

FORUM

Species diversity and productivity: why do results of diversity-manipulation experiments differ from natural patterns?

Lin Jiang^{1*}, Shiqiang Wan² and Linghao Li²¹*School of Biology, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA; and* ²*Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China*

Summary

1. Experiments that directly manipulate species diversity often report a positive diversity effect on productivity, whereas observations of natural communities reveal various productivity–diversity relationships and nutrient addition to natural plant communities generally results in negative productivity–diversity relationships.

2. We hypothesize that this apparent paradox may be potentially explained by the reduced roles of complementarity and positive selection effects, and the increased importance of competitive exclusion in natural communities compared to diversity-manipulation experiments. This hypothesis arises from the difference in species distribution and abundance patterns between immature synthetically assembled communities in diversity-manipulation experiments and more mature natural communities.

3. Our hypothesis applies best to small-scale studies within homogenous habitats and complements the environmental heterogeneity hypothesis that explains diversity–productivity patterns across heterogeneous habitats.

4. *Synthesis.* Our analysis highlights important differences between synthetic communities in diversity-manipulation experiments and natural communities that may translate into different diversity–productivity patterns, and cautions against indiscriminate extrapolations of results of diversity-manipulation experiments to natural communities.

Key-words: biodiversity and ecosystem functioning, competitive exclusion, complementarity, environmental heterogeneity, productivity, selection effects, species diversity

Introduction

During the past two decades ecologists have devoted considerable effort to understanding functional significances of biodiversity (Kinzig *et al.* 2002; Loreau *et al.* 2002; Hooper *et al.* 2005; Srivastava & Vellend 2005). Much of the experimental work in this area has been conducted in synthetically assembled plant communities involving direct manipulations of plant diversity. This research has thus far revealed generally positive effects of biodiversity on ecosystem functioning and in particular positive effects of plant species diversity on primary productivity (Balvanera *et al.* 2006; Cardinale *et al.* 2006, 2007). This positive relationship between plant species diversity and productivity, however, is in striking contrast with emerging

patterns in natural communities that are revealed by studies exploring productivity as a driver of species diversity – a perspective that has historically received more attention (e.g. Hutchinson 1959; Connell & Orias 1964). Such studies include observations of diverse forms of productivity–diversity relationships (Waide *et al.* 1999; Mittelbach *et al.* 2001; Gillman & Wright 2006), and nitrogen fertilization experiments that reported nearly ubiquitous negative productivity–diversity relationships (Gough *et al.* 2000; Crawley *et al.* 2005; Suding *et al.* 2005). Understandably, these patterns of different diversity–productivity relationships have led to debates on whether results of diversity-manipulation experiments are relevant for natural communities (Thompson *et al.* 2005; Hector *et al.* 2007) and some conceptual models have been proposed to reconcile these different patterns (Loreau *et al.* 2001; Schmid 2002; Hector *et al.* 2007). The central message

*Correspondence author. E-mail: lin.jiang@biology.gatech.edu

of these conceptual models is that diversity tends to have a positive effect on productivity in the relatively homogenous environments that characterize small-scale diversity-manipulation experiments, but that the positive diversity effect tends to be overwhelmed by the environmental heterogeneity (e.g. spatial variation in soil nutrient concentration) that characterizes N-addition experiments and large-scale observational studies. While this environmental heterogeneity hypothesis may resolve some of the controversy, it is unable to explain the negative productivity–diversity relationships reported for plant communities in small-scale observational studies (i.e. those comparing small plots within a single, relatively homogeneous field site; e.g. Crawley *et al.* 2005; Thompson *et al.* 2005). Here, we offer possible explanations for the different plant diversity–productivity relationships observed in diversity-manipulation experiments and small-scale studies of natural communities (including both observations and N-addition experiments conducted within a single field site), without resorting to environmental heterogeneity as in previous hypotheses (Loreau *et al.* 2001; Schmid 2002; Hector *et al.* 2007).

