

From selection to complementarity: shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment

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In a 10-year (1996–2005) biodiversity experiment, the mechanisms underlying the increasingly positive effect of biodiversity on plant biomass production shifted from sampling to complementarity over time. The effect of diversity on plant biomass was associated primarily with the accumulation of higher total plant nitrogen pools (N g m^{-2}) and secondarily with more efficient N use at higher diversity. The accumulation of N in living plant biomass was significantly increased by the presence of legumes, C4 grasses, and their combined presence. Thus, these results provide clear evidence for the increasing effects of complementarity through time and suggest a mechanism whereby diversity increases complementarity through the increased input and retention of N, a commonly limiting nutrient.

Keywords: biodiversity; selection effect; complementarity effect; sampling effect; nitrogen

1. INTRODUCTION

A number of experiments have documented a positive relationship between biodiversity and productivity (reviewed in Wardle 1999; Schwartz *et al.* 2000; Diaz & Cabido 2001; Loreau *et al.* 2001, 2002; Hector 2002; Schmid *et al.* 2002; Hooper *et al.* 2005; Spehn *et al.* 2005). However, the mechanisms behind these effects are debated. Two general hypotheses have been offered to explain this positive relationship: the ‘sampling effect’ and the ‘niche complementarity’ (Aarssen 1997; Huston 1997; Tilman *et al.* 1997b, 2001; Loreau 2000). The sampling effect hypothesis suggests that diversity effects are caused by the greater chance of one or a few dominant, high-biomass species being present in the polyculture. The niche complementarity hypothesis states that niche differences among species, such as interspecific differences in resource use, should lead to more efficient acquisition of limiting resources and therefore higher productivity. Thus, each hypothesis proposes an ecologically distinct mechanism, complementarity involving interactions among two or more species and sampling involving the presence of a particular species.

Our long-term grassland biodiversity experiment manipulates species number, a component of biodiversity. Transgressive overyielding (i.e. when polyculture plots

have higher biomass than any monoculture plot) is strong evidence of complementarity. It has previously been shown that the percentage of plots exhibiting this type of overyielding increased with increasing species richness in later years, but not in the first year of data collection (Tilman *et al.* 2001).

However, sampling and complementarity effects are not mutually exclusive, and both effects can operate simultaneously to affect productivity. This highlights the need to quantify both components, which analyses of transgressive overyielding fail to do. Here, we apply a technique developed by Loreau & Hector (2001) to quantify the relative contributions of complementarity and dominance by a particular species. Specifically, we use data for the 3rd to 12th year of our biodiversity experiment to quantify for the first time the long-term temporal trends in selection and complementarity effects. Loreau & Hector (2001) coined the term ‘selection effect’ to replace the term ‘sampling effect’ because both the selection and the complementarity effects result from a sampling process. A positive selection effect operates via the increased probability of sampling a dominant, high-biomass species in polyculture, and a positive complementarity effect operates via the increased probability of sampling a suite of complementary species in polyculture. In the context of Loreau & Hector’s technique, the ‘sampling effect hypothesis’ predicts specifically that biodiversity experiments will have both (i) a large, positive selection effect and (ii) no significant complementarity effect. We use the sampling effect hypothesis to refer to these dual predictions and the selection effect to refer to the tendency for species

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2006.0351> or via <http://www.journals.royalsoc.ac.uk>.

with either high (positive selection) or low (negative selection) biomass to dominate mixtures.

To further address the mechanisms behind the biodiversity effects in this nitrogen (N)-limited system (Tilman 1990), we examine the trends in plant tissue N. This allows us to test the hypothesis that positive complementarity effects are associated with legumes increasing N availability (Huston & McBride 2002; Lee *et al.* 2003; Scherer-Lorenzen *et al.* 2003; Hooper & Dukes 2004), and to test for additional mechanisms. Specifically, we test for the effects of four functional groups on the plant N pools, and for the increased efficiency of N use in diverse communities. Increased efficiency of N use in diverse communities is an untested mechanism by which diverse communities may increase productivity. If diverse communities are more competitive, then plants in these communities may have lower tissue N concentrations. Therefore, we test the hypothesis that diverse communities have lower tissue N concentrations (higher biomass: N ratios), which would indicate higher productivity per unit of limiting resource and could partially explain the higher productivity observed at higher diversity.

