

REPORT

Mechanisms responsible for the positive diversity–productivity relationship in Minnesota grasslands

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Abstract

Species' extinctions have spurred debate on whether interactions among few or among many species cause a positive diversity–productivity relationship in experimentally assembled grasslands. We addressed this question by quantifying the productivity of 14 species across an experimental diversity gradient in Minnesota. We found that interspecific interactions leading to coexistence and competitive displacement both determine which species overyield; i.e. are more productive at high diversity. Overyielding species were either superior N competitors (C4 grasses) or N fixers (legumes). Surprisingly, these species were not most productive in monoculture, thus, the 'selection' of productive species in diverse plots did not cause the positive diversity–productivity relationship. Both positive (with legumes) and negative interspecific interactions (with C4 grasses) determined whether individual species overyielded. Foliar pathogens did not cause overyielding, although other natural enemies may be responsible. Overyielding species are not displacing underyielding species over time, implying that other diversity-promoting interactions also operate in this experiment.

Keywords

Competition, diversity, facilitation, frequency-dependent disease, niches, selection effects.

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INTRODUCTION

Interspecific interactions are often studied by population and community ecologists interested in species coexistence or competitive exclusion (Bever *et al.* 1997; Callaway *et al.* 2002; McKane *et al.* 2002; Mitchell *et al.* 2002). Recently, ecosystem ecologists have also become interested in these interactions, because the consequences of species extinctions for ecosystem metrics such as aboveground productivity may depend on the same species interactions that determine community dynamics (Naeem *et al.* 1994; Petchey 2000; Cardinale *et al.* 2002; Mouquet *et al.* 2002). For example, niche differentiation, facilitation, and frequency-dependent growth all promote diversity by increasing population growth rates of rare species (Chesson 2000; Bruno *et al.* 2003). Rare species are buffered from extinction because they are less limited by intraspecific competition (if niche differentiated), more often facilitated (if positively

interacting with other species), and/or less impacted by host-specific natural enemies (if limited by these density- or frequency-dependent agents) than when abundant. Under these diversity-promoting mechanisms, individuals surrounded by heterospecific neighbors may outperform individuals surrounded by conspecific neighbors, thus causing total community productivity to rise with diversity (Tilman *et al.* 1997a; Petchey 2000; Mouquet *et al.* 2002; Drake 2003; Fox 2003). This suggests that species extinctions may have implications for aboveground productivity.

A positive relationship between diversity and productivity across experimental diversity gradients is often interpreted as evidence that diversity-promoting interactions operate among many species, and therefore, that extinctions may negatively affect productivity (e.g. Hector *et al.* 1999; Reich *et al.* 2001; Tilman *et al.* 2001). However, this positive diversity–productivity relationship could also arise from species interactions that lead to competitive exclusion. If

productive species dominate diverse plots, a positive diversity–productivity relationship could still be observed because these species are more likely to be present at high diversity (a ‘positive selection’ or ‘sampling’ effect; Aarssen 1997; Huston 1997; Tilman *et al.* 1997a; Loreau & Hector 2001). In this case, a positive diversity–productivity relationship would arise from the increased probability that a competitive, productive species would be present (‘sampled’) in diverse communities, rather than from diversity-promoting interactions among many species.

Understanding the performance of individual species in biodiversity experiments is critical for determining which mechanisms are responsible for the positive diversity–productivity relationship, unfortunately, few studies have done so (but see Tilman *et al.* 1997b; Craine *et al.* 2003). To address this issue, we quantify the productivity of 14 prairie species in a biodiversity experiment at Cedar Creek, MN, USA. We next determine whether the identity and traits of species that benefit from interspecific interactions (i.e. overyield) are consistent with processes that lead to competitive exclusion or with diversity-promoting mechanisms, as follows. We ask (1) whether overyielding is correlated with a species’ competitive ability as represented by two traits; monoculture productivity and competitive ability for nitrogen; (2) if dominant competitors (C4 grasses) suppress overyielding of other species; (3) if overyielding species displace underyielding species over time; (4) whether the traits of overyielding species are consistent with niche differentiation; (5) whether nitrogen-fixing legumes facilitate overyielding; and (6) whether overyielding species are most released from diversity-dependent foliar pathogens.