As stated above, most diversity-manipulation experiments are based on synthetic communities, typically with multiple species compositions at each diversity level randomly drawn from a prescribed species pool (e.g. Tilman *et al.* 1997a; Hector *et al.* 1999). Under this design, two mechanisms, complementarity (including both species-complementary resource use and facilitation) and positive selection effects (i.e. the increased probability of productive species being included and dominant in more diverse communities), could work individually or in concert to make community productivity an increasing function of diversity (Tilman *et al.* 1997b; Loreau 2000). Recent syntheses indicate that both mechanisms gave rise to positive diversity–productivity relationships in many diversity-manipulation experiments (Cardinale *et al.* 2007).

The reduced role of the positive selection effect in natural communities

We suggest that one important reason for the frequently reported natural patterns of non-positive diversity–productivity relationships is the greatly diminished role of the positive selection effect in natural communities. A general pattern characterizing natural communities is that species that are more abundant also tend to be more broadly distributed (Brown 1984; Hanski *et al.* 1993). This positive correlation between species abundance and distribution, when applied to small-scale observational studies and N-addition experiments, means that plant species that are abundant in a study site will also be widespread in local subplots being sampled. As an example, the dominant perennial bunchgrass, *Stipa krylovii*, was present in each randomly selected 1 × 1 m quadrat in each of the 64 10 × 15 m plots of our ongoing N-addition experiment in a semiarid temperate steppe of Inner Mongolia, China, for each year between 2004 and 2007. This pattern, however, does not apply to most diversity-manipulation experiments, in which members of the species pool have equal chances of being present in multi-species plots, regardless of

their productivity; the positive selection effect is therefore often important in driving positive diversity–productivity relationships in these experiments (Cardinale *et al.* 2006, 2007). Another general pattern that exists in natural communities is that changes in species diversity often result from the addition or the loss of rare species, which are subject to greater extinction risks than more abundant species (Fischer & Stocklin 1997; Suding *et al.* 2005). Under these circumstances, the reduction in diversity does not necessarily result in the reduced presence of productive species. In situations where the primary production of a natural community is dominated by productive plants (e.g. Harpole & Tilman 2006), the importance of the positive selection effect would thus be greatly reduced, potentially translating into non-positive diversity–productivity relationships. Consistent with this idea, Smith & Knapp (2003) reported no effect of plant diversity on primary productivity in a tallgrass prairie experiment that removed only the subordinate grass species and therefore left primary productivity being controlled by productive dominant grasses. In alternative situations where relatively unproductive species become dominant components of the community (e.g. Hooper & Vitousek 1997), the negative selection effect (i.e. the increased probability of unproductive species being included and dominant in more diverse communities) may instead operate, which may also lead to non-positive diversity–productivity relationships (Loreau 2000; Jiang *et al.* 2008).

The reduced role of complementarity in natural communities

We suggest that natural patterns of non-positive diversity–productivity relationships may also be due to the diminished role of the complementarity effect in natural communities, as dictated by patterns of relative species abundance in nature. A well-recognized pattern characterizing many natural communities is that many rare species co-occur with few abundant species, with the former contributing predominantly to species richness in the community and latter making up the bulk of community biomass (Grime 1998). This many-rare-species-few-abundant-species pattern even characterizes theoretically assembled neutral communities in which all organisms are assumed to be ecologically equivalent, regardless of species identity, leading to rank-abundance curves similar to those of natural communities (Hubbell 2001). Most diversity-manipulation experiments, however, employ a design in which initial abundance or biomass of each species was comparable (sometimes identical) within a synthetically assembled community (e.g. Tilman *et al.* 1997a; Hector *et al.* 1999). This choice of relative species abundance may not matter much if experiments are allowed to run for a sufficiently long time, as long-term interactions within the synthetic communities may likely adjust species abundances towards those seen in natural communities. However, results of diversity-manipulation experiments using plants as focal organisms are typically reported after only one or a few growing seasons, even for communities composed of perennial plants. For example, the longest-running diversity-manipulation experiment to date,

which started in 1994 and mimics random species loss in perennial grassland communities in Cedar Creek, MN, USA, has reported consistently positive diversity–productivity patterns since its commencement (Tilman *et al.* 1997a, 2001; Fargione *et al.* 2007). The short-term nature (relative to the generation times of the experimental organisms) of most diversity-manipulation experiments, however, suggests that their results may be strongly influenced by initial species abundances. In particular, complementary and facilitative interactions in these artificial communities may be inflated as a result of elevated initial densities of species that may naturally be uncommon.