2. MATERIAL AND METHODS

Our experiment, previously described in Tilman *et al.* (1997a, 2001), is located at Cedar Creek Natural History Area in central Minnesota, USA. In the summer of 1993, an old field was treated with herbicide, burned, bulldozed to remove the top 6–8 cm of A horizon soil to reduce the seed bank, and ploughed and harrowed. In the spring of 1994, 168 plots, each 9 × 9 m, were seeded to contain 1, 2, 4, 8 or 16 grassland–savannah perennial species with 39, 35, 29, 30 and 35 replicates, respectively. The species composition of these plots was randomly selected from a pool of 18 species that included C4 and C3 grasses, legumes, forbs and trees. The plots received a total of 10 g seed m⁻² in 1994 and 5 g seed m⁻² in 1995; this total was composed of equal masses of each selected species. All species were planted in at least duplicate monoculture plots, but three species (*Elymus canadensis*, *Poa pratensis* and *Panicum virgatum*) did not establish in one of their two monoculture plots, and these plots were then abandoned.

We excluded the two woody species (*Quercus ellipsoidalis* and *Quercus macrocarpa*) from all years for our analyses because the aboveground biomass of the woody species is not an estimate of annual productivity (in contrast to our herbaceous perennials), and because these two species occurred infrequently and thus had high sampling variance compared with other species. We used the 35 non-oak monocultures, the 29 two-species plots that exclude oaks and all higher diversity plots in our data analyses. *Solidago rigida* did not germinate in 1994, so plots were reseeded with *Monarda fistulosa*. However, *S. rigida* subsequently germinated, and plots now contain both species.

Total aboveground biomass was measured in 0.1 × 3.0 m strips (four strips in 1996–1999 and eight strips in 2000–2005) from which all vegetation was clipped, dried and weighed. In 2001–2005, clipped aboveground biomass was sorted to species for two 0.1 × 3.0 m strips and then dried and weighed. For 1996–2000, per cent cover was visually estimated in four permanent 1.0 × 0.5 m² quadrats, and was converted to biomass estimates for each species by assuming that each

species' proportion of total cover was equivalent to its proportion of total aboveground biomass. Our results are not dependent on this shift in methods: analyses on only the first 5 years of data were qualitatively similar to analyses on all 10 years of data. In addition, compatibility of cover and biomass estimates has been quantitatively confirmed in an adjacent experiment. Using 24 species, all grown together in 24 replicate plots, we found that average cover was well correlated with average biomass (in 1997: $p < 0.0001$, $r^2 = 0.85$, $t = 11.05$, $N = 24$; in 1998: $p < 0.0001$, $r^2 = 0.75$, $t = 8.04$, $N = 24$).

We measured the tissue N concentrations in the aboveground biomass in 1996–2000 and 2002, and in the root biomass in 1997–2000 and 2002. In addition, in 2002, we measured the tissue N concentrations for four species across the biodiversity gradient. These species included the most abundant species from each of the four functional groups (*Schizachyrium scoparium*, C4 grass; *P. pratensis*, C3 grass; *Lupinus perennis*, legume; *S. rigida*, forb). The aboveground biomass was harvested as described above, and the root biomass was harvested with three 5 cm diameter × 30 cm deep cores. We measured the tissue N concentration in the dried and ground plant root and the aboveground material using a Carlo Erba Carbon–Nitrogen analyzer.

We used the technique of Loreau & Hector (2001) to calculate net, selection and complementarity effects. The net effect is defined as $\sum Y - \bar{M}$, where Y is the observed biomass for each species in a plot ($\sum Y$ is the biomass of all the species in a plot) and \bar{M} is the average monoculture biomass of all the species in that plot. The net effect can be partitioned into two additive components: the selection effect and the complementarity effect. Selection is calculated as $D \times \text{cov}(M, \Delta RY)$, where D is the diversity (i.e. species number), M represents a species' average monoculture biomass and ΔRY is the difference between the observed relative yield (Y/M) and the expected relative yield ($1/D$). Complementarity is calculated as $\bar{M} \times D \times \Delta \bar{RY}$, where $\Delta \bar{RY}$ is the average ΔRY of all the species in a plot.

