivity–diversity relationships: (1) increasing environmental heterogeneity among ponds with increasing mean productivity at the regional scale; (2) increasing numbers of alternative stable states (i.e. different communities that result from different starting conditions but identical environmental conditions) with higher levels of productivity; or (3) increasing rates of compositional turnover through time at higher levels of productivity, so long as turnover is asynchronous among localities. Because these data are patterns of a single snapshot in time, we cannot fully discern which among these mechanisms lead to our observed scale-dependent pattern in the distantly connected ponds (Figs 2a,b). Chase & Leibold (2002) presented evidence to suggest that the first possibility, increasing heterogeneity with increasing productivity was unlikely to have caused this result because they found no statistical relationships between interpond heterogeneity in environmental variables and productivity. Furthermore, Chase (2003a) argued on empirical and theoretical grounds that this result was more consistent with the idea that more alternative stable states were expressed at higher levels of productivity. Alternatively, in a simulation model, Steiner & Leibold (2004) have found evidence for scale-dependent productivity–diversity patterns that appear to result from variation in the temporal turnover among localities within regions.

In opposition to the results when localities were relatively distant from one another, scale-dependence in the productivity–diversity relationship did not emerge when connectance was higher among localities (Figs 2c,d). One possible explanation for this result could simply be that these habitats were more proximate to one another; they were more similar in environmental conditions. However, we specifically chose ponds and watersheds where this possible effect was minimised, and did not find any significant correlations to that effect. Nevertheless, each of the three mechanisms that could lead to scale-dependence discussed above—increased heterogeneity, alternative states, or temporal turnover with productivity—are likely to be dimin-

ished by increased dispersal rates and connectance among localities. For example, a variety of theoretical models predict that increased connectance homogenises community composition among habitats that vary in their environmental conditions (Amarasekare & Nisbet 2001; Mouquet & Loreau 2002, 2003). Similarly, other theoretical models show that increased connectance decreases the number of alternative stable states a community can achieve (Shurin *et al.* 2004). Finally, although not theoretically examined as such, we expect that increased connectance would increase the synchronisation in temporal compositional turnover among localities. Thus, we can say with some confidence that the connectance among these regions homogenised species composition; e.g. the maximum species richness in distantly aligned ponds was considerably higher than the maximum species richness in more closely aligned ponds (see also Chase 2003a). Furthermore, this homogenisation is what most likely eliminated the scale-dependent effect. Unfortunately, these are observational data from a narrow temporal window, and we cannot discern by which of the above mechanisms this may have occurred.

Despite decades of research, there is still little consensus on the specific shape of the relationship between productivity and diversity. The most common relationship between productivity and diversity at local spatial scales is hump-shaped, whereas at regional spatial scales, it is most often monotonically increasing (Mittelbach *et al.* 2001). However, several other shapes of the relationship exist, and the relationship is influenced by several factors, including disturbance, consumers, niche specialisation, resource heterogeneity, and community history (Kassen *et al.* 2000; Mittelbach *et al.* 2001; Wilson & Tilman 2002; Worm *et al.* 2002; Fukami & Morin 2003; Weitz & Rothman 2003). Fukami & Morin (2003), for example, have shown that the history of community assembly (i.e. which species were introduced to the community first) produced different productivity–diversity relationships; this was likely because communities achieved multiple stable states depending on the order in which species entered the community. However, as discussed above in theoretical and empirical work, more connected systems should be less likely to exhibit multiple stable states (Chase 2003a; Shurin *et al.* 2004). As such, we expect that the results of Fukami & Morin (2003) resulted because their communities were isolated from one another; in more connected communities, we would expect that assembly sequence would have a weaker effect, and not express the same level of variation in the shape of the productivity–diversity relationship.

In conclusion, we have shown that the degree of scale-dependence in the productivity–diversity relationship depends critically on the degree of connectance and

dispersal rates among localities. This also emphasises the potential subjectivity involved when delimiting scale on natural communities (see also Loreau 2000). Connectivity homogenises local communities so that they behave as a single unit. This is analogous to the fact that in population genetics, spatially segregated populations behave more like a single population in increasingly connected systems. The degree to which a group of species will respond primarily as a single locality or a region of linked localities (i.e. a metacommunity) will depend on rates of connectivity among localities as well as a suite of other interacting meta-community attributes. We suggest that perhaps it is best to avoid the subjective determination of localities and regions in deference to more fluid depictions of species diversity (e.g. species–area curves).

ACKNOWLEDGEMENTS

We thank J. Kneitel, T. Knight, P. Van Zandt, and the Chase lab discussion group for discussion and comments. In addition, we thank J. Knops and three anonymous referees for their very useful comments and suggestions. This work was supported by a grant from the National Science Foundation to JMC (DEB 01-08118, 02-41080).