METHODS

Cedar Creek Natural History Area is a 2200 ha research site located on a sandy glacial outwash with nitrogen poor soils in central Minnesota. The biodiversity experiment at Cedar Creek was established in early spring of 1994 (Tilman *et al.* 1997b, 2001). The experiment contains 168 plots, each 9 × 9 m, planted at five levels of species richness: 1 (39 plots), 2 (35 plots), 4 (29 plots), 8 (30 plots), and 16 (35 plots). Per plot, species composition was determined by a random draw from a species pool of 18 late-successional species representing C4 grasses, C3 grasses, legumes, forbs and woody trees. The same total mass of seeds, equally divided among component species, was added to each plot. Thus, the number of seeds (per species) added to each plot was an inverse function of the species richness treatment. Plots were annually weeded to remove non-planted species. For consistency with previous studies we use the term diversity to refer to species richness (Hector *et al.* 1999; Reich *et al.* 2001; Tilman *et al.* 2001).

We sampled aboveground biomass in a 0.1 by 6 m strip in each plot August of 2001 and 2002 (a proxy for annual productivity; Knapp *et al.* 1998). Biomass was sorted to species, dried in drying ovens, and weighed. Four of the 18 species were excluded from our analyses – woody trees (whose aboveground biomass does not represent annual productivity) and two species present in less than half of the plots they were planted in (*Agropyron smithii* and *Elymus canadensis*). Previous studies have found that competitive ability for nitrogen, the limiting soil resource in these grasslands, is well described by the level to which nitrate is drawn down in monoculture soils (R^* for nitrate; Tilman & Wedin 1991). To determine this index of competitive ability we measured 0.01 M KCl extractable soil nitrate from a composite of five 20 cm deep by 2.5 cm diameter soil cores per monoculture plot. We used the average of five samples taken biweekly in late July and August of 2001 and once in August of 2002.

Analysis

We used statistical modeling to identify those species that benefit from interspecific interactions (i.e. overyield) vs. those species that do not (i.e. underyield). Our model relates the productivity of species i in plot j (b_{ij}) to monoculture productivity (m_i) and the diversity (species richness) of plot j (d_j):

$$b_{ij} = m_i d_j^{y_i} \quad (1)$$

Because the amount of seed (per species) added to plots was an inverse function of diversity, aboveground productivity of each species should decline with diversity, as described by parameter y_i (the yield exponent). The magnitude of y_i depends on the interspecific and intraspecific interactions each species experienced during germination, growth and survival in the 7 years since the experiment was initiated. In the simplest case (our ‘null’ model), productivity scales with the amount of seed added to each plot, and y_i equals -1 (Tilman *et al.* 1997b; Petchey 2000). For species conforming to this ‘null’ model, interspecific interactions are equal in magnitude to intraspecific interactions.

Species for which inter- and intraspecific interactions differ in magnitude have yield exponents that differ from -1 . If interspecific interactions are less inhibitory than are intraspecific interactions (e.g. through niche differentiation), productivity is greater in diverse plots than predicted by the ‘null’ model and species ‘overyield’ (y_i greater than -1). Alternatively, interspecific interactions may be more inhibitory than intraspecific interactions (e.g. because the species is an inferior competitor), and productivity in diverse plots less than predicted by the ‘null’ model. Yield exponents of such ‘underyielding’ species are less than -1 .

We used maximum likelihood and a lognormal distribution to estimate parameters m_i (monoculture productivity) and y_i (the yield exponent) from the aboveground productivity (b_{ij} 's) of individual species in plots of different diversity (d_j 's); and likelihood ratio tests to test whether y_i 's are significantly different from -1 (i.e. whether species overyield or underyield; Hilborn & Mangel 1997). Our analyses do not depend on adequate replication of monoculture plots (as other analyses do; Loreau & Hector 2001; Reich *et al.* 2001; Tilman *et al.* 2001), because the yield exponent is quantified from the productivity of individual species across a diversity gradient, not just from monoculture relative to mixture productivity. The assumptions of our analyses are equivalent to those of Loreau & Hector (2001), but we explicitly focus on species level, not community level relationships between diversity and productivity. To reduce subsampling variance, we applied our analyses to the average of 2001 and 2002 biomass data. We added 1/10 of the smallest non-zero biomass value observed (for that species) to all biomass values, because a lognormal likelihood does not accommodate zero biomass.

