

Biodiversity and ecosystem functioning at local and regional spatial scales

Emily M. Bond* and
Jonathan M. Chase¹
Department of Biological
Sciences, University of
Pittsburgh, Pittsburgh,
Pennsylvania, 15260, USA.

¹Present address: Department of
Biology, Washington University,
St. Louis, Missouri, 63130, USA.

*Correspondence: E-mail:
emily0515@hotmail.com

Abstract

Local niche complementarity among species (the partitioning of species based upon niche differentiation) is predicted to affect local ecosystem functioning positively. However, recent theory predicts that greater local diversity may hinder local ecosystem functioning when diversity is enhanced through source–sink dynamics. We suggest community assembly as a way to incorporate both the local and regional processes that determine biodiversity and its consequent effects on ecosystem functioning. From this, we propose a hump-shaped relationship between diversity and ecosystem functioning at local scales, but a linear increase of functioning with diversity at regional scales due to regional complementarity.

Keywords

Biodiversity, community assembly, ecosystem functioning, niche complementarity, regional processes, spatial scale.

Ecology Letters (2002) 5: 467–470

In recent years, several investigators have demonstrated that species richness within local communities can influence ecosystem functioning, such as productivity and stability (reviewed in Kinzig *et al.* 2002). A wide variety of experiments conducted in disparate ecosystems have shown that greater species diversity positively affects ecosystem functioning (reviewed in Schwartz *et al.* 2000; Cottingham *et al.* 2001; Loreau *et al.* 2001). These studies have been used to make an important argument for the conservation of species (Schwartz *et al.* 2000; Hector *et al.* 2001; Lawler *et al.* 2002). However, other studies have found neutral or sometimes negative results (Huston *et al.* 2000; Schwartz *et al.* 2000). Thus, although there is often an overall effect of diversity on ecosystem functioning, the shape of the relationship is not always predictable and it is unclear why this variation among studies occurs.

We use theoretical models as a tool for understanding the variation in studies of diversity and ecosystem functioning. Two recent models have provided a framework for understanding the relationship between biodiversity and ecosystem functioning; however, they predict opposing patterns. The first model is based on local niche complementarity and assumes that each species possesses certain traits that allow species to utilize available resources differently (Tilman *et al.* 1997; Loreau 1998; Tilman 1999). As species diversity increases, each species utilizes a different component of the resource base. Thus, diversity

positively contributes to ecosystem functioning in the local community. However, as species diversity continues to increase, the probability that species will overlap in their resource use increases, thus creating a decelerating relationship. The second model is based on regional processes and source–sink dynamics and suggests that, when immigration from a region is high, local diversity increases, but ecosystem functioning decreases (Loreau & Mouquet 1999; Mouquet *et al.* 2002). This can be due to interspecific competition between the superior competitor in the patch and the inferior competitors that are maintained locally as sink populations when immigration is high. The decline in ecosystem functioning may occur when interspecific competition between the competitors is greater than intraspecific competition within a species. Here we connect these two theories to provide a synthetic view of the diversity–functioning relationship when community assembly controls local species diversity. Further, we suggest that ecosystem functioning can be viewed from the regional scale when environmental heterogeneity allows species to exist in different patch types and thus, coexist regionally. This regional complementarity among species may then cause ecosystem functioning to increase as regional species diversity increases.

We link these two models by assuming that when species diversity is low, the addition of new species complement one another (local niche complementarity). Alternatively,

when species diversity exceeds the number of local limiting factors, competition for these factors may cause a decline in local ecosystem functioning (Fig. 1a). Below, we provide a simple verbal model describing how this relationship might come about based on community assembly; but, note that the shape of this relationship does not necessarily rely on these specific assumptions. First, we assume that there are several local patches within a regional landscape. Within each local patch, there are several functional roles that species could fill. For example, these functional roles could be based on resource utilization (i.e. different nutrients). For each functional role we assume that there is a single species that can maximize functioning and outcompete all other

species (Mouquet *et al.* 2002). This superior competitor may maximize functioning by most efficiently transferring their resources to biomass (net primary productivity) or by providing resources to other biota through their tissues (nutrient cycling). Under the assumption of community assembly (Weiher & Keddy 1999), as species diversity increases each species falls into a particular functional role in the community. Thus, ecosystem functioning will increase until the number of species equals the number of functional roles in the local community (ascending part of Fig. 1a).

Given our assumption that a single species can outcompete all others for a particular functional role, the only way for species diversity to exceed the available functional roles in a local community is through source–sink dynamics (Loreau & Mouquet 1999; Amarasekare & Nisbet 2001; Mouquet *et al.* 2002). In order to explore the consequences of species diversity at these higher levels, we assume that there is environmental heterogeneity among patches, such that local patches vary in some other environmental factor (i.e. pH or temperature) in addition to resource availability. Therefore, a species that is a superior competitor in one patch type may be an inferior competitor in another. That is, a species cannot exist in sinks throughout the entire region or it would become regionally extinct (Holt 1997). Based on source–sink dynamics, both superior and inferior competitors may be present in the local patch. As a result, if immigration is high and if the inferior competitor can detract from the overall functioning of the superior competitor (through source–sink dynamics), ecosystem functioning may decline (descending part of Fig. 1a).