Intuitively, positive complementarity occurs when species on average have higher than the expected relative yield (RY), where the expected RY is that each species will produce biomass in proportion to the number of species planted in a plot (i.e. one-half as much biomass in two species plots as in monoculture, one-quarter as much in four species plots, etc.). Positive selection occurs when species have a positive covariance between the relative yield and the monoculture biomass, such that species abundant in monoculture are the competitive dominants in polyculture.

Following Loreau & Hector (2001), we did not include species with extremely low monoculture biomass values because RY approaches infinity as monoculture biomass approaches zero. We excluded species in only those years when their average estimated monoculture biomass was lower than 2.5 g m⁻² (eight cases in total). Results were qualitatively similar when we did not exclude these species from the analyses. Data were analysed using JMP v. 6.0.2 (SAS Institute, Inc. 2006). Repeated measures analyses were conducted using the Geisser & Greenhouse (1958) adjustment.

3. RESULTS

The net and complementarity effects increased over time, whereas the selection effect decreased over time such that it was strongly negative by the end of the experiment. Figure 1 shows how, on an average, the addition of one

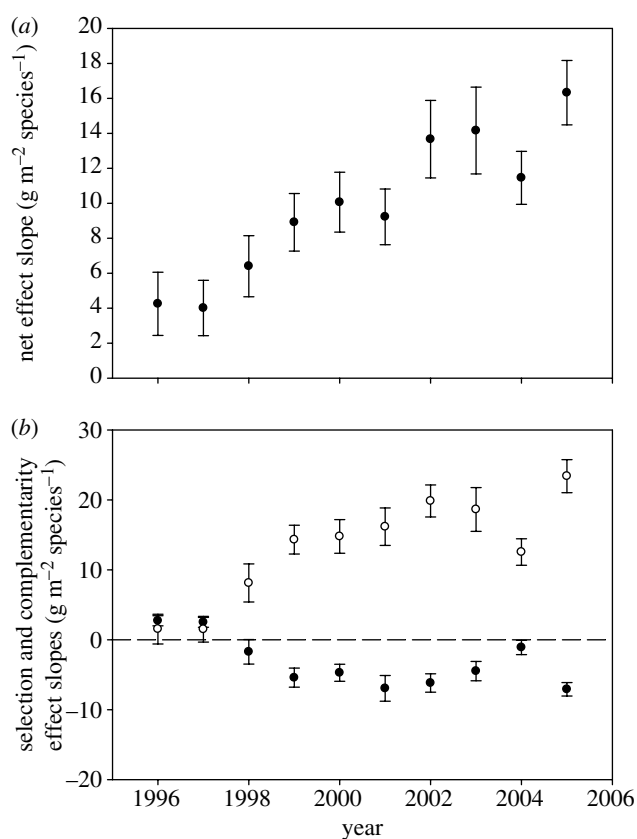


Figure 1. Temporal trends in the slopes of the net, selection and complementarity effects versus species number in 1996–2005. Error bars indicate 1 s.e. Only four of the slopes are not significantly different from zero: complementarity in 1996 and 1997 and selection in 1998 and 2004.

more species affected the net, complementarity and selection effects during each year of the experiment (i.e. the values plotted on the *y*-axis are the slopes of regressions conducted on values from a single year for the net, complementarity or selection effect versus species number). These temporal trends were also evident as interactions between species number and time in repeated measures analyses (table 1). The relationship between the net, complementarity and selection effects versus species number, for each year, is available online (see electronic supplementary material).

The effect of species number on the net effect was significantly positive in each of the 10 years ($p < 0.03$ in 1996 and 1997; $p < 0.0001$ in 1998–2005). The effect of species number on complementarity was not significant in the first 2 years, but was significantly and increasingly positive in each of the eight subsequent years ($p > 0.41$ in 1996 and 1997; $p < 0.01$ in 1998; $p < 0.0001$ in 1998–2005). The selection effect increased with species number in the first 2 years ($p < 0.001$), showed no relationship with species number in the third year ($p = 0.33$) and decreased with species number in the subsequent years ($p < 0.001$; except for 2004, $p = 0.28$) (figure 1). Note that the complementarity effect increased more than the selection effect decreased; this is why their sum, the net effect, increased over time even though the selection effect became negative over time.