Is overyielding determined by competitive processes?

We used simple correlations (Pearson's r , one-tailed tests) to determine whether the traits of overyielding (and underyielding species) are consistent with competitive processes. First, we tested whether the yield exponent is positively correlated with monoculture productivity (thought to correlate with competitive ability – Huston 1997; Tilman *et al.* 1997a; Loreau & Hector 2001). As nitrogen is the limiting soil resource at Cedar Creek, we also correlated yield exponents with R^* for nitrate, an index of competitive ability for nitrogen. We excluded legumes from this comparison, because nitrogen fixers do not compete strongly for soil nitrogen, since they have access to atmospheric nitrogen. We also excluded two species not planted in monoculture from both of these comparisons (*Monarda fistulosa* and *Solidago rigida*). We hypothesized that the presence of strong competitors would negatively affect yield exponents of other species, if competitive processes are responsible for overyielding. To test for this possibility, we asked how C4 grasses, superior nitrogen competitors (Tilman & Wedin 1991), impact yield exponents of other species by quantifying yield exponents in plots with and without C4 grasses, and performing a t -test on their difference. Finally, we asked whether overyielding species are displacing underyielding species over time, by using repeated measures analysis to test whether temporal trends in relative abundance (from per species biomass or percentage cover in 16 species plots) are correlated to yield exponents.

Is overyielding associated with niche differentiation, facilitation, or diversity-dependent foliar pathogens?

First, we asked whether the traits of overyielding species are consistent with niche differentiation: do overyielding species differ in functional group identity and phenology? Next, we determined how nitrogen-fixing legumes (expected to stimulate productivity) affect overyielding of other species (Huston & McBride 2002), in the same way that we tested for effects of C4 grasses. Finally, we determined if diversity-dependent effects of foliar pathogens correlate with overyielding. We used disease severity (the proportion of leaf area covered by foliar pathogens) collected from this and two other diversity experiments (Knops *et al.* 1999; Mitchell *et al.* 2002, 2003) to quantify the per species release from host-specific foliar pathogens with increasing diversity. We then correlated the slope of this log–log regression (between diversity and disease severity) to species-specific yield exponents (Pearson's r , one-tailed test), to test whether overyielding species are most released from foliar pathogens with increasing diversity.

RESULTS

We found that species varied greatly in how they responded to increasing diversity (Fig. 1, Table 1). There were six significantly overyielding species including a C3 grass species, three C4 grass species, and two legume species. Thus, overyielding species were generally grasses (three of four C4 grass species and one of two C3 grass species), but also legumes (two of three species). Underyielding species came exclusively from the forb functional group (four of five species). Analyses of early season productivity (not shown) generated yield exponents that were tightly correlated with yield exponents in Table 1 ($r = 0.925$). Analyses of yield exponents over time (not shown) indicate that the processes that lead to over- and underyielding in this experiment primarily occurred after germination and seedling establishment.

Yield exponents were not correlated to monoculture productivity (Fig. 2a, $r = -0.22$, $P = 0.75$) and negatively correlated (for non-nitrogen fixing species) to R^* for soil nitrate (Fig. 2b, $r = -0.64$, $P = 0.03$). In the presence of C4 grasses, yield exponents of many species declined (Fig. 3, $t = -2.7$, $P = 0.02$) while three forbs became overyielders in the absence of C4 grasses (*Achillea millefolium*, *Monarda fistulosa*, *Solidago rigida*, Table 1). There was no evidence that overyielding species are displacing underyielding species in this experiment: trends in relative abundance are not consistently associated with overyielding and underyielding species (Fig. 4a–c, time \times yield exponent interaction, $F = 0.518$, $P = 0.722$).

