

## LETTER

## Diversity decreases invasion via both sampling and complementarity effects

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### Abstract

Complementarity and sampling effects may both contribute to increased invasion resistance at higher diversity. We measured plant invader biomass across a long-term experimental plant diversity gradient. Invader species' biomass was inhibited in more diverse plots, largely because of the presence of strongly competitive C<sub>4</sub> bunchgrasses, consistent with a sampling effect. Invader biomass was negatively correlated with resident root biomass, and positively correlated with soil nitrate concentrations, suggesting that competition for nitrogen limited invader success. Resident root biomass increased and soil nitrate concentrations decreased with the presence of C<sub>4</sub> grasses and also across the diversity gradient, suggesting that diverse plots are more competitive because of the presence of C<sub>4</sub> grasses. In addition to this evidence for a sampling effect, we also found evidence for a complementarity effect. Specifically, the percentage of plots that had lower invader biomass than did the best resident monoculture (i.e. that had invader 'underyielding') increased across the species richness gradient. This pattern cannot be explained by a sampling effect and is a unique signature of complementarity effects. Our results demonstrate the importance of multiple mechanisms by which diversity can increase invasion resistance.

### Keywords

Biodiversity, C<sub>4</sub> grass, complementarity, invasion, nitrogen, sampling effect, species diversity, underyielding.

*Ecology Letters* (2005) 8: 604–611

### INTRODUCTION

What determines the success or failure of an invading species? The properties that make communities resistant to invasions are relevant both for management (D'Antonio & Vitousek 1992; OTA 1993; Wilcove *et al.* 1998; Pimentel *et al.* 2000) and for understanding community assembly and structure (e.g. Fargione *et al.* 2003). Biodiversity is one feature of communities that has long been hypothesized to reduce invasions (Elton 1958; Levine & D'Antonio 1999). Invader success has been shown to decrease across diversity gradients in studies where diversity has been experimentally manipulated (Knops *et al.* 1999; Stachowicz *et al.* 1999; Levine 2000; Naeem *et al.* 2000; Symstad 2000; Dukes 2001; Hector *et al.* 2001; Lyons & Schwartz 2001; Kennedy *et al.* 2002; Fargione *et al.* 2003; van Ruijven *et al.* 2003; see Levine *et al.* 2004 for a meta-analysis). Negative effects of native diversity on invading species have also been shown in natural communities at small scales but not at larger scales

(Stohlgren *et al.* 1999), perhaps because factors promoting native diversity also promote invasions (Levine 2000) or because more diverse regions have greater anthropogenic disturbance (Taylor & Irwin 2004).

The invasion resistance effect has been attributed to the ability of diverse communities to occupy more space, generate more biomass, and use more resources (e.g. Stachowicz *et al.* 1999; Tilman 1999; Tilman *et al.* 2001; Kennedy *et al.* 2002; Levine *et al.* 2003). Such effects could be due to both the increased probability of presence of highly competitive species at high diversity (the 'sampling effect'; Huston 1997; Tilman *et al.* 1997) and to complementary resource use among species (Loreau 2000; Loreau & Hector 2001). Complementarity could have numerous causes. For example, complementarity can result if species have tradeoffs in their efficiency of using different resources, tradeoffs in colonization and competitive abilities, or tradeoffs in their success under different environmental conditions. One form of complementarity

often hypothesized to contribute to diversity effects in plant communities are differences among species in both the timing and the depth of resource uptake (e.g. McKane *et al.* 1990). Because diverse plots are more likely to contain species that acquire resources at different times and from different depths, they may exhibit more complete resource capture, leaving less resource left over for invaders. In addition, complementary species may confer competitive resistance to a community if resident species compete more strongly with invader species that have the same spatial and temporal uptake patterns. Thus, both sampling and complementarity effects occur because of the increased probability of species being present at high diversity, the sampling effect because of the presence of strong competitors, and the complementarity effect because of the presence of combinations of complementary species (e.g. strong competitors under different conditions). Both of these effects can be in operation simultaneously.

Although it is difficult to separate these effects, they each have their own signatures. The sampling hypothesis predicts that invader biomass is reduced primarily by the presence of one or a few highly competitive species. In our system, nitrogen (N) is the primary limiting resource. Highly competitive species may reduce invader biomass by increasing root biomass and decreasing soil nitrate concentrations, an index of the efficiency of exploitative plant competition. Complementarity predicts that diverse plots can inhibit invaders more than any monoculture plot can inhibit invaders (Loreau 1998; Stachowicz *et al.* 2002). Otherwise stated, diverse plots may 'underyield' in terms of invader biomass, just as diverse plots have been shown to 'overyield' in terms of the biomass of the resident community (e.g. Tilman *et al.* 2001).

