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Mutualistic fungus promotes plant invasion into diverse communities

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Abstract Reducing the biological diversity of a community may decrease its resistance to invasion by exotic species. Manipulative experiments typically support this hypothesis but have focused mainly on one trophic level (i.e., primary producers). To date, we know little about how positive interactions among species may influence the relationship between diversity and invasibility, which suggests a need for research that addresses the question: under what conditions does diversity affect resistance to invasion? We used experimental manipulations of both plant diversity and the presence of an endophytic fungus to test whether a fungal mutualist of an invasive grass species (*Lolium arundinaceum*) switches the relationship between plant community diversity and resistance to invasion. Association with the fungal endophyte (*Neotyphodium coenophialum*) increased the ability of *L. arundinaceum* to invade communities with greater species diversity. In the absence of the endophyte, the initial diversity of the community significantly reduced the establishment of *L. arundinaceum*. However, establishment was independent of initial diversity in the presence of the endophyte. Fungal symbionts, like other key species, are often overlooked in studies of plant diversity, yet their presence may explain variation among studies in the effect of diversity on resistance to invasion.

Keywords Diversity · Ecosystem functioning · Invasibility · *Neotyphodium* · Prairie

Introduction

Reducing the biological diversity of a community is often predicted to decrease its resistance to invasion by exotic species (Tilman et al. 1997; Levine and D'Antonio 1999; Levine et al. 2003). Both the loss of diversity and the introduction of exotic, invasive species into communities are major threats to natural ecosystems (Mack et al. 2000; Pimentel et al. 2000; Hector et al. 2001). Understanding the role of diversity in resistance to invasion will not only advance our basic understanding of community dynamics, but also may improve conservation by focusing attention on the processes critical to sustaining natural ecosystems (Chapin et al. 1998).

During the past decade, many observational and manipulative studies have looked for a relationship between plant diversity and resistance to invasion (reviewed by Levine and D'Antonio 1999; Wardle 2001). The two most common mechanisms proposed to underlie this relationship include complementarity effects, in which the addition of greater phenotypic diversity to species assemblages enhances resource utilization or positive interactions among species, thereby leaving fewer resources available for invaders, and the selection effect, whereby communities with higher diversity have a greater probability of including a species with a strong effect on the invader (Burke and Grime 1996; Foster et al. 2002; Wilsey and Polley 2002). The importance of diversity to invasion varies across studies, with experiments often finding the predicted negative effect of increases in diversity on invasibility (Naeem et al. 2000; Lyons and Schwartz 2001; Kennedy et al. 2002; Stachowicz et al. 2002), whereas many observational and some manipulative studies report an opposite (positive) relationship (Robinson et al. 1995; Foster et al. 2002; Brown and Peet 2003; Stohlgren et al. 2003; Weltzin et al. 2003). Although these discrepancies have largely been attributed to the scale of studies and to covarying factors that are not

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accounted for in observational studies (Levine 2000, 2001), other factors may also contribute to variation in the importance of diversity. This variation suggests a need for research that addresses the question: under what conditions does diversity affect resistance to invasion?

One condition that may reduce the effect of diversity on resistance to invasion is the presence of a mutualism that benefits the invader (Richardson et al. 2000; Bruno et al. 2003; Rudgers et al. 2004). For example, the invasion of exotic *Myrica* may be facilitated by mutualistic interactions with nitrogen-fixing bacteria (Walker et al. 1986) and by mutualisms with seed-dispersing birds (Woodward et al. 1990). Similarly, diverse webs of interactions with native pollinators may sustain non-native plants (Memmott and Waser 2002). However, to our knowledge, the hypothesis that a mutualist can modify the relationship between diversity and resistance to invasion has not yet been tested using manipulative experiments (but see Klironomos et al. (2000) for diversity–productivity relationships).

Many cool season grasses host endophytic fungi that can render the grass resistant to herbivory (Clay 1996), pathogen attack (Clay et al. 1989; Gwinn and Gavin 1992), drought stress (Elmi and West 1995), and competition with other plants (Clay et al. 1993). Interactions between plants and endophytic fungi can span the range from parasitic to mutualistic (Saikkonen et al. 1998, 2004). However, systemic endophytes that are strictly vertically transmitted from the host plant to its seeds are commonly mutualistic (Clay and Schardl 2002). As these endophytes produce no externally visible symptoms, they are often overlooked in studies of plant diversity and invasion (see Rudgers et al. 2004). Therefore, systemic, endophytic fungi, which are estimated to occur in 20–30% of all grass species (Leuchtman 1992), represent a hidden factor that may help explain the varied results of prior studies on resistance to invasion and plant diversity.