By assuming that community assembly controls local species diversity, we propose a hump-shaped relationship between local species diversity and local ecosystem functioning when immigration rates are high among patches in the region (Fig. 1a). The peak of this hump is dependent on the number of available functional roles in a local community and may be predicted *a priori* for the ecosystem of interest. Also, the descent of the curve may depend on the rate of immigration and strength of competition from the inferior competitor. If immigration is low or the inferior competitor is not able to detract from the superior competitor's functioning, then this decline may be weak or nonexistent.

So far, ecosystem functioning has primarily been considered on the local scale. However, the average functioning of an entire region may not necessarily be additive across all local patches. In our verbal model, local ecosystem functioning is reduced when species diversity increases through source–sink dynamics (see also Mouquet *et al.* 2002), but this effect might not be seen when we consider environmentally heterogeneous patches in a region. On the regional scale, different species are superior competitors in different patch types. When we pool across all patches in the

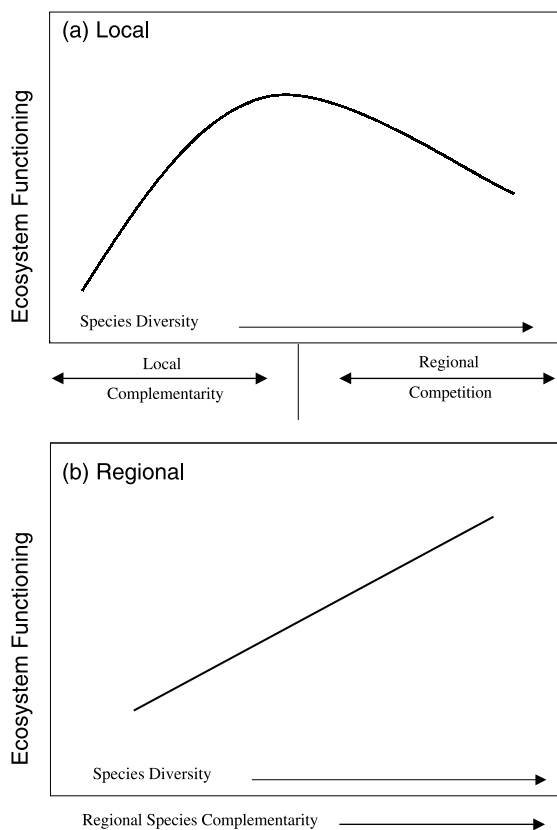


Figure 1 Species diversity and ecosystem functioning in local and regional spatial scales. At the local scale (a), niche complementarity allows an increase in functioning until all available niches are filled. After this point, local competition from sink populations (maintained through high immigration) detracts from the local functioning of established species. At the regional scale (b), regional species complement one another across patches, thus linearly increasing the functioning of the entire region. With loss of species locally, ecosystem functioning may actually be improved up to a certain point, whereas regional loss of species overall is detrimental to ecosystem functioning.

region, all species may now coexist and complement one another regionally (Mouquet & Loreau 2002). This can be considered niche complementarity at the regional spatial scale. Thus, even though local functioning is not maximized at high levels of local diversity (within patches), as regional complementarity (among patches) and regional species diversity increases, there may be a linear increase in regional ecosystem functioning (Fig. 1b). As a result, we suggest that ecosystem functioning can be highest when all species are maintained in the region, whereas, within any local patch, ecosystem functioning might actually be lower when all species are present.

In our discussion of the effects of biodiversity on ecosystem functioning, such as primary productivity, we have ignored a possible feedback of the effect of primary productivity on biodiversity. In fact, in a recent paper, Chase & Leibold (2002) have shown that the relationship between primary productivity (independent variable) and diversity (dependant variable) shows a scale-dependent pattern that is superficially similar to the one that we predict here. However, there is a problem with cause and effect in the relationship between biodiversity and productivity (this paper) and the relationship between productivity and biodiversity (Chase & Leibold 2002). In this paper, we are assuming that environmental variables which influence primary productivity (e.g. nutrients) other than species diversity are held constant. In Chase & Leibold (2002), the productivity gradient was driven primarily by variation in environmental factors (i.e. nutrients), and we suspect that the feedback of diversity on productivity was probably much weaker than the influence of environmental variation on productivity. Nevertheless, the complexity of cause and effect in the relationship between biodiversity and productivity illustrates an important issue in need of further exploration.

Our conceptual investigation may also be applied to temporal variation in environmental conditions. Recent models (Yachi & Loreau 1999; Chesson *et al.* 2002) have shown that, as environmental conditions vary through time, higher species diversity may be important in maintaining ecosystem functioning. Indeed, empirical evidence already supports the idea that greater species diversity may have different contributions to ecosystem functioning as environmental conditions shift through time (Reich *et al.* 2001; Mulder *et al.* 2001; Pfisterer & Schmid 2002). Thus, while empirical evidence is accruing to support the notion that increased species diversity is important through time, we suggest that spatial scale is also an important component to consider empirically when investigating the relationship between diversity and ecosystem functioning.