Complementary interactions should be especially strong between equally abundant species with some form of resource partitioning, such as plants with different rooting architectures that allow them to absorb nutrients from different soil locations. However, these interactions should be much weaker in natural communities between species differing substantially in their abundances, as they are constrained by limited contributions from the low-abundance species. In support of this idea, experimental manipulations of species relative abundance have shown that plant communities with greater evenness tend to be more productive (Wilsey & Potvin 2000; Kirwan *et al.* 2007). Likewise, complementarity associated with facilitation, particularly the effect of legumes on other plants through the fixation of atmospheric nitrogen, may also be abnormally large in diversity-manipulation experiments. Notably, almost all diversity-manipulation experiments conducted in terrestrial plant communities contain legumes (but see Van Ruijven & Berendse 2005), and the presence of legumes accounted for substantial variation in productivity in many of these experiments (e.g. Spehn *et al.* 2005; Fargione *et al.* 2007). In natural communities, however, where legumes typically represent only a small fraction of total plant biomass (e.g. Silvertown *et al.* 2006), one might expect their facilitative effects on other plants to be of much less importance. Taken together, the reduced role of complementarity associated with resource partitioning and facilitation may be another reason why diversity–productivity relationships are frequently non-positive in natural communities.

The reduced role of competitive exclusion in short-term diversity-manipulation experiments

As stated above, most diversity-manipulation experiments are relatively short-term, generally lasting no more than a few growing seasons. Synthetic communities in these experiments thus may be viewed as immature communities, contrasting with more mature natural communities in later successional stages (Thompson *et al.* 2005). This difference may carry significant consequences for understanding the different diversity–productivity patterns in synthetic and natural communities. During early stages of diversity-manipulation experiments, all species would be able to grow largely unchecked as afforded by the availability of abundant resources, and each community would be dominated by its fastest growing constituent species. As a consequence, the positive

selection effect is likely to dominate at this stage, resulting in positive diversity–productivity relationships (Pacala & Tilman 2002). As experiments progress further, resource availability declines and competitive dominants increase in abundance at the expense of others. Although competition operates to limit species abundances during this intermediate stage, many species will be still able to coexist, because competitive dominants have yet to attain substantial biomass and also because competitive exclusion of subordinate and rare species takes time. Because temporally coexisting species in diverse communities may be able to exploit a broad spectrum of resources, complementarity is likely to be the important mechanism leading to positive diversity–productivity relationships at this stage. In agreement with this idea, Cardinale *et al.* (2007) found in a recent meta-analysis that the strength of complementarity increased over time in synthetic plant communities where positive diversity–productivity relationships were commonly found. These authors also showed that the strength of selection effects remained roughly constant over the course of many diversity-manipulation experiments, a surprising result that they considered tentative and attributed to the lack of successional dynamics in these experiments.

We suggest that the elevated importance of complementarity during intermediate stages of succession may not carry over into later successional stages where competition limits species diversity and realistic species rank-abundance patterns develop. It is notable, however, that aside from those based on microbial microcosms, few diversity-manipulation experiments have lasted long enough for communities to reach stages in which competitive exclusion has run its course. Under general scenarios in which more productive plant species also tend to be competitive dominants (Gaudet & Keddy 1988; Harpole & Tilman 2006), one may still expect the positive selection effect to be important in long-term diversity-manipulation experiments, causing primary productivity to increase with initial plant diversity as established by the experimenters. However, it is likely that this positive diversity–productivity relationship may no longer hold when productivity is plotted against realized species richness, as competitive dominants may have excluded many species in these mature communities in which they are present, especially the initially diverse ones. Therefore, by concentrating its effect in mature communities, competitive exclusion may have the potential to alter diversity–productivity patterns from those observed in short-term diversity-manipulation experiments in which it plays a relatively minor role (see also Thompson *et al.* 2005). Thus contrary to the interpretation that the observed positive diversity effect on productivity in diversity-manipulation experiments represents the ‘true’ biodiversity effect (Loreau *et al.* 2001; Schmid 2002; Hector *et al.* 2007), here we view it as a possibly transient effect associated with the relatively short durations of these experiments. In accordance with this idea, several protist microcosm experiments have reported neutral or negative diversity–productivity relationships in late successional stages (Fox 2004; Jiang 2007; Weis *et al.* 2007). Plant communities in most diversity-manipulation experiments, including those in the decade-old Cedar Creek experiment that exhibited consistently