In a prior study assessing the role of mutualisms in diversity–invasibility relationships, observational data from long-term field plots revealed that the negative correlation between the diversity of the plant community and the success of an invader was stronger for invasive plants that lacked vertically transmitted fungal symbionts as compared to plants with these endophytes (Rudgers et al. 2004). To provide a conceptual framework for our work, we also developed a model (adapted from Tilman et al. 1997; Klironomos et al. 2000; see model in Rudgers et al. 2004). In this model, plants exploit niches along two resource axes (e.g., light and water). As species are added to the community, remaining resources become diminished. For a finite pool of resources, when a mutualist is added to a dominant or invading plant species in the community, other plant species are expected to achieve lower biomass than when competing with a plant lacking its mutualist. These other species

will contribute less to the productivity of the community and also have a smaller effect on the community's resistance to spread by the dominant (or invading) plant. Put simply, our model predicts that diversity should matter less when the dominant (or invading) plant has a mutualist because mutualists enhance (directly or indirectly) the competitive ability of their host (see Rudgers et al. 2004).

Experimental manipulations of plant diversity are necessary to establish whether the invader's mutualist disrupts a causal effect of diversity on resistance to invasion. In the present study, we manipulated both plant diversity and the presence of a fungal endophyte to test whether a fungal mutualist enhances the ability of the invasive grass, *Lolium arundinaceum*, to invade diverse plant communities.

Methods

Natural history of the invader

Lolium arundinaceum (Schreb.) S.J. Darbyshire (tall fescue, Poaceae) is a hexaploid, perennial grass that is native to Mediterranean Europe and Africa. It was introduced to the United States during the 1800s (Ball et al. 1993; Clay and Holah 1999). Since its introduction, *L. arundinaceum* has been widely planted for forage and turf, occupying more than 15 million ha of the eastern United States (Ball et al. 1993). *L. arundinaceum* has also invaded native communities and is now considered an important exotic pest in several states (Stubbendieck et al. 1994; Uva et al. 1997).

More than 75% of the *L. arundinaceum* in the United States is found in association with the fungal endophyte *Neotyphodium coenophialum* (Latch, Christensen and Samuels) Glenn, Bacon and Hanlin (Ball et al. 1993). *N. coenophialum* grows in the intercellular spaces of the aboveground tissues of its host, where it typically accounts for less than 0.1% of the aboveground biomass (Hiatt and Hill 1997). Under natural conditions, the fungus has only been documented to reproduce asexually via hyphal growth into the seeds of symbiotic plants (Clay 1989). Although the endophyte produces no externally visible symptoms, it can be detected microscopically after staining thin sections of the inner leaf sheath with lactophenol cotton blue (Clark et al. 1983).

Greenhouse experiment

We manipulated both plant richness and the presence of an endophyte in *L. arundinaceum* in a 2×4 factorial design with an endophyte treatment [with (*E+*) or without (*E-*) the endophyte] and four levels of plant richness (1, 2, 4 or 8 native prairie species). The treatments were applied in large pots in the green-

house. All pots were filled with sterilized soil (193–3–98 ppm N–P–K) and fertilized after 70, 85, and 99 days (450–450–450 ppm N–P–K). The greenhouse was maintained at 21–24°C with a photoperiod of 14 h using artificial lighting until day 55, when the artificial lights were eliminated due to an increase in the natural photoperiod.

Altering plant diversity

We used North American prairie plants to manipulate plant diversity. Four levels of plant richness were created (1, 2, 4 or 8 species) by drawing from a pool of 18 species: *Asclepias tuberosa* (Apocynaceae); *Coreopsis lanceolata*, *Echinacea purpurea*, *Rudbeckia hirta*, *Vernonia fasciculata*, *Symphyotrichum novae-angliae* (Asteraceae); *Amorpha canescens*, *Dalea candida*, *Desmodium canadense* (Fabaceae); *Monarda fistulosa*, *Pycnanthemum verticillatum* (Lamiaceae); *Andropogon gerardii*, *Schizachyrium scoparium*, *Bromus kalmii*, *Elymus canadensis*, *Bouteloua curtipendula*, *Panicum virgatum*, and *Sorghastrum nutans* (Poaceae). Seeds were obtained commercially (Prairie Moon Nursery, Winona, MN, USA), cold stratified (4°C) for 7 days in wet vermiculite, and initially planted into 26×52×6 cm flats filled with pasteurized Metromix 360 soil (Scotts-Sierra Horticultural Products Co., Marysville, OH, USA).