We have only begun to understand the implications of biodiversity on ecosystem functioning (Schwartz *et al.* 2000; Hector *et al.* 2001; Kinzig *et al.* 2002). The ideas presented

here suggest that species diversity may become increasingly important to ecosystem functioning at higher spatial scales. As environmental conditions vary across space, a variety of species with different environmental tolerances would be required to maintain ecosystem functioning across the landscape (i.e. regional complementarity). Previous studies have determined a variety of results between species diversity and ecosystem functioning (reviewed in Schwartz *et al.* 2000; Cottingham *et al.* 2001; Loreau *et al.* 2001; Schmid *et al.* 2002). Through synthesizing two previous models and increasing the spatial scale under consideration, our ideas may be used to describe the combination of processes (local and regional) which may influence the relationship found in empirical investigations.

ACKNOWLEDGEMENTS

We thank J. Butzler, A. Downing, S. Kalisz, T. Knight, A. Randle, N. Schoeppner, J. Steets and S. Tonsor for their helpful suggestions. We thank Nicolas Mouquet, Peter Morin, and two anonymous reviewers for their comments on the manuscript. This work was funded by NSF grant DEB-0108118 (to J.M.C.).

REFERENCES

- Amarasekare, P. & Nisbet, R.M. (2001). Spatial heterogeneity, source–sink dynamics, and the local coexistence of competing species. *Am. Nat.*, 158, 572–584.
- Chase, J.M. & Leibold, M.A. (2002). Spatial scale dictates the productivity–biodiversity relationship. *Nature*, 416, 427–430.
- Chesson, P., Pacala, S. & Neuhauser, C. (2002). Environmental niches and ecosystem functioning. In: *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. (eds Kinzig, A.P., Pacala, S.W. & Tilman, D.). Princeton University Press, Princeton, pp. 213–245.
- Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecol. Lett.*, 4, 72–85.
- Hector, A., Joshi, J., Lawler, S.P., Spehn, E.M. & Wilby, A. (2001). Conservation implications of the link between biodiversity and ecosystem functioning. *Oecologia*, 129, 624–628.
- Holt, R.D. (1997). Consequences of spatial heterogeneity. In: *Metapopulation Biology: Ecology, Genetics and Evolution* (eds Hanski, I. & Gilpin, M.E.). Academic Press, San Diego, pp. 149–164.
- Huston, M.A., Aarssen, L.W., Austin, M.P., Cade, B.S., Fridley, J.D., Garnier, E., *et al.* (2000). No consistent effect of plant diversity on productivity. *Science*, 289, 1255.
- Kinzig, A.P., Pacala, S.W. & Tilman, D. (eds). (2002). *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. Princeton University Press, Princeton, NJ.
- Lawler, S.P., Armesto, J.J. & Kareiva, P. (2002). How relevant to conservation are studies linking biodiversity and ecosystem functioning? In: *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. (eds Kinzig, A.P., Pacala, S.W.

- & Tilman, D.). Princeton University Press, Princeton, pp. 294–313.
- Loreau, M. (1998). Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Nat. Acad. Sci. USA*, 95, 5632–5636.
- Loreau, M. & Mouquet, N. (1999). Immigration and the maintenance of local species diversity. *Am. Naturalist*, 154, 427–440.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., *et al.* (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, 294, 804–808.
- Mouquet, N. & Loreau, M. (2002). Coexistence in metacommunities: The regional similarity hypothesis. *Am. Nat.*, 159, 420–426.
- Mouquet, N., Moore, J.L. & Loreau, M. (2002). Plant species richness and community productivity: why the mechanism that promotes coexistence matters. *Ecol. Lett.*, 5, 56–65.
- Mulder, C.P.H., Uliassi, D.D. & Doak, D.F. (2001). Physical stress and diversity–productivity relationships: the role of positive interactions. *Proc. Nat. Acad. Sci. USA*, 98, 6704–6708.
- Pfisterer, A.B. & Schmid, B. (2002). Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature*, 416, 84–86.
- Reich, P.B., Knops, J., Tilman, D., Craine, J., Ellsworth, D., Tjoelker, M., *et al.* (2001). Plant diversity enhances ecosystem responses to elevated CO₂ and nitrogen deposition. *Nature*, 410, 809–812.
- Schmid, B., Joshi, J. & Schlapfer, F. (2002). Empirical evidence for biodiversity–ecosystem functioning relationships. In: *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. (eds Kinzig, A.P., Pacala, S.W. & Tilman, D.). Princeton University Press, Princeton, NJ.
- Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H. & van Mantgem, P.J. (2000). Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia*, 122, 297–305.
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, 80, 1455–1474.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300–1302.
- Weiher, E. & Keddy, P. (1999). *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge.
- Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Nat. Acad. Sci. (USA)*, 96, 57–64.

Editor, P. J. Morin

Manuscript received 14 February 2002

First decision made 11 March 2002

Second decision made 2 April 2002

Manuscript accepted 18 April 2002