The selection effect is determined by the covariance of relative yield (*RY*, a measure of competitive ability) and monoculture biomass. The early positive selection effect

was associated with the successful establishment of a few species, notably *S. scoparium*, in both monocultures and in polycultures with competition. The switch from a positive to a negative selection effect over time indicates a change in the relationship between monoculture biomass and *RY*, such that the species with high monoculture biomass were no longer those with the highest *RY*.

Shifts in the species hierarchy of monoculture biomass, rather than *RY*, account for this decreasing selection effect. Species' initial and long-term *RY* were significantly positively correlated ($p < 0.0032$, $R^2 = 0.47$, $n = 16$ for regression of 2001–2002 versus 1996–1997 species' average *RY*). However, species' monoculture biomasses changed over time, causing the initial and the final monoculture biomasses of species to be uncorrelated ($p > 0.71$, for regressions of each year's monoculture biomass in 1999–2005 versus monoculture biomass in 1996). The initial and the final monoculture biomasses were uncorrelated because the biomass of monocultures of some species increased over time, whereas the monoculture biomass of others decreased. Specifically, regressions of monoculture biomass versus year for each of our 16 species found parameter estimates for year to be negative for nine species and positive parameter estimates for seven species. In particular, averaged across the second half of the experiment, the three highest monoculture biomasses belonged to *Amorpha canescens*, *Liatris aspera* and *P. virgatum*, all of which are poor competitors that initially had low monoculture biomass. Thus, in the long term, monoculture biomass was not a good indicator of competitive dominance (as measured by *RY*) in our experiment (Hille Ris Lambers *et al.* 2004).

Greater biomass at higher species number could be associated with either higher biomass: N ratio (i.e. lower tissue N concentrations) or simply a greater total amount of N in plant biomass (hereafter plant N pools). Both factors contributed to greater biomass at higher diversity, but the increase in plant N pools was responsible for an increasing majority of the biodiversity effect over time. As an index of the relative importance of these two factors, we calculated the percentage increases in biomass: N ratios and N pools across the biodiversity gradient (i.e. comparing monocultures and 16 species plots) for the first and the last years for which data were available (1996 and 2002). The percentage increase in biomass: N ratios gives an indication of the effects on the productivity associated with lower tissue N (if plant N pools were constant). The percentage increase in plant N pools gives an indication of the effects on the productivity associated solely with larger plant N pools (if tissue N were constant). In 1996 and 2002, a 44 and a 15% increase in biomass, respectively, were associated solely with observed changes in tissue N. In 1996 and 2002, a 74 and a 119% increase in biomass, respectively, were associated solely with observed changes in plant N pools.

Although the biodiversity–productivity gradient was associated more with increases in plant N pools than with decreases in plant N concentrations, N concentrations did significantly decrease across the diversity gradient. Specifically, per cent tissue N in the aboveground biomass slightly decreased with increasing diversity, more so in some years than in others (repeated measures analysis: for species number $p = 0.015$, d.f. = 1,159, $F = 6.0$; for time \times species number $p < 0.0001$, d.f. = 4.2,669, $F = 8.4$).

Table 1. Repeated measures analysis for each of the three biodiversity effects for the years 1996–2005.

	net effect				selection effect				complementarity effect			
	num d.f.	den d.f.	<i>F</i>	<i>p</i>	num d.f.	den d.f.	<i>F</i>	<i>p</i>	num d.f.	den d.f.	<i>F</i>	<i>p</i>
species number	1	120	47.6	<0.0001	1	120	20.8	<0.0001	1	120	52.2	<0.0001
year	6.6	791.3	3.8	0.0006	5.9	710.9	1.9	0.075	6.9	830.3	4.3	0.0001
year × species number	6.6	791.3	11.7	<0.0001	5.9	710.9	10.6	<0.0001	6.9	830.3	20.5	<0.0001