Greater understanding of the mechanisms of biodiversity effects are needed to inform management and conservation decisions affecting biodiversity in natural and designed systems (Hooper *et al.* 2005). Here we report the results from 3 years of natural invasion into a 6-year-old biodiversity experiment. We present analyses to detect sampling and complementarity effects, and to test competition for N as a mechanism behind these effects.

## MATERIALS AND METHODS

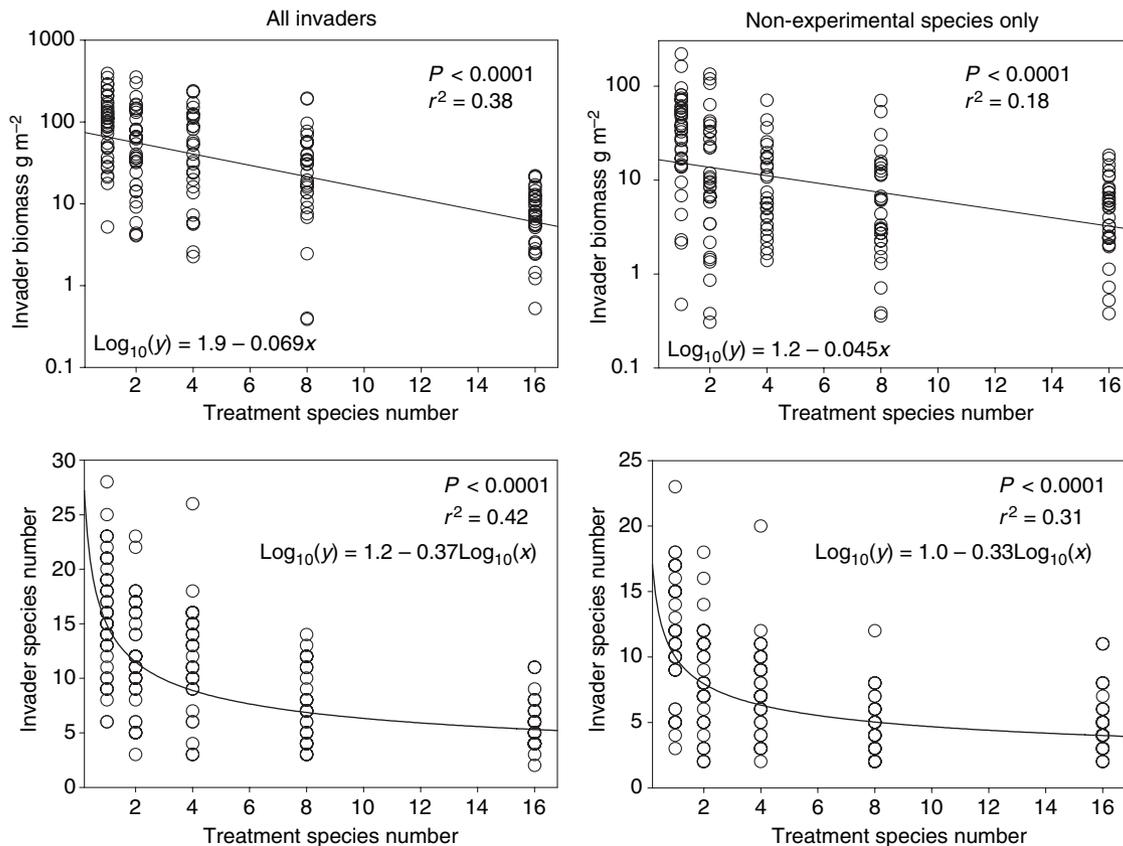
A long-term biodiversity experiment (Tilman *et al.* 2001) was established in 1994, consisting of 168  $13 \times 13$  m experimental plots planted with 1, 2, 4, 8 or 16 randomly selected prairie-savannah species from a pool of 18 possible species. These plots were weeded to maintain the planted species composition. Plots were weeded three or four times a year in an effort to remove individual invaders when they were small so as to minimize differences in the amount of biomass removed between plots differing in susceptibility to