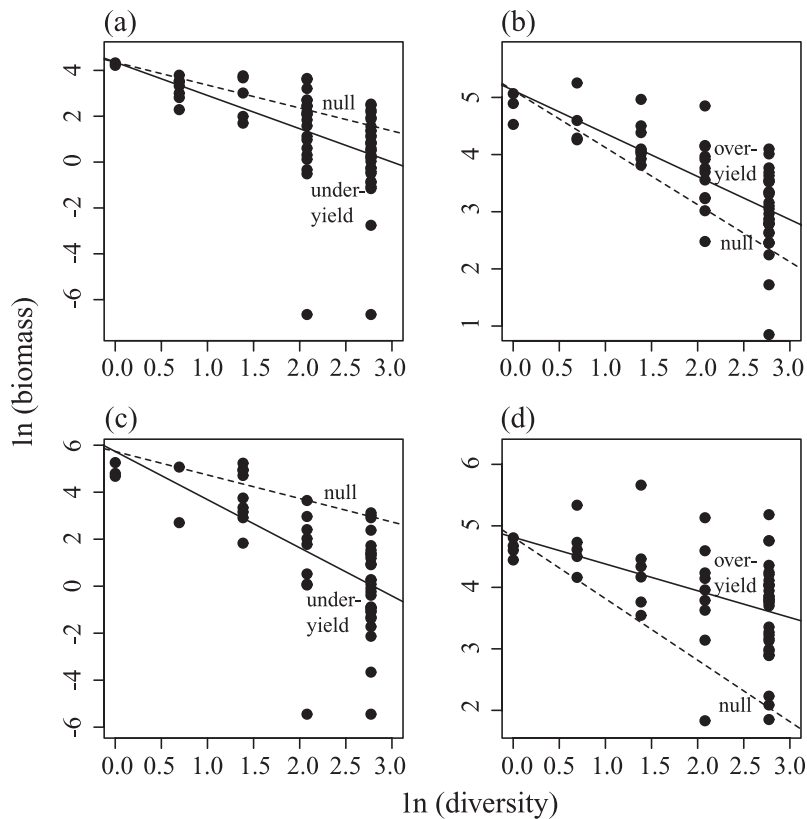


Figure 1 The aboveground productivity of four species [(a) *Koeleria cristata*, (b) *Lespedeza capitata*, (c) *Liatris aspera* and (d) *Sorghastrum nutans*] across a diversity gradient (log–log scale). Each point represents the average of 2001 and 2002 productivity (g m^{-2}) in one of the approximately 60 plots each species was planted in. Solid lines represent best-fitting lines through the scatter of points, dashed lines have slopes of -1 , representing our ‘null’ model. All species shown, except *Koeleria cristata* (a), have yield exponents that are significantly different from -1 .

Functional group <i>Species</i> (abbreviation)	Yield exponent		
	Full data set ($n = 52\text{--}65$)	No legumes ($n = 7\text{--}10$)	No C4 grasses ($n = 6\text{--}16$)
C3 grass			
<i>Koeleria cristata</i> (Kc)	-1.45	-1.25	-0.635
<i>Poa pratensis</i> (Pp)	0.315	-2.57	-0.0865
C4 grass			
<i>Andropogon gerardii</i> (Ag)	-0.281	-0.658	NA
<i>Panicum virgatum</i> (Pv)	-1.50	-1.25	NA
<i>Schizachyrium scoparium</i> (Ss)	-0.184	0.111	NA
<i>Sorghastrum nutans</i> (Sn)	-0.436	-1.12	NA
Forb			
<i>Achillea millefolium</i> (Am)	-0.801	-2.62	-0.485
<i>Asclepius tuberosa</i> (At)	-2.76	-3.56	-1.363
<i>Liatris aspera</i> (La)	-2.05	-1.37	-1.05
<i>Monarda fistulosa</i> (Mf)*	-2.70	-2.78	-0.249
<i>Solidago rigida</i> (Sr)*	-2.27	-1.62	-0.336
Legume			
<i>Lespedeza capitata</i> (Lc)	-0.754	NA	-0.593
<i>Lupinus perennis</i> (Lp)	-0.0822	NA	-0.00555
<i>Petalostemum purpureum</i> (Ppu)	-1.95	NA	-1.77

*Species not present in monoculture plots.

Column values in bold represents overyielding species whose likelihood ratio tests indicate the yield exponent is significantly greater than -1 (at $P < 0.05$).

Column values in italics represents underyielding species whose likelihood ratio tests indicate the yield exponent is significantly less than -1 (at $P < 0.05$).