Table 2. Regressions of tissue N concentrations of selected species on species number. ((a) The tissue N of two forbs (*L. perennis*, a leguminous forb, and *S. rigida*, a non-leguminous forb) significantly decreased with increasing diversity. (b) The tissue N of two grasses (*P. pratensis*, a C3 grass, and *S. scoparium*, a C4 grass) significantly increased with increasing diversity. The species identity term shows how much greater, on average, tissue N concentration is for *L. perennis* compared to *S. rigida* and for *P. pratensis* compared to *S. schizachyrium*, for the forb and the grass regressions, respectively. For both regressions, a model including an interaction term between species identity and species richness showed no significant effect ($p > 0.4$).

parameter	per cent N of two forb species			per cent N of two grass species		
	estimate	standard error	<i>p</i>	estimate	standard error	<i>p</i>
intercept	1.23	0.04	<0.0001	0.902	0.03	<0.0001
species number	−0.0074	0.0034	0.029	0.0054	0.0020	0.010
species identity	0.237	0.019	<0.0001	0.082	0.011	<0.0001
overall model						
R^2		<i>p</i>		<i>n</i>		
0.60		<0.0001		107		
0.37		<0.0001		109		

However, at the species level, the tissue N of some species decreased, and the tissue N of other species increased, over the diversity gradient. Specifically, the tissue N of two forb species (*L. perennis*, legume, and *S. rigida*, forb) significantly decreased with increasing diversity (table 2); in contrast, the tissue N of two grass species (*S. scoparium*, C4 grass, and *P. pratensis*, C3 grass) significantly increased across the diversity gradient (table 2). This increase may have been due to the increased probability of growing with legumes at higher diversity; when the presence or absence of legumes was included in the model, the effect of species number on the grass tissue N concentration became non-significant ($p = 0.22$).

The diverse communities accumulated N in plant tissues more quickly than the simple communities ($p < 0.0001$, d.f. = 3.7, 587.5, $F = 40.5$ for the interaction between species number and year in a repeated measures analysis of the plant N pool). Although there was no significant change in the amount of N in plant biomass across the diversity gradient at the beginning of the experiment ($p > 0.05$ in 1997), the faster rates of N accumulation at high diversity soon created one. In subsequent years, the amount of N in total plant biomass was significantly higher at higher diversity ($p < 0.0001$ in 1998, 1999, 2000 and 2002).

The faster accumulation of N in the diverse communities was associated with the presence of legumes, C4 grasses, and their interaction (i.e. $L \times Y$, $C4 \times Y$ and $L \times C4 \times Y$ in the repeated measures analysis were all significant, see table 3). The presence of legumes increased the rate of N accumulation in total plant

biomass by about fourfold. Plots with legumes compared with plots of the same diversity treatment without legumes had 5.5, 3.8 and 3.7 times faster rates of N accumulation in 1, 2 and 4 species plots, respectively. Consequently, by 2002, we found that the total N in plant biomass of plots with both legumes and C4 grasses (11.6 g m^{-2}) was higher than for plots with legumes but no C4 grasses (9.5 g m^{-2}), and plots with legumes were higher than plots with C4 grasses but no legumes (4.1 g m^{-2}) or plots with neither C4 grasses nor legumes (3.5 g m^{-2}) (Tukey–Kramer test, $\alpha = 0.05$).

4. DISCUSSION

In our long-term biodiversity experiment, we found that the positive relationship between species number and biomass was explained largely by a positive selection effect in the first 2 years of the experiment, but by complementarity among species in the following 8 years (figure 1). This shift occurred because the selection effect decreased over time and the complementarity effect increased over time. The overall net effect increased over time because the complementarity effect increased more strongly than the selection effect decreased. In the later years of the experiment, the selection effect was significantly negative, rejecting the sampling effect hypothesis.