We planted 18 replicate pots per endophyte × richness combination. For the treatments with more than one species, we chose species at random from the pool and duplicated each random combination to create pairs of pots, one of which was assigned at random to either an *E+* or *E-* *L. arundinaceum* addition. For the single species treatment, we planted pairs of pots for each of the 18 species in the original species pool. On 20 November 2003, we transplanted 3-week old prairie seedlings into large, round pots (21 cm diameter×21 cm depth). Forty seedlings were planted into each pot with equal spacing (approximately 2 cm) between each plant (Fig. 1a). For each pot with more than one species, we planted a single individual of each species in a randomly chosen order. We repeated this random order throughout the pot. Paired pots (*E+* and *E-*) of a given richness treatment were randomly assigned to locations in the greenhouse. Three weeks after the initial planting, we replaced seedlings that died from transplant shock.

Each replicate consisted of an independent random draw; therefore, we could test for an effect of species richness (or diversity) but not of species composition (Loreau and Hector 2001; Mikola et al. 2002). Random draw experiments make the assumption that species loss from communities occurs at random. Although important criticisms have been raised against this approach (Huston 1997; Wardle 1999), random draws do mimic some biologically plausible scenarios of biodiversity loss (Chapin et al. 2000; Hector 2000). Furthermore, because

our primary interest was whether the mutualist altered the diversity–invasibility relationship, we did not attempt to isolate mechanisms underlying this relationship (i.e., selection versus complementarity effects), which would require an alternative experimental design.

We estimated the initial diversity of each pot to increase the statistical power and biological realism for detecting an effect of plant diversity. An initial diversity measure allowed us to use a regression approach with the initial diversity treatment as the predictor variable rather than an ANOVA approach with richness as the treatment. This method accounts for initial differences in size among species. We obtained an initial estimate of plant diversity by determining the initial biomass of each native species at the time of planting. Seedlings were dried (3 days at 60°C) and weighed to the nearest 0.001 g ($n=20$ individuals of each prairie species). We then determined the initial Shannon-Weiner diversity index (Peet 1974) for each pot by using the mean initial aboveground biomass of each species in our calculations.

Eliminating the endophyte

Viability of the fungal endophyte was originally reduced by long-term seed storage to create uninfected (*E-*) seeds from endophyte-infected (*E+*) seeds (var. Jesup, Pennington Seed, Madison, GA, USA). These original seeds were then propagated in field plots; seeds from these plots were used to create new field plots, and so on for several generations. Therefore, seeds used in the experiment were several generations removed from the original treatment to eliminate the endophyte and were harvested at the same time (2001) as *E+* seeds. Four weeks after prairie seedlings were planted, all pots received ten seeds of either *E+* or *E-* *L. arundinaceum* (Fig. 1b). This treatment was intended to mimic the effect of seeds invading a community of newly established prairie plants. At the end of the experiment, endophyte status was verified for 30 randomly selected live individuals of *L. arundinaceum* per treatment by staining sections of leaf sheaths with lactophenol cotton blue (Clark et al. 1983). These data were analyzed with a log-linear model that included whether or not the individual had the endophyte as the response variable and the endophyte treatment as the predictor variable (Proc Genmod, SAS Institute 2000).

We tested for initial differences in biomass and germination for *E+* and *E-* seeds of *L. arundinaceum*. For biomass, we weighed 50 samples of ten seeds each. The endophyte did not affect seed mass (mean mass per seed (g) ± SE, $E+ = 0.024 \pm 0.001$, $E- = 0.023 \pm 0.001$; ANOVA, $F_{1,98} = 2.12$, $P = 0.15$). For germination, we placed seeds in sealed plastic trays lined with moist blotter paper ($n=6$ trays per endophyte treatment with 20 seeds per tray). Seeds were maintained in the same greenhouse as the pots

Fig. 1 Pots in the greenhouse experiment **a** at time of initial planting and **b** at the time of tall fescue seed addition, 4 weeks after planting



for 21 days. Germination was recorded every 2–8 days, and differences in proportional germination per tray (angular-transformed) were analyzed with a repeated measures ANOVA that included the main effect of the endophyte treatment and the repeated effect of time. The endophyte did not affect total seed germination (endophyte $F_{1,10}=0.25$, $P=0.62$) or the rate of germination (Fig. 2, endophyte \times time interaction $F_{4,7}=1.07$, $P=0.44$).