weed invasion. In 2002, we measured resident root biomass in these weeded plots in 8 5-cm diameter by 20-cm deep cores. In 2000, weeded plots were shrunk to  $9 \times 9$  m plus an unweeded  $1 \times 9$  m strip along one edge of the plots where invaders were allowed to colonize. In 2002, a  $6 \times 0.1$  m strip of the aboveground plant biomass in these invasion plots was harvested, sorted to species, dried and weighed. Also in the invasion plots, on 7 August 2002 10-g subsamples from four pooled 2-cm diameter cores were extracted for nitrate using 0.01 M KCl (a weak extractant that still fully extracts nitrate) shaken for 30 min, and allowed to settle overnight at 4 °C. The supernatant was removed the following day, and was frozen until analysed for nitrate on an Alpkem analyzer (Pulse Instruments Ltd, Saskatoon, Canada). In 2001, in the weeded portion of the plots, soil nitrate concentrations at the depths of 0–10 and 10–20 cm were similarly measured 10 times throughout the growing season on four pooled 2-cm diameter cores in each plot.

We present analyses based on two types of invader species: 'non-experimental invaders' and 'all invaders'. Non-experimental invaders include only those species not planted anywhere in the full biodiversity experiment. 'All invaders' is defined for each plot to include all species not planted in that plot. When species that were planted somewhere in the experiment invade a plot in which they were not planted, they are considered invaders by the 'all invaders' criterion, but not the 'non-experimental invaders' criterion. Thus, using the 'all invaders' criterion, some species are considered residents in some plots and invaders in other plots, depending upon which species were planted in a given plot. Patterns detected using this approach could be confounded because individuals that invade a plot in which that species is a planted resident are considered residents rather than invaders. Using the non-experimental invaders criterion avoids this problem. Although we recognize the limitations of interpretation with the 'all invaders' approach, for completeness and comparison we present results for both measures of invader success. Invader biomass and invader species number values, for both all invaders and non-experimental invaders, were all greater than zero. These values were log transformed to improve normality for statistical analyses, performed with JMP version 4.0.4 (SAS Institute Inc. 2001).

## RESULTS

Sixty-two species of non-experimental invaders and all 21 experimental species occurred as invaders in our experiment (see Appendix S1). Both the biomass and the number of species of invaders decreased significantly across the gradient of resident species number (Fig. 1). Comparing 1 and 16 species plots, invader species number decreased by



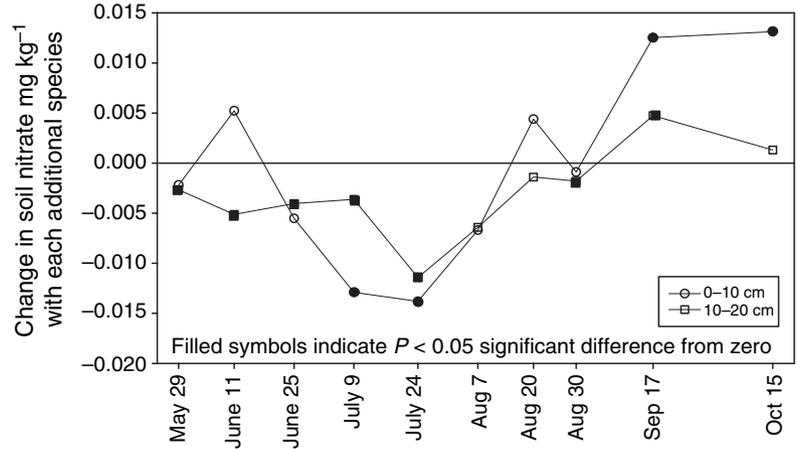
**Figure 1** Invader success vs. species number. Invader biomass and number decreased with increasing resident species richness for both non-experimental and all invaders.

76% and 68% for non-experimental and all invaders, respectively. Invader biomass decreased by 81% and 92% for non-experimental and all invaders, respectively. When the biomass of resident species was included as a predictor, resident species number was still a highly significant predictor of invader biomass (for non-experimental invaders  $P = 0.0002$  and  $P = 0.1836$  for resident species number and resident biomass, respectively; for all invaders  $P < 0.0001$  and  $P = 0.873$  resident species number and resident biomass respectively). Resident species number also still significantly predicted invader species number when resident biomass was included in the model (for non-experimental invaders  $P < 0.0001$  and  $P < 0.0049$  for resident species number and resident biomass, respectively; for all invaders  $P < 0.0001$  and  $P = 0.0037$  resident species number and resident biomass respectively).