REFERENCES

- Amarasekare, P. (2000). The geometry of coexistence. *Biol. J. Linn. Soc.*, 71, 1–31.
- Amarasekare, P. & Nisbet, R.M. (2001). Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *Am. Nat.*, 158, 572–584.
- Bohonak, A.J. & Jenkins, D.G. (2003). Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecol. Lett.*, 6, 783–796.
- Box, G.E.P. & Draper, N.R. (1987) *Empirical Model Building and Response Surfaces*. John Wiley and Sons, New York, NY.
- Chase, J.M. (2003a). Community assembly: when should history matter? *Oecologia*, 136, 489–498.
- Chase, J.M. (2003b). Strong and weak trophic cascades along a productivity gradient. *Oikos*, 101, 187–195.
- Chase, J.M. & Leibold, M.A. (2002). Spatial scale dictates the productivity–biodiversity relationship. *Nature*, 416, 427–430.
- Clesceri, L.S., Greeberg, A.E. & Eaton, A.D. (1998). *Standard Methods for the Examination of Water and Wastewater*, 20th edn. American Public Health Association, USA.
- Forbes, A.E. & Chase, J.M. (2002). The role of habitat connectivity and landscape geometry in experimental zooplankton meta-communities. *Oikos*, 96, 433–440.
- Fukami, T. & Morin, P.J. (2003). Productivity–biodiversity relationships depend on the history of community assembly. *Nature*, 424, 423–426.
- Harrison, S. (1997). How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. *Ecology*, 78, 1898–1906.
- Harrison, S. (1999). Native and alien species diversity at the local and regional scales in a grazed California grassland. *Oecologia*, 121, 99–106.
- Harrison, S. & Quinn, J.F. (1989). Correlated environments and the persistence of metapopulations. *Oikos*, 56, 293–298.
- Hastings, A. & Gavrilets, S. (1999). Global dispersal reduces local diversity. *Proc. R. Soc. Lond. B Biol. Sci.*, 266, 2067–2070.
- Kalff, J. (2001) *Limnology*. Prentice Hall, Upper Saddle River, NJ.
- Kassen, R., Buckling, A., Bell, G. & Rainey, P.B. (2000). Diversity peaks at intermediate productivity in a laboratory microcosm. *Nature*, 406, 508–512.
- Kneitel, J.M. & Miller, T.E. (2003). Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *Am. Nat.*, 162, 165–171.
- Leibold, M.A. (1999). Biodiversity and nutrient enrichment in pond plankton communities. *Evol. Ecol. Res.*, 1, 73–95.
- Loreau, M. (2000). Are communities saturated? On the relationship between alpha, beta and gamma diversity. *Ecol. Lett.*, 3, 73–76.
- Merritt, R.W. & Cummins, K.W. (1996) *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt Publishing, Dubuque, IA.
- Mitchell-Olds, T. & Shaw, R.G. (1987). Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution*, 41, 1149–1161.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B. *et al.* (2001). What is the observed relationship between species richness and productivity? *Ecology*, 82, 2381–2396.
- Mouquet, N. & Loreau, M. (2002). Coexistence in metacommunities: the regional similarity hypothesis. *Am. Nat.*, 159, 420–426.
- Mouquet, N. & Loreau, M. (2003). Community patterns in source-sink metacommunities. *Am. Nat.*, 162, 544–557.
- Peckarsky, B.L., Fraissinet, P., Penton, M.A. & Conklin, D.J. (1990) *Freshwater macroinvertebrates of Northeastern North America*. Cornell University Press, Ithaca, NY.
- Schindler, D.W. (1978). Factors regulating phytoplankton production and standing crop in the world's lakes. *Limnol. Ocean.*, 23, 478–486.
- Shurin, J.B., Amarasekare, P., Chase, J.M., Holt, R.D., Hoopes, M.F. & Leibold, M.A. (2004). Alternative stable states and regional community structure. *J. Theor. Biol.*, 227, 359–368.
- Steiner, C.F. & Leibold, M.A. (2004). Cyclic assembly trajectories and scale dependent productivity–diversity relationships. *Ecology*, 85, 107–113.
- Thorpe, J.W. & Covich, A.P. (1991) *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, San Diego, CA.
- Veech, J.A., Summerville, K.S., Crist, T.O., & Gering, J.C. (2002). The additive partitioning of species diversity: recent revival of an old idea. *Oikos*, 99, 3–9.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I. *et al.* (1999). The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.*, 30, 257–300.
- Weitz, J.S. & Rothman, D.H. (2003). Scale-dependence of resource–biodiversity relationships. *J. Theor. Biol.*, 225, 205–214.
- Wilson, S.D. & Tilman, D. (2002). Quadratic variation in old-field species richness along gradients of disturbance and nitrogen. *Ecology*, 83, 492–504.
- Worm, B., Lotze, H.K., Hillebrand, H. & Sommer, U. (2002). Consumer versus resource control of species diversity and ecosystem functioning. *Nature*, 417, 848–851.

Wright, D.H., Currie, D.J. & Maurer, B.A. (1993). Energy supply and patterns of species richness on local and regional scales. In: *Diversity in Ecological Communities* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 66–74.

Editor, Johannes Knops
Manuscript received 11 February 2004
First decision made 11 March 2004
Manuscript accepted 20 May 2004