Response variables and analysis

At the end of the experiment, we assessed the effectiveness of the diversity manipulation as well as the success of *L. arundinaceum*. We harvested all aboveground biomass by cutting plants at the soil surface on 16 March 2004. Mean total aboveground biomass across

all pots was 47.99 ± 2.44 g. Belowground biomass was not assessed because it was impossible to identify and detangle the roots of each species. For each pot, we counted the number of individuals of each species and assessed the aboveground biomass of each species after drying for 3 days at 60°C . For two species, *P. virgatum* and *S. novae-anglicae*, we had a minor amount of seed contamination by *Setaria faberi* (Poaceae, $n=7$ of 144 pots) and an unknown Asteraceae ($n=1$ of 144 pots), respectively. We included these contaminants in the estimates of final diversity.

Two measures of final diversity were determined by calculating Shannon-Weiner diversity indices (Peet 1974) for each pot using (1) the total number of individuals of each species or (2) the final aboveground biomass of each species in the calculation. To assess the effectiveness of the richness treatment, the relationship

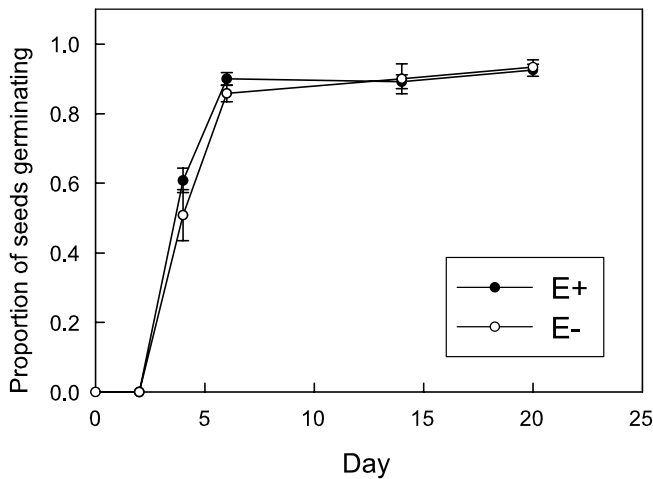


Fig. 2 Proportion of *L. arundinaceum* seeds that germinated on blotter paper in the greenhouse for seeds with (*E+* black circles) or without (*E-* open circles) the endophyte *N. coenophialum*. Bars represent SEs

between initial diversity and final diversity was examined with regression analysis (Proc Reg, SAS Institute 2000).

We examined two response variables to determine the success of the invader: the number of individuals and biomass per individual. To assess the effect of diversity on these responses of *L. arundinaceum*, we constructed ANCOVA models that included the initial species diversity (a continuous variable), the endophyte treatment (*E+* or *E-*), and the initial species diversity \times endophyte treatment interaction (Proc Glim, SAS Institute 2000). We conducted the same analysis using final diversity in place of initial diversity. To address whether an increase in total aboveground biomass (an increase in the level of competition) may be one mechanism underlying an effect of initial diversity, we also conducted the same analysis using total aboveground biomass in place of initial diversity. When interactions between the covariate (initial species diversity, final species diversity, or total aboveground biomass) and the endophyte treatment were statistically significant, we then examined the correlations between the covariate and the number of tall fescue individuals (or biomass per individual) in both the presence and absence of the endophyte. We also determined the magnitude of the effect by comparing the slope of the relationship between diversity and the response of *L. arundinaceum* in the presence and absence of the endophyte; we used bias-corrected accelerated bootstrap analysis to estimate 95% confidence intervals around each slope (Efron and Tibshirani 1993, 10,000 iterations, Jackboot macro; SAS Institute 1995). Analyses met assumptions of normality and equality of variances following log transformation of biomass. The number of tall fescue individuals was rank-transformed for nonparametric analysis (Conover and Iman 1981).