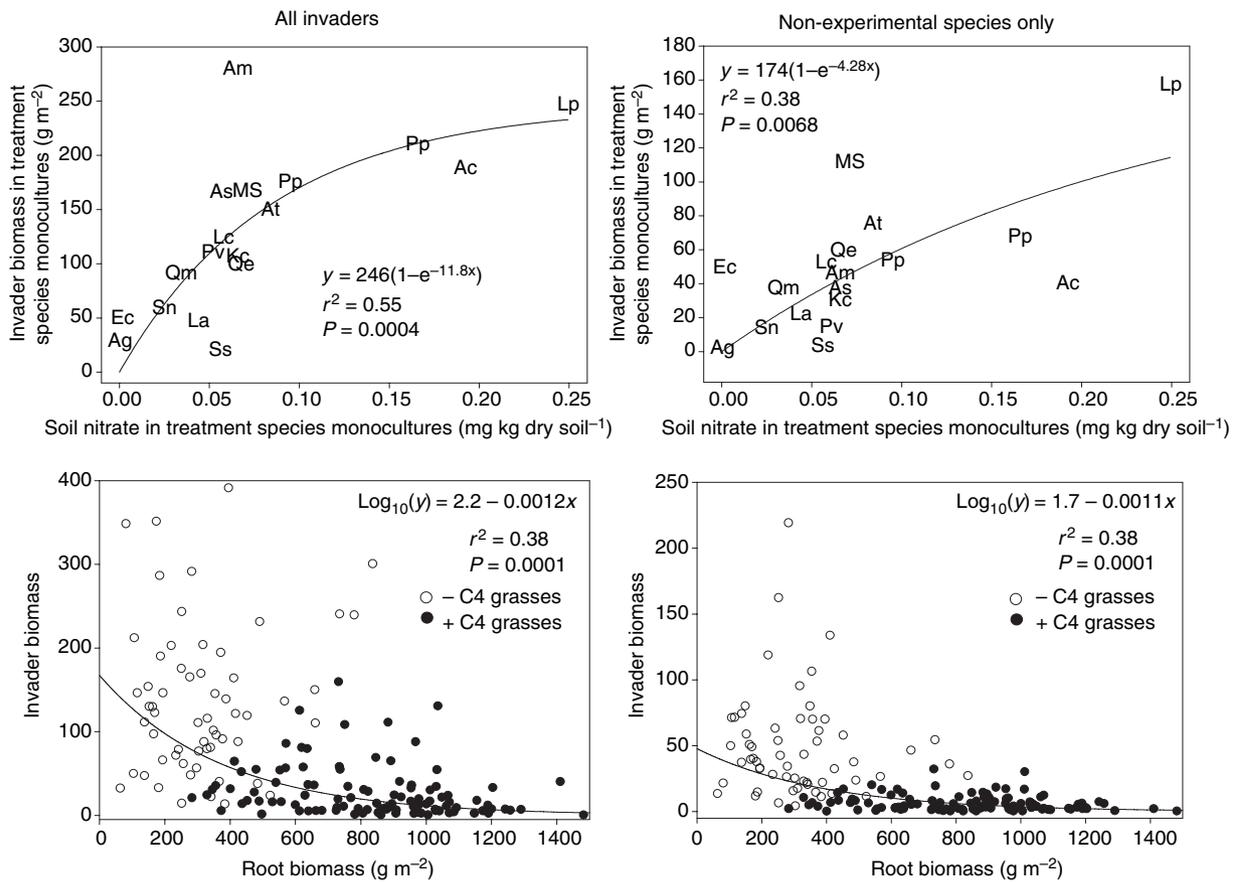
Species number affected resident root biomass and soil nitrate, indicators of the strength of competition experienced by invaders. Resident root biomass increased with increasing species number ( $r^2 = 0.31$ ,  $P < 0.0001$ ). We measured soil nitrate at 0–10 cm and at 10–20 cm 10 times throughout the growing season in 2001 (Fig. 2). Species number had

significant negative effects on soil nitrate at one or both depths for the first five sampling dates, 29th May to 24th July. Species number had significant positive effects on soil nitrate at one or both depths for the last two sampling dates, 17 September and 15 October. This pattern suggests that soil nitrate pools are responding to greater uptake of N at higher species richness during the beginning and middle of the growing season, and greater decomposition and N supply at higher species richness after plant uptake has ceased for the season. Temporal trends were similar for both depths, but the shallow depths had more extreme values, both negative and positive. Thus, the magnitude of the diversity effect on soil nitrate was greater at this shallower depth. In total, species number affects soil nitrate across multiple times and depths, with negative effects during the part of the growing season in which plant uptake occurs.