Table 1. The perceived importance of different mechanisms underlying the different diversity–productivity relationships in short-term diversity-manipulation experiments vs. small-scale observations and N-addition experiments on natural communities

	Short-term diversity-manipulation experiments	Small-scale observations and N-addition experiments
The importance of the positive selection effect	High	Low
The importance of complementarity	High	Low
The importance of competitive exclusion	Low	High
Diversity–productivity patterns	Commonly positive	Typically negative

positive diversity–productivity relationships over its course (Tilman *et al.* 1997a, 2001; Fargione *et al.* 2007), probably have yet to reach late successional stages, precluding explicit tests of this idea.

Small-scale observations and N-addition experiments in natural communities are similar to diversity-manipulation experiments in that both examine diversity–productivity patterns at the scale of local plots within a single field. In contrast to the common positive diversity–productivity relationships in short-term diversity-manipulation experiments, however, plant diversity generally declines with increasing productivity in these studies (Gough *et al.* 2000; Crawley *et al.* 2005; Thompson *et al.* 2005; Suding *et al.* 2005). Note that this result, which is often attributed to increased competition at higher productivities leading to more frequent competitive exclusions (Rajaniemi 2003), emerges in mature natural communities where competitive dominants tend to be present in many local plots. It may not necessarily apply to long-term diversity-manipulation experiments where competitive dominants from the species pool are absent in many experimental plots.

Concluding remarks

Although increasing diversity tends to have a positive effect on productivity in short-term diversity-manipulation experiments, a negative productivity–diversity relationship often emerges in small-scale observations and N-addition experiments. Here we suggest that this discrepancy may arise from the difference in the relative importance of three factors (complementarity, selection and competitive exclusion) contributing to diversity–productivity relationships between the two types of studies. Specifically, we argue that complementarity and positive selection effects may be much more important in short-term diversity-manipulation experiments than in small-scale observations and N-addition experiments, and that the reverse may apply for competitive exclusion (Table 1). We note that our hypothesis is most relevant for investigations at the scale of species interactions within relatively homogenous habitats (e.g. plots within a single field site) and acknowledge that spatial variation in environmental factors may influence diversity–productivity relationships in heterogeneous habitats (e.g. Maestre *et al.* 2006; Maestre & Reynolds 2006, 2007; Grace *et al.* 2007; Wacker *et al.* 2008). Our hypothesis thus complements the environmental heterogeneity

hypothesis (Loreau *et al.* 2001; Schmid 2002; Hector *et al.* 2007) in explaining the difference in diversity–productivity patterns between diversity-manipulation experiments and natural communities.

Our hypothesis emphasizes on important differences between synthetic communities in diversity-manipulation experiments and natural communities that give rise to potentially different diversity–productivity patterns. While diversity-manipulation experiments aim to elucidate the effects of biodiversity on productivity and, more generally, the functional consequences of biodiversity loss currently threatening many of the world's ecosystems, our analyses call into question the direct relevance of these experiments for understanding ecosystem consequences of realistic biodiversity loss scenarios, an issue also raised by several other researchers (e.g. Wardle 1999; Diaz *et al.* 2003; Thompson *et al.* 2005). In this regard, we agree with Diaz *et al.* (2003) that removal experiments, which manipulate biodiversity by eliminating species of high extinction risks from natural communities, may be more informative when it comes to assessing impacts of species loss on specific natural assemblages. Indeed, empirical tests of our hypothesis may be facilitated by the combined use of removal and synthetic experiments. Specifically, our predictions of the reduced roles of complementarity and positive selection effects and increased importance of competitive exclusion in natural communities relative to synthetic communities could be tested by comparing results of the two types of experiments that use the same species pool, that include monoculture treatments of each species to allow the estimation of the strength of complementarity and selection effects (*sensu* Loreau & Hector 2001), and that last for multiple generations of experimental organisms to allow competitive exclusion to run its course.

Acknowledgements

We thank Fernando Maestre, Bernhard Schmid, Hank Stevens, Cyrille Violle, and one anonymous referee for valuable comments that significantly improved this manuscript. This project was supported by a US NSF grant (DEB-0640416) to L. J. and a grant (No. KZCX2-XB2-01) from the Knowledge Innovation Program of Chinese Academy of Sciences to L. L.