Table 1 The response of 14 species to increasing diversity in the Cedar Creek Biodiversity experiment; in the full experiment (column 1), plots without nitrogen-fixing legumes (column 2), and plots without C4 grasses (column 3)

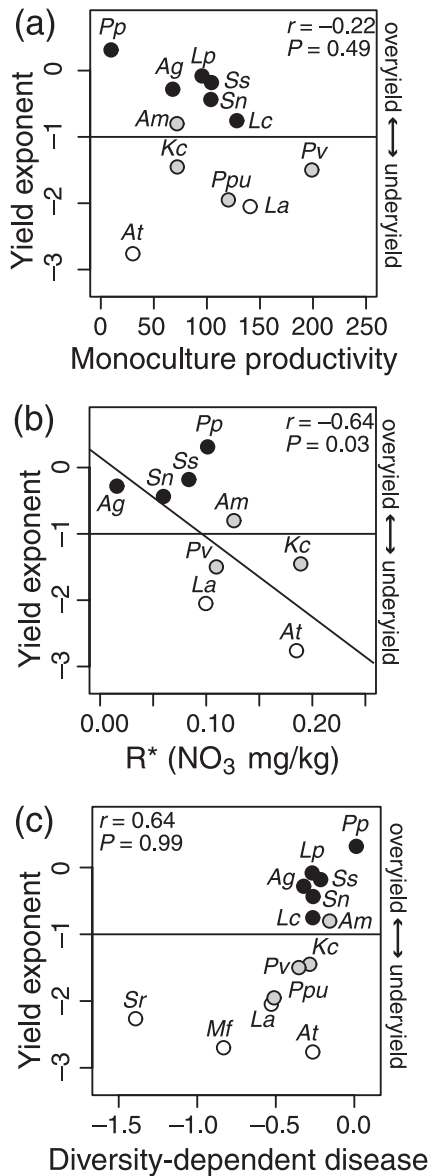


Figure 2 The relationship between (a) monoculture productivity and overyielding of 12 species (all species in Table 1 except those not present in monoculture), (b) R^* for nitrogen and overyielding of nine species (all non-legume species present in monoculture) and (c) the strength of diversity-dependent disease (the slope between diversity and disease severity) and overyielding of 14 species. Black circles represent overyielding species, grey circles species conforming to the null model, and white circles underyielding species.

Overyielding species are both good competitors for soil nitrogen and nitrogen-fixing legumes (C4 grasses vs. legumes), and are active both early (*Lupinus perennis* and *Poa pratensis*) and late (overyielding C4 grasses, *Lespedeza capitata*) in the growing season (Table 1). The presence of legumes positively affected the yield exponents of most

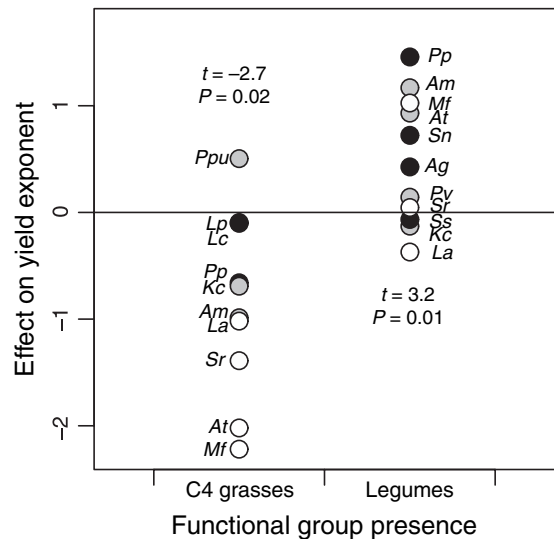


Figure 3 The effects of legume and C4 grass presence on the yield exponent. Black circles represent overyielding species, grey circles species conforming to the null model, and white circles underyielding species in the full data set (i.e. column 1 of Table 1).