Variation in soil nitrate and resident root biomass explained the majority of variation in invader biomass (Fig. 3). In the monoculture plots, where effects of individual resident species could be isolated, the average soil nitrate concentration and average invader biomass were well-correlated (Fig. 3). When all plots were considered,



**Figure 2** Soil nitrate concentrations over time. Data are from weeded plots in 2001.



**Figure 3** Invader success is correlated with soil nitrate concentrations and root biomass. Soil nitrate concentrations explained most of the variation in invader biomass among monocultures of different species. Averages across monocultures are used for both invader biomass and soil nitrate, both of which were measured in the invasion strips. Root biomass, which was highly correlated with the presence of C<sub>4</sub> grasses, was the best predictor of invader biomass across all 168 plots. Root biomass was measured in the adjacent unweeded plots. The regression results are for log (invader biomass) regressed on root biomass. Analyses including C<sub>4</sub> grasses are reported in the text.

resident root biomass was a better predictor of invader biomass than was soil nitrate (for soil nitrate as a predictor,  $P = 0.0002$  and  $P = 0.0034$ ,  $r^2 = 0.08$  and  $0.05$  for non-

experimental and all invaders respectively; for root biomass as a predictor  $P < 0.0001$  and  $r^2 = 0.38$  for both non-experimental and all invaders, see Fig. 3).

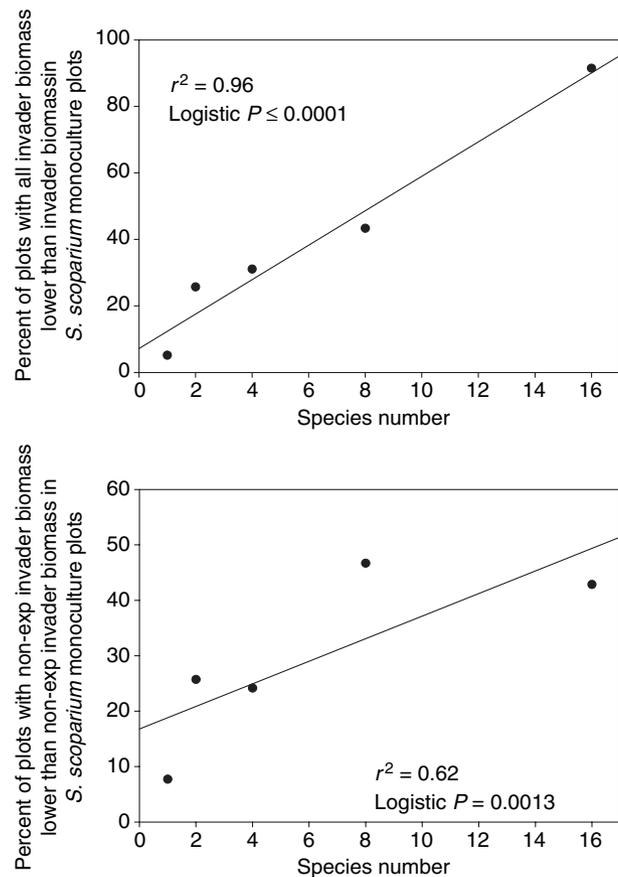
Predictors	Responses					
	Log biomass all invaders			Log biomass non-experimental invaders		
	Effect	<i>F</i>	<i>P</i>	Effect	<i>F</i>	<i>P</i>
C <sub>3</sub> presence/absence	-0.23	9.0	0.0031	-0.18	6.3	0.0128
C <sub>4</sub> presence/absence	-0.76	101.3	<0.0001	-0.89	167.1	<0.0001
Forb presence/absence	-0.23	9.2	0.0028	-0.10	2.0	0.1554
Legume presence/absence	-0.06	0.6	0.4497	0.11	2.4	0.1218
Overall <i>r</i> <sup>2</sup>	0.52			0.57		
Overall <i>P</i>	<0.0001			<0.0001		