Results

Effectiveness of treatments

Both the diversity and endophyte manipulations were effective. The initial Shannon-Weiner diversity index was strongly positively correlated with final diversity, both using the biomass of individuals ($r=0.88$, $P<0.0001$, $n=144$) and using the number of individuals ($r=0.98$, $P<0.0001$, $n=144$). The proportion of individuals with endophytes was 100% for the infected treatment and 3% for the uninfected treatment (likelihood ratio $\chi^2=74.34$, $P<0.0001$, $n=30$ individuals per treatment).

Endophytes, diversity and invasion

Association with the fungal endophyte increased the ability of the invasive grass, *L. arundinaceum*, to invade more diverse plant communities (endophyte \times initial species diversity $F_{1,143}=6.56$, $P=0.012$). The number of *L. arundinaceum* individuals that successfully established was significantly reduced by higher initial species diversity of the community when *L. arundinaceum* lacked the endophyte (Fig. 3a; $r=-0.36$, $P=0.002$). However, in the presence of the endophyte, establishment of *L. arundinaceum* was independent of the initial species diversity of the community (Fig. 3b; $r=-0.08$, $P=0.53$). The magnitude of the effect of diversity (as estimated by the slope of the number of seedlings regressed on initial diversity) was 331% greater in the absence of the endophyte (β [95% CI] = -1.352 [-2.105 to -0.575]) than in the presence of the endophyte (β [95% CI] = -0.314 [-1.350 to 0.744]). Averaged over diversity treatments, the endophyte did not affect the number of fescue seedlings established by the end of the experiment (i.e., there was no main effect of the endophyte, $F_{1,143}=0.00$, $P=0.99$). Overall, initial diversity had a negative effect on the number of seedlings ($F_{1,143}=6.43$, $P=0.012$). Patterns for the effect of final diversity paralleled those for initial diversity, with a significantly negative effect of final diversity on the number of fescue individuals in the absence of the endophyte ($r=-0.39$, $P=0.001$), and a nonsignificant effect of diversity in the presence of the endophyte ($r=-0.06$, $P=0.61$; endophyte \times final species diversity, $F_{1,143}=5.40$, $P=0.022$; endophyte $F_{1,143}=0.12$, $P=0.73$; final diversity $F_{1,143}=6.19$, $P=0.014$).

Despite the effects on the number of *L. arundinaceum*, the endophyte did not alter the effect of diversity on the biomass per individual plant (endophyte \times initial species diversity $F_{1,134}=0.67$, $P=0.41$). Overall, higher initial diversity reduced the biomass per individual tall fescue plant (Fig. 4; $r=-0.33$, $F_{1,134}=16.64$, $P<0.0001$), but the endophyte had no effect ($F_{1,134}=0.53$, $P=0.47$). The same pattern was observed when final, rather than initial, diversity was included in the model (endo-