References

- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. & Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146–1156.

- Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.
- Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L. & Sankaran, M. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989–992.
- Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M. & Weis, J.J. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences USA*, **104**, 18123–18128.
- Connell, J.H. & Orias, E. (1964) The ecological regulation of species diversity. *American Naturalist*, **98**, 399–414.
- Crawley, M.J., Johnston, A.E., Silvertown, J., Dodd, M., de Mazancourt, C., Heard, M.S., Henman, D.F. & Edwards, G.R. (2005) Determinants of species richness in the park grass experiment. *American Naturalist*, **165**, 179–192.
- Diaz, S., Symstad, A.J., Chapin, F.S., Wardle, D.A. & Huenneke, L.F. (2003) Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution*, **18**, 140–146.
- Fargione, J., Tilman, D., Dybzinski, R., HilleRisLambers, J., Clark, C., Harpole, W.S., Knops, J.M.H., Reich, P.B. & Loreau, M. (2007) From selection to complementarity: shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 871–876.
- Fischer, M. & Stocklin, J. (1997) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. *Conservation Biology*, **11**, 727–737.
- Fox, J.W. (2004) Effects of algal and herbivore diversity on the partitioning of biomass within and among trophic levels. *Ecology*, **85**, 549–559.
- Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature*, **334**, 242–243.
- Gillman, L.N. & Wright, S.D. (2006) The influence of productivity on the species richness of plants: A critical assessment. *Ecology*, **87**, 1234–1243.
- Gough, L., Osenberg, C.W., Gross, K.L. & Collins, S.L. (2000) Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos*, **89**, 428–439.
- Grace, J.B., Anderson, T.M., Smith, M.D., Seabloom, E., Andelman, S.J., Meche, G., Weiher, E., Allain, L.K., Jutila, H., Sankaran, M., Knops, J., Ritchie, M. & Willig, M.R. (2007) Does species diversity limit productivity in natural grassland communities? *Ecology Letters*, **10**, 680–689.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.
- Hanski, I., Kouki, J. & Halkka, A. (1993) Three explanations of the positive relationship between distribution and abundance of species. *Species Diversity in Ecological Communities* (eds R.E. Ricklefs & D. Schluter), pp. 108–116. The University of Chicago Press, Chicago, Chicago.
- Harpole, W.S. & Tilman, D. (2006) Non-neutral patterns of species abundance in grassland communities. *Ecology Letters*, **9**, 15–23.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hoegberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S. & Lawton, J.H. (1999) Plant diversity and productivity experiments in European grasslands. *Science (Washington)*, **286**, 1123–1127.
- Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Spehn, E.M., Wacker, L., Weilenmann, M., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M.C., Dimitrakopoulos, P.G., Finn, J.A., Huss-Danell, K., Jumpponen, A., Leadley, P.W., Loreau, M., Mulder, C.P.H., Nesshoover, C., Palmberg, C., Read, D.J., Siamantziouras, A.S.D., Terry, A.C. & Troumbis, A.Y. (2007) Biodiversity and ecosystem functioning: reconciling the results of experimental and observational studies. *Functional Ecology*, **21**, 998–1002.
- Hooper, D.U. & Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302–1305.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, **93**, 145–159.
- Jiang, L. (2007) Density compensation can cause no effect of biodiversity on ecosystem functioning. *Oikos*, **116**, 324–334.
- Jiang, L., Pu, Z. & Nemergut, D.R. (2008) On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. *Oikos*, **117**, 488–493.
- Kinzig, A.P., Pacala, S.W. & Tilman, D. (2002) The functional consequences of biodiversity: empirical progress and theoretical extensions. Princeton University Press, Princeton.
- Kirwan, L., Luescher, A., Sebastia, M.T., Finn, J.A., Collins, R.P., Porqueddu, C., Helgadottir, A., Baadshaug, O.H., Brophy, C., Coran, C., Dalmannsdottir, S., Delgado, I., Elgersma, A., Fothergill, M., Frankow-Lindberg, B.E., Golinski, P., Grieu, P., Gustavsson, A.M., Hoglind, M., Huguenin-Elie, O., Iliadis, C., Jorgensen, M., Kadziulienė, Z., Karyotis, T., Lunnan, T., Malengier, M., Maltori, S., Meyer, V., Nyfeler, D., Nykanen-Kurki, P., Parente, J., Smit, H.J., Thumm, U. & Connolly, J. (2007) Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. *Journal of Ecology*, **95**, 530–539.
- Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, **91**, 3–17.
- Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72–76.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, **294**, 804–808.
- Loreau, M., Naeem, S. & Inchausti, P. (2002) *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford University Press, Oxford.
- Maestre, F.T. & Reynolds, J.F. (2006) Spatial heterogeneity in soil nutrient supply modulates nutrient and biomass responses to multiple global change drivers in model grassland communities. *Global Change Biology*, **12**, 2431–2441.
- Maestre, F.T. & Reynolds, J.F. (2007) Biomass responses to elevated CO₂, soil heterogeneity and diversity: an experimental assessment with grassland assemblages. *Oecologia*, **151**, 512–520.
- Maestre, F.T., Bradford, M.A. & Reynolds, J.F. (2006) Soil heterogeneity and community composition jointly influence grassland biomass. *Journal of Vegetation Science*, **17**, 261–270.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381–2396.
- Pacala, S.W. & Tilman, D. (2002) The transition from sampling to complementarity. *The functional consequences of biodiversity* (eds A.P. Kinzig, S.W. Pacala & D. Tilman), pp. 151–166. Princeton University Press, Princeton.
- Rajaniemi, T.K. (2003) Explaining productivity–diversity relationships in plants. *Oikos*, **101**, 449–457.
- Schmid, B. (2002) The species richness–productivity controversy. *Trends in Ecology and Evolution*, **17**, 113–114.
- Silvertown, J., Poulton, P., Johnston, E., Edwards, G., Heard, M. & Biss, P.M. (2006) The Park Grass Experiment 1856–2006: Its contribution to ecology. *Journal of Ecology*, **94**, 801–814.
- Smith, M.D. & Knapp, A.K. (2003) Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters*, **6**, 509–517.
- Spehn, E.M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Jumpponen, A., Koricheva, J., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Palmberg, C., Pereira, J.S., Pfisterer, A.B., Prinz, A., Read, D.J., Schulze, E.D., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S. & Lawton, J.H. (2005) Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs*, **75**, 37–63.
- Srivastava, D.S. & Vellend, M. (2005) Biodiversity–ecosystem function research: Is it relevant to conservation? *Annual Review of Ecology and Systematics*, **36**, 267–294.
- Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., Milchunas, D.G. & Pennings, S. (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences USA*, **102**, 4387–4392.
- Thompson, K., Askew, A.P., Grime, J.P., Dunnett, N.P. & Willis, A.J. (2005) Biodiversity, ecosystem function and plant traits in mature and immature plant communities. *Functional Ecology*, **19**, 355–358.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997a) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.
- Tilman, D., Lehman, C.L. & Thomson, K.T. (1997b) Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academy of Sciences USA*, **94**, 1857–1861.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001)

- Diversity and productivity in a long-term grassland experiment. *Science*, **294**, 843–845.
- van Ruijven, J. & Berendse, F. (2005) Diversity–productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences USA*, **102**, 695–700.
- Wacker, L., Baudois, O., Eichenberger-Glinz, S. & Schmid, B. (2008) Environmental heterogeneity increases complementarity in experimental grassland communities. *Basic and Applied Ecology*, **9**, 467–474.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The relationship between productivity and species richness. *Annual Review of Ecology & Systematics*, **30**, 257–300.
- Wardle, D.A. (1999) Is ‘sampling effect’ a problem for experiments investigating biodiversity–ecosystem function relationships? *Oikos*, **87**, 403–407.
- Weis, J.J., Cardinale, B.J., Forshay, K.J. & Ives, A.R. (2007) Effects of species diversity on community biomass production change over the course of succession. *Ecology*, **88**, 929–939.
- Wilsey, B.J. & Potvin, C. (2000) Biodiversity and ecosystem functioning: Importance of species evenness in an old field. *Ecology*, **81**, 887–892.

Received 8 December 2008; accepted 9 March 2009

Handling Editor: Fernando Maestre