The C<sub>4</sub> grasses strongly inhibited invaders, and their effects largely explain the patterns observed with soil nitrate and root biomass. Although initially planted in relatively equal amounts, by the end of our experiment resident functional groups in the invasion strips had markedly different abundances, with C<sub>4</sub> grasses comprising 50% of the total resident biomass, legumes 35%, forbs 16% and C<sub>3</sub> grasses only 3%. Comparing average functional group traits measured in the monoculture plots, C<sub>4</sub> grasses had the lowest soil nitrate values and were less invaded than the other functional groups. C<sub>4</sub> grasses also had high-root biomass, and the presence of C<sub>4</sub> grasses strongly increased the root biomass of resident communities (Fig. 3). The presence of C<sub>4</sub> grasses explained 54% of the variation in root biomass. It is difficult to separate whether increased root biomass is the mechanism by which C<sub>4</sub> grasses competitively inhibited invaders, or whether root biomass is significant only because it is well-correlated with the presence of C<sub>4</sub> grasses. When both factors are included in a model, they are both significant (for non-experimental invaders *P* = 0.0428 and *P* < 0.0001 for root biomass and C<sub>4</sub> presence, respectively; for all invaders *P* = 0.0011 and *P* < 0.0001 for root biomass and C<sub>4</sub> presence respectively). This suggests both that the increased root biomass is a mechanism inhibiting invaders and that the C<sub>4</sub> grasses have inhibitory effects on invaders in addition to those mediated through increased root biomass.

The strong effects of C<sub>4</sub> grasses are also shown in Table 1. The presence of C<sub>4</sub> grasses strongly inhibited both non-experimental and all invaders. There were additional effects of C<sub>3</sub> grasses on both non-experimental and all invaders, and of forbs on all invaders. The majority of the effect of species number on invader biomass was likely because of the presence of C<sub>4</sub> grasses. Regressions of log-invader biomass on the number of C<sub>4</sub> grass species explained more variation (*r*<sup>2</sup> = 0.51 and 0.31 for non-experimental and all invaders respectively) than did species number (*r*<sup>2</sup> = 0.38 and 0.18 for non-experimental and all invaders respectively). Although the number of resident C<sub>4</sub>

**Table 1** Multiple regression of invader biomass (all and non-experimental) on the presence of functional groups, the number of C<sub>4</sub> species, and the total number of species

grass species and resident species number are collinear variables, when both are included as predictors of log-invader biomass, the number of C<sub>4</sub> grass species was significantly negatively correlated with invader biomass



**Figure 4** The percentage of plots with invader biomass lower than the average biomass in *Schizachyrium scoparium* plots increased with species number. *Schizachyrium scoparium* was the species most resistant to invasion. The y-axis reports the percentage of plots with invader biomass >20.45 or 3.84 g m<sup>-2</sup>, for all invaders and non-experimental invaders respectively.

while resident species number was not significantly correlated with invader biomass (data not shown).

Although these results suggest a sampling effect, might complementary interactions among established species also inhibit invasion? The species with the lowest invader biomass in monoculture was *Schizachyrium scoparium*. We used the average invader biomass from the monocultures of *S. scoparium* as a cutoff, and calculated for each diversity treatment the percentage of plots that had invader biomass that were below this cutoff (Fig. 4). This analysis addresses the question: 'do diverse plots tend to resist invaders more than does the most resistant species in monoculture?' We found that, as diversity increased, there was a highly significant increase in the percentage of plots that had lower invader biomass (i.e. that had underyielding invaders) than did average *S. scoparium* monocultures (Fig. 4). In the most diverse plots, 43 and 91% of the plots had lower invader biomass than did the average *S. scoparium* monoculture, for non-experimental and all invaders respectively. In combination with earlier results, this result suggests that both interspecific complementarity and sampling contribute to the greater inhibition of invaders observed in higher diversity plots in this experiment.

## DISCUSSION

Our results are consistent with previous invasion experiments, which have shown negative effects of resident species number on invasion (Knops *et al.* 1999; Stachowicz *et al.* 1999; Levine 2000; Naeem *et al.* 2000; Hector *et al.* 2001; Lyons & Schwartz 2001; Kennedy *et al.* 2002; Fargione *et al.* 2003; van Ruijven *et al.* 2003; but see Crawley *et al.* 1999; Dukes 2001), positive effects of legumes on invaders (Prieur-Richard *et al.* 2002), and strong negative effects of a subset of resident species (e.g. Crawley *et al.* 1999; Symstad 2000; Fargione *et al.* 2003; Xu *et al.* 2004). Here, we show that the strong negative effect of  $C_4$  grasses on invader biomass is associated with specific functional traits (Diaz & Cabido 2001): high-root biomass and low soil nitrate concentrations. Both root biomass and soil nitrate are measures of the efficiency of exploitative competition for N, suggesting that a community's ability to efficiently consume N leads to invasion resistance.