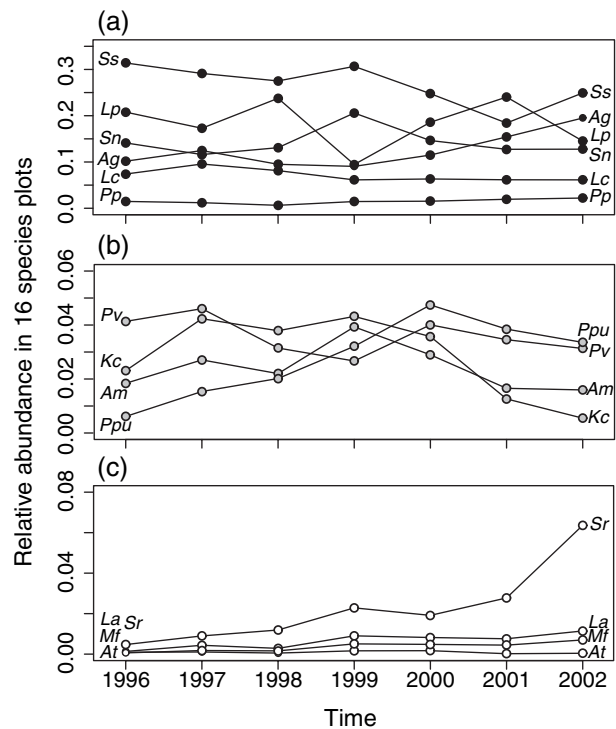


Figure 4 Relative abundance in 16 species plots (as a proportion of biomass or percentage cover) of (a) overyielding, (b) species conforming to the null model and (c) underyielding species over 7 years.

species (Fig. 3, $t = 3.2$, $P = 0.01$). Of the overyielding grasses, only *Schizachyrium scoparium* remained an overyielder in the absence of legumes (Table 1). The yield exponent was

not negatively correlated with slopes between diversity and disease severity as hypothesized, rather, a strong positive correlation was found (Fig. 2c, $r = 0.64$, $P = 0.99$ for a one-tailed test, $P < 0.01$ for a two-tailed test).

DISCUSSION

Our results indicate that the productivity of individual species across this experimental diversity gradient results from both interspecific interactions that could lead to competitive displacement and interspecific interactions that promote diversity. There is strong evidence for competition because the greater than expected productivity (overyielding) of non-legume species is positively correlated with their ability to compete for nitrogen (Fig. 2b), and the presence of these superior nitrogen competitors negatively affects other species (Table 1, Fig. 3). However, several lines of evidence suggest that competitive processes alone are insufficient to explain the positive diversity–productivity relationship in this experiment. First, this would require that overyielding species be the most productive monoculture species (i.e. a ‘positive selection’ effect; Huston 1997; Tilman *et al.* 1997a; Loreau & Hector 2001), which they are not (Fig. 2a). Additionally, this would require that overyielding species be displacing underyielding species over time, which is not occurring (Fig. 4a–c). This suggests that diversity-promoting interspecific interactions are at least in part responsible for the positive diversity–productivity relationship in this experiment (Mouquet *et al.* 2002).

Resource limitation appears to strongly influence the community composition and dynamics of these experimentally assembled communities. Most species that benefit from interspecific interactions (i.e. overyield) belong to the C4 grass and legume functional groups (Fig. 1, Table 1), both adept at acquiring nitrogen, the limiting soil resource in these grasslands (Tilman & Wedin 1991). Collectively, these species make up ~80% of aboveground biomass in diverse plots (Fig. 4). The negative effects of C4 grasses and positive effects of nitrogen-fixers on other species (Fig. 3) further supports the idea that limiting resources may determine the nature of species interactions within these communities. Therefore, although a traditional ‘sampling’ or ‘positive selection’ effect does not operate within this experiment (Fig. 2a), the greater probability of jointly ‘sampling’ both C4 grasses and legumes in diverse plots may contribute to a positive diversity–productivity relationship when nitrogen is limiting (Huston & McBride 2002). Interestingly, C3 grasses and non-nitrogen-fixing forbs (species that do not compete well for nitrogen) were important overyielders in a nearby biodiversity experiment on more nitrogen-rich soils (P. Reich and colleagues, unpublished data), suggesting that the identity of overyielding species may depend on the strength of resource

limitation, as well as other environmental factors (Cardinale *et al.* 2002; Fridley 2003).

Niche differentiation may also contribute to the positive relationship between diversity and productivity in this experiment. C4 grasses and legumes (Fig. 1, Table 1), important overyielding functional groups in this experiment, have different strategies for acquiring nitrogen, the limiting soil resource. Thus, legumes may overyield because they have access to atmospheric nitrogen, while C4 grasses may overyield because they are superior competitors for soil nitrogen. Overyielding species can also be differentiated by their phenology; both cool-season (Table 1; the C3 grass *Poa pratensis* and the legume *Lupinus perennis*) and warm-season species (Table 1; overyielding C4 grasses and the legume *Lespedeza capitata*) were overyielders. Thus, temporal partitioning in resource use may also contribute to the positive diversity–productivity relationship. The results of a nearby experiment, where a positive diversity–productivity relationship was found within functional groups (including the C4 and legume functional groups; Reich *et al.* 2004), suggest that other, as yet unknown, niche differences (e.g. temporal differences in nitrogen uptake; McKane *et al.* 2002) also contribute to the coexistence and overyielding of legumes and C4 grasses (van Ruijven & Berendse 2003).