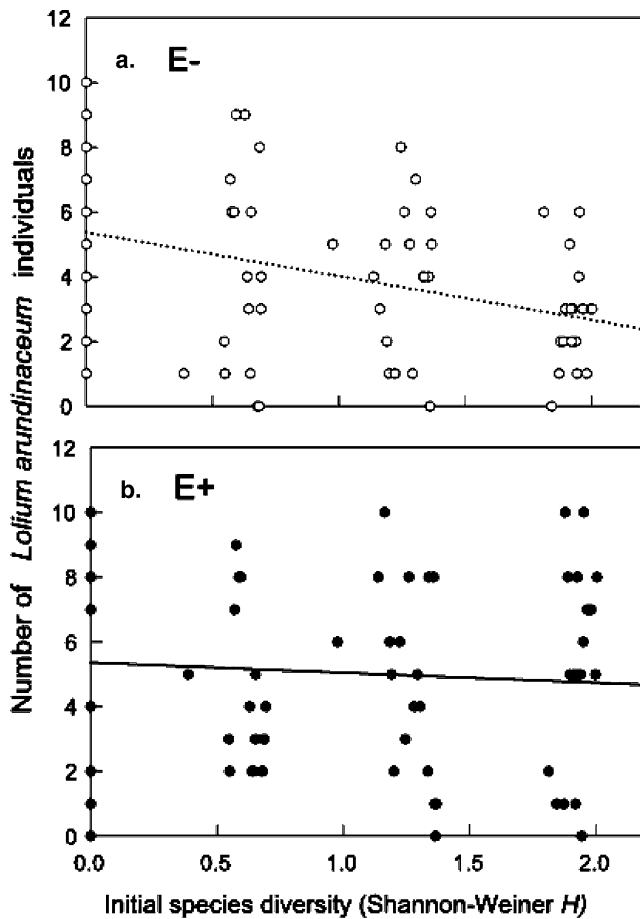


Fig. 3 The number of surviving *L. arundinaceum* individuals by initial plant species diversity **a** without the endophyte, *N. coenophialum* (E^-) (regression: Number = $-1.35 \times$ initial diversity + 5.37, $r = -0.36$, $P = 0.0018$, $n = 72$) and **b** with the endophyte (E^+) (regression: Number = $-0.31 \times$ initial diversity + 5.37, $r = -0.08$, $P = 0.53$, $n = 72$)

phyte \times final species diversity $F_{1,134} = 0.55$, $P = 0.46$; endophyte $F_{1,134} = 0.40$, $P = 0.53$; final diversity $F_{1,134} = 19.15$, $P < 0.0001$).

Total aboveground biomass (a measure of primary productivity) was positively correlated with initial diversity ($r = 0.23$; $F_{1,143} = 7.56$, $P = 0.007$). However, this relationship did not vary with the presence of the endophyte (endophyte \times initial species diversity, $F_{1,143} = 0.09$, $P = 0.77$), nor did the endophyte have an overall effect on total biomass ($F_{1,143} = 0.21$, $P = 0.65$). The same patterns for total aboveground biomass were observed when final, rather than initial, diversity was examined (J. A. Rudgers, W. B. Mattingly, and J. M. Koslow, unpublished data). These results suggest that the endophyte shifts the relative contribution of tall fescue to the community rather than affect the total productivity of the community.

The concurrent increase in total productivity (an increase in the level of competition) with increased initial diversity may be a mechanism driving the effect of diversity on the number of tall fescue that are estab-

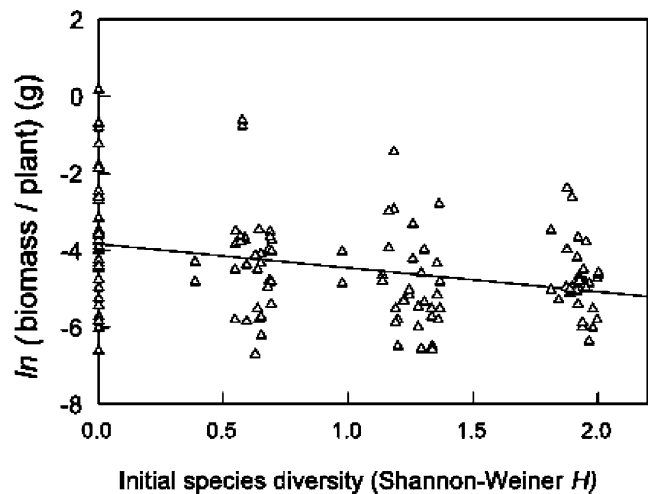


Fig. 4 Biomass per individual *L. arundinaceum* (natural log-transformed) by initial plant species diversity (regression: $\ln(\text{mass}) = -0.62 \times$ initial diversity - 3.84, $r = -0.33$, $P < 0.0001$, $n = 144$). The endophyte, *N. coenophialum*, did not alter this relationship

lished. The presence of the endophyte weakened the correlation between total aboveground biomass (aboveground productivity) and the number of tall fescue individuals that established (total aboveground biomass \times endophyte, $F_{1,143} = 4.34$, $P = 0.039$; total aboveground biomass, $F_{1,143} = 8.84$, $P = 0.0035$; endophyte, $F_{1,143} = 0.23$, $P = 0.63$). In the absence of the endophyte, total aboveground biomass was more strongly negatively correlated with the number of tall fescue ($r = -0.27$, $P = 0.0157$), than in the presence of the endophyte ($r = -0.25$, $P = 0.0272$), suggesting that an increase in competition may underlie the effect of diversity.