In support of this interpretation that competition for N is the mechanism inhibiting invasion at high diversity, we found that diversity reduced soil nitrate at multiple depths during the early and middle part of the growing season when plant N uptake occurs (Fig. 2). Diverse plots had lower soil nitrate concentrations during the early and middle part of the growing season in spite of diverse plots in this experiment having higher mineralization rates (Zak *et al.* 2003). Our results are consistent with this previously observed positive effect of diversity on N mineralization;

diversity had a positive effect on soil nitrate pools during the latter part of the growing season, when belowground plant senescence and decomposition may be contributing to N mineralization rates. Thus, the shifting effect of diversity on soil nitrate concentrations during the growing season (from negative to positive) appears to be caused by high uptake in diverse plots during the early and mid-season leading to lower nitrate concentrations, followed by high mineralization rates in diverse plots during the late season leading to higher soil nitrate concentrations.

Although data were not collected on individual plants, both personal observation and the fact that invaders were reduced both in biomass and in number of invader species suggests that high diversity limited both invader size and number. However, invaders commonly set seed, suggesting that invaders were establishing viable populations, rather than persisting solely because of propagule pressure from outside the plot. Reduced invader size suggests reduced invader growth rates, whereas reduced invader numbers could be caused either by decreased establishment or increased mortality. Competitive effects could operate to decrease growth rates, decrease establishment, and/or increase mortality; further research is necessary to reveal the life history stages at which biodiversity effects on invaders occur.

The strong negative effect of the presence of  $C_4$  grasses (Table 1) is evidence for a strong sampling effect that contributes to invasion resistance in diverse communities. In addition, we detected a clear signature of complementarity, the underyielding of invader biomass. Such underyielding occurs when diverse plots resist invaders more successfully than the best species in monoculture. In our experiment this was *S. scoparium*, and the percentage plots with lower invader biomass than the average *S. scoparium* monocultures increased with diversity (Fig. 4). A similar result has also been found in a sessile epibenthic invertebrate community (see Fig. 3 in Stachowicz *et al.* 2002). This provides clear evidence for underyielding by invaders, demonstrating that the presence of additional species increases the ability of communities to resist invaders beyond what can be achieved even by the strongest competitor alone.

The evidence presented in this study for complementarity as a mechanism of diversity effects inhibiting invasion is consistent with previous studies documenting complementarity as a mechanism for biodiversity effects on productivity (Loreau & Hector 2001; Tilman *et al.* 2001; Spehn *et al.* 2005) and with studies discussing different forms of complementarity (e.g. Tilman *et al.* 1997; Loreau 1998; Loreau *et al.* 2001; Kinzig *et al.* 2002; Scherer-Lorenzen *et al.* 2003). We hypothesize that complementarity contributes to invasion resistance by diversity in our experiment for reasons that are generally applicable in other systems. Specifically, that resident species compete more strongly

with species of invaders more similar to themselves (Fargione *et al.* 2003; Xu *et al.* 2004) and that differences amongst resident species in phenology and rooting depth lead to more complete uptake of N and stronger competition with invaders (Fargione 2004). In total, our results demonstrate the importance of multiple mechanisms by which diversity can increase invasion resistance.

## ACKNOWLEDGEMENTS

We thank Sarah Hobbie, Claudia Neuhauser, Dennis Cook, Gary Oehlert, Keri Holland and two anonymous referees for helpful comments and Troy Mielke and many Cedar Creek interns for field help. Funding for the project was provided by the National Science Foundation (NSF/DEB 0080382 and NSF/DEB 9629566) and the Andrew Mellon Foundation, and funding for JEF was provided by the University of Minnesota Graduate School.

## SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE753/ELE753sm.htm>

**Appendix S1** Table of invader species' abundances and functional groups.

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Editor, Marcel Rejmanek

Manuscript received 12 January 2005

First decision made 20 February 2005

Manuscript accepted 28 February 2005