Our results confirm that nitrogen-fixing legumes stimulate overyielding of other herbaceous perennials, which may strongly contribute to the positive relationship between diversity and productivity in this experiment (Fig. 3; Loreau & Hector 2001; Tilman *et al.* 2001; Spehn *et al.* 2002). In the absence of legumes, only one species significantly overyields (*Schizachyrium scoparium*), and yield exponents of most species increase in the presence of legumes (Table 1, Fig. 3). Yield exponents of two forbs (*Achillea millefolium* and *Monarda fistulosa*) were positively affected by nitrogen-fixing legumes and these two species overyielded in plots without C4 grasses, the dominant competitors for nitrogen (Table 1). This raises the interesting possibility that legumes may stimulate overyielding of other species besides the three overyielding grasses (Table 1), as long as superior nitrogen competitors (C4 grasses) are not present.

The greater than expected productivity of overyielding species at high diversity is not explained by the decreased severity of host-specific foliar pathogens (Mitchell *et al.* 2002, 2003). In fact, species with host-specific foliar pathogens that declined least in severity with increasing diversity were most likely to overyield (Fig. 2c). This strong relationship between overyielding and foliar pathogen disease severity (opposite in direction than expected) may be explained by host-specific foliar pathogens that respond to the density, not frequency of their hosts (Mitchell *et al.* 2002). The productivity of overyielding species, by definition, declines less with diversity than that of underyielding species. If host-specific foliar pathogens are responding to

density (i.e. biomass) and not frequency (i.e. diversity), the slopes of diversity on disease severity should be less negative for overyielding species, as observed. This suggests that foliar pathogens are responding to rather than driving shifts in productivity with diversity. It is possible that other host-specific diversity-dependent natural enemies (e.g. soil pathogens, herbivores) contribute to overyielding of individual species (Bever *et al.* 1997; Carson & Root 2000; Klironomos 2002), although the extremely low rates of insect herbivory on overyielding C4 grasses relative to other functional groups (Haddad *et al.* 2001; Burt-Smith *et al.* 2003) suggests that host-specific insect herbivores are not likely to contribute to overyielding of C4 grasses.

The long-term coexistence of 14 species that are both overyielding as well as underyielding (Fig. 1, Fig. 4a–c) raises the following question: what mechanism prevents the local extinction of underyielding species from this experiment? One possibility is that, because of spatial heterogeneity, underyielding species do experience sufficient complementary interactions that allow them to persist in these experimental grasslands (e.g. facilitation by legumes; Fig. 3), but that these interactions are masked when we quantify the strength of average interspecific interactions rather than interactions between specific species pairs. The fact that several forbs went from underyielding to overyielding in the absence of C4 grasses (Table 1) certainly supports this idea. Another possibility is that the frequency-dependent effects of host-specific natural enemies besides foliar pathogens (e.g. soil mutualists or pathogens; Bever *et al.* 1997; Klironomos 2002) prevent overyielding species from displacing underyielding species (Fig. 4c). Underyielding species may also be buffered from extinction because they occupy different temporal niches than do overyielding species (i.e. the ‘storage effect’; Chesson 2000). Other, as yet unidentified diversity-promoting mechanisms may also be responsible for the persistence of underyielding species in this experiment.

In conclusion, we found that both competition for limiting resources as well as diversity-promoting interactions contribute to the positive relationship between diversity and productivity at Cedar Creek. Several diversity-promoting interactions between species appear to affect total community productivity at high diversity; overyielding species differ in how they acquire limiting resources and in their phenology, suggesting that niche differentiation may play a role in their overyielding. The presence of nitrogen-fixing legumes stimulates overyielding of many species, indicating that facilitation by legumes may strongly contribute to the positive diversity–productivity relationship. Other diversity-promoting interactions probably also operate in this experiment, because underyielding species appear to be buffered from extinction.

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