Discussion

Our results suggest that mutualistic fungal endophytes can switch the relationship between plant diversity and invasibility. Increases in species diversity reduced the abundance of the invasive grass, *L. arundinaceum*; however, this effect was contingent on the absence of a mutualistic fungal endophyte. Increases in diversity reduced the invader's establishment only when the invader lacked its mutualist. In contrast to the response of *L. arundinaceum* number, the biomass per individual was reduced by diversity regardless of the endophyte treatment. This result suggests that the endophyte may be more important during the initial establishment phase of the invader than during the growth phase following establishment. Regardless of the mechanism, the overall success of the invader in diverse communities (number of individuals established times biomass per individual) depended strongly on the presence of the mutualistic endophyte. Studies on other invasive plants known to host fungal endophytes (e.g., *Agrostis gigantea*, *Elymus*

repens, *Festuca ovina*, *F. rubra*, *L. perenne*, *L. multiflorum*) and on other plant mutualists are needed before we can draw generalizations about how mutualists affect species invasions into diverse communities. In addition, experiments manipulating mutualisms involving resident community members could provide additional insights into the role of mutualists in diversity–ecosystem functioning relationships.

Accounting for the potentially hidden effects of endophytes may help to make future experiments more realistic and enhance predictive power (Rudgers et al. 2004). For example, the viability of endophytes can be lost during long-term or improper seed storage (Rolston et al. 1986; Welty et al. 1987), and experiments using these seeds may not reproduce natural hierarchies of competition. Prior work has shown that > 50% of the Pooidae grasses that are commonly used in studies on plant diversity are known to host systemic, endophytic fungi (Rudgers et al. 2004). In addition, we examined the endophyte status of the prairie grasses in our experiment and found that 60% of the individuals of one species, *E. canadensis*, had a systemic endophyte. Given the potential for endophytes to alter the effects of diversity on ecosystem properties (Rudgers et al. 2004), future investigations using cool season grasses may gain predictive power by knowing the endophyte status of the species involved and determining whether the endophyte is mutualistic with its host.

Mutualistic endophytic fungi may enhance the success of exotic grasses in novel habitats through several mechanisms. Endophytes can enhance hosts' intrinsic competitive ability (Clay et al. 1993), resistance to herbivores and pathogens (Breen 1994; Clay 1996; Clay et al. 1989; Gwinn and Gavin 1992), nutrient acquisition (Lyons et al. 1990; Malinowski et al. 2000), and tolerance to drought stress (Elmi and West 1995; Hill et al. 1996). Endophytes can also affect organisms in the rhizosphere (Matthews and Clay 2001), for example, by reducing mycorrhizal fungi (Chu-Chou et al. 1992). The mechanisms underlying the patterns in our study are currently unresolved. Most likely, the endophyte modifies diversity–invasibility relationships by increasing the competitive ability of its host grass because our experiments were conducted in the absence of herbivores, pathogens, and soil organisms and because plants experienced relatively benign conditions with respect to nutrient and water availability. However, allelopathy cannot be ruled out. In our experiment, in the absence of the endophyte, diversity explained 13% of the variation in the number of invaders surviving per pot, whereas in the presence of the endophyte diversity accounted for less than 1% of variation. We predict that under field conditions (with herbivory, pathogens, and soil microbes, etc.), this difference caused by the endophyte would be even greater due to the negative interactions between endophytes and other plant associates.

Mutualists of all types may play important roles in increasing species' distributions into novel habitats (reviewed by Richardson et al. 2000). For example, in

competition with native plant species, invasive knapweed grew larger in the presence of mycorrhizal fungi than when mycorrhizae were experimentally reduced (Callaway et al. 2004). This effect may be due in part to a transfer of nutrients from the native plants to the invader via the fungi (Carey et al. 2004). In addition, some plant species fail to set seed in novel habitats until pollinators from their native habitat are introduced (reviewed by Richardson et al. 2000). As with protective mutualisms between endophytes and plants, nutritive and dispersal mutualisms may also play important roles in the success of invasive species. Furthermore, mutualisms are predicted to switch the relationship between diversity and ecosystem functioning (Stachowicz et al. 2002; Bruno et al. 2003). Many experiments to test the effects of diversity on invasibility have ignored the role of mutualistic symbionts, such as mycorrhizal fungi or fungal endophytes. Experiments are often conducted under benign conditions, potentially reducing the ability to detect the facilitative interactions among species that may be most important under stressful conditions (e.g., Bertness and Callaway 1994). In this study, we found that more diverse communities can resist invasion by *L. arundinaceum*, but only when it lacks a key mutualist. Integrating mutualistic and facilitative interactions into current ecological theory may afford new insights into factors that extend the distributions and dominance of invasive species.

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