The selection effect was initially positive because a few species were able to establish and grow well in both monoculture and polyculture. The selection effect became negative in the long term because aboveground biomass in monoculture is not associated with competitive ability in

Table 3. Repeated measures analysis of the effect of functional group presence on the amount of N in total plant biomass. (Significant *p*-values are in bold. All significant effects are positive. A similar repeated measures analysis including all two-way interactions between functional groups did not reveal any additional interactions.)

effect	total plant N			
	<i>p</i> -value	<i>F</i>	d.f.	den d.f.
C3 grasses	0.9323	0.01	1	157
C4 grasses	0.0077	7.3	1	157
forbs	0.8497	0.04	1	157
legumes	<0.0001	148.1	1	157
L×C4	0.5903	0.3	1	157
year (Y)	<0.0001	53.7	3.62	568.7
Y×C3	0.7984	0.4	3.62	568.7
Y×C4	0.0253	2.9	3.62	568.7
Y×F	0.7666	0.4	3.62	568.7
Y×L	<0.0001	25.4	3.62	568.7
Y×L×C4	0.0449	2.5	3.62	568.7

this N-limited system, where many poor competitors eventually achieved high monoculture biomass. This shift in the direction of the selection effect was not associated with successional change, as the most abundant species in monoculture initially was the late-successional species *S. scoparium*.

The shift to complementarity was associated with higher rates of N accumulation at high diversity. More N at higher diversity should contribute to the complementarity effect rather than the selection effect because it should allow all species, on an average, to exceed their expected biomass. Higher rates of N accumulation at high diversity were associated with the presence of legumes, C4 grasses, and their interaction (table 3). Legumes increase N supply because they are able to fix atmospheric N. C4 grasses have high root biomass, high C : N ratio and low root turnover, and thus more efficient nutrient capture and retention, which probably explains their significant effects on the rates of accumulation and the amount of N in plant biomass (Tilman & Wedin 1991; Craine *et al.* 2002). The positive interaction between these two functional groups suggests that the amount of N retained by the addition of C4 grasses is higher under the increased supply associated with legumes. Such effects are commonly observed in annual agricultural systems (e.g. Vandermeer 1989). Our work shows that these effects of legumes and C4 grasses increase over time in this perennial prairie.

Diverse plots not only had more N, but also used it more efficiently. This more efficient use of N was associated with decreases in tissue N across the diversity gradient by leguminous and non-leguminous forbs, but not by C3 and C4 grasses. We hypothesize that forbs had lower tissue N concentrations when planted in higher diversity owing to increased competition, especially from grasses. In contrast, we hypothesize that grasses had higher N concentrations at higher diversity owing to the fertilizing effect of legumes.

Numerous experiments have found a positive relationship between species number and productivity or above-ground biomass in grassland communities (reviewed in Wardle 1999; Schwartz *et al.* 2000; Diaz & Cabido 2001; Loreau *et al.* 2001, 2002; Hector 2002; Schmid *et al.* 2002;

Spehn *et al.* 2005). Kenkel *et al.* (2000) however observed no relationship between species number and productivity. These existing studies demonstrate that the short-term net effect of biodiversity is often positive, but that this can be primarily due to either selection or complementarity effects. We suggest that the initial effect of biodiversity may depend upon the relationship between monoculture biomass and relative yield (which determines the selection effect), while the long-term effect of biodiversity may prove to be consistently positive due to complementarity effects. In general, the complementarity effects will increase over time if diverse communities are able to acquire and retain more limiting resource, as found in this experiment.

5. CONCLUSION

Our study found a shift in the mechanisms of the biodiversity effect on the productivity over time. Initially, a few species, notably *S. scoparium*, established and grew well in both monocultures and polycultures relative to other species. Over time, diverse plots acquired more N and exhibited increasing complementarity. The increased rate of N accumulation in polycultures was associated with the presence of legumes, C4 grasses, and their interaction. Plots containing legumes had increased N inputs, while those with C4 grasses probably had more efficient nutrient capture and retention because C4 grasses have high root biomass, high C : N ratio and low root turnover. These results provide clear evidence for increasing effects of complementarity through time and suggest a mechanism by which diversity increases the input and retention of N, a commonly limiting nutrient.

We thank Troy Mielke and many Cedar Creek interns for fieldwork, and NSF/DEB 0080382, NSF/DEB 9629566 and the Andrew Mellon Foundation for support.

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