



# Dominant species identity regulates invasibility of old-field plant communities

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Dominant species are known to exert strong influence over community dynamics, although little work has addressed how they affect invasibility. In this study, we examined whether dominant species identity and abundance affected invasibility of old-field plant communities. To quantify invasibility, we added seeds of 19 plant species into plots dominated by one of four different herbaceous perennial species (*Andropogon virginicus*, *Bromus inermis*, *Centaurea maculosa*, or *Solidago canadensis*). We found that, independent of species richness and abiotic variables, plots dominated by *Andropogon* were the least invasible, while *Bromus* and *Centaurea* plots had the highest invasibility. We examined several potential mechanisms by which these dominant species might influence invasibility, and found invasion to increase with decreasing litter biomass and increasing community species richness. The abundance of the dominant species was not a significant predictor of invasion. These results indicate that dominant species identity plays an important role in determining invasibility of plant communities, though exact mechanisms underlying these effects still need to be explored.

Invasibility- in the broadest sense- describes the ease with which any new species establishes in a community. This concept is important for more than just predicting success of invasive exotic species. While growing concern over the negative ecological and economic impacts of non-native species makes understanding what factors drive the invasibility of native communities critical (Lonsdale 1999), understanding the invasibility of non-native communities may enhance the effectiveness of restoration efforts designed to facilitate planned “invasions” of degraded habitats by native species (Seabloom et al. 2003, Suding et al. 2004). More generally, increased insight into the mechanisms driving invasibility in all types of systems will inform studies of succession, community assembly, and the maintenance of community stability (Crawley 1987).

While community invasibility is fundamental to our understanding of community dynamics, including species coexistence (species-packing) and compositional stability (Levine and D’Antonio 1999), factors that control a community’s invasibility are still not well resolved. Most studies examining factors that influence invasibility have focused on how invasion by non-

resident species is influenced by species richness, and have not explicitly examined other components of community structure, such as species dominance and composition (reviewed by Hector et al. 2001, Levine et al. 2004). While many studies have indicated that identities of species in a community can alter invasibility (Smith and Knapp 1999, Dukes 2002, Prieur-Richard et al. 2002), fewer studies have demonstrated that dominant species in particular can regulate invasion, despite the fact that dominant species are known to exert strong influence over community dynamics and ecosystem function (McNaughton and Wolf 1970, Crawley et al. 1999, Grime 2001, Dangles and Malmqvist 2004). While many of the experiments manipulating community species richness do attribute some of the negative relationships between diversity and invasibility to a “sampling effect” (Huston 1997), where increased experimental species richness increased the likelihood of including a strong competitive dominant in the community (Crawley et al. 1999, Hodgson et al. 2002, Lennon et al. 2003, van Ruijven et al. 2003), there are very few studies directly

addressing the role of different competitive dominant species in regulating invasibility.

Further, while Wardle (2001) proposed that the relative abundance of a dominant species, not just its presence, should affect invasibility in both experimental and observational studies, there is some debate over whether communities with high dominance (e.g. large proportion of community biomass or density contributed by a single species) should be more or less invulnerable than communities with high evenness. In part, this depends on whether biomass dominants are also competitive dominants. High dominance in communities may be due to complete use of a limiting resource by the dominant species (Tilman 1982, Robinson et al. 1995), or may indicate underutilization of other resources and so provide a variety of unused niches for minor species (Wilsey and Polley 2002). These mechanisms of dominance should apply to both native and non-native species, allowing us to make predictions about invasion in a wide variety of plant communities. Most evidence for the role of dominant species identity or abundance in mediating invasibility comes from experimental studies, and these have reported mixed results. In a few cases, invasion was positively related to community dominance (Wilsey and Polley 2002, Smith et al. 2004), suggesting that invading species can exploit underused resources, or that the dominant can facilitate invasion. In other cases, invasion declined with increased dominance (Robinson et al. 1995, Smith and Knapp 1999, Lindig-Cisneros and Zedler 2002), with evidence suggesting that this was mediated by strong effects of the dominant on productivity, light or litter.

Experimental studies usually only focus on the ability of a single species to invade synthetic communities constructed from a pre-determined species pool (Naeem et al. 2000), or confound manipulation of community species richness with disturbance caused by species removal (Smith et al. 2004). Because different processes may influence the assembly of natural and experimental communities (Ricklefs 2004), there is a need for experiments in natural systems to address the role of dominance in regulating invasion.

In this study, we asked three questions: Does the identity of the dominant species affect invasibility? Does the relative abundance of the dominant affect invasibility? And by what mechanisms do dominant species alter invasibility? We examined these effects of dominant species after accounting for effects of other factors such as community species richness, biomass, and soil properties. We tested these questions in a seed-addition study in three mid-successional old-field plant communities in southwest Michigan which were similar in vegetation composition.

## Methods

### Experimental design

In 2003, we established 96 1 × 1 m plots across three old-field sites (32 plots in each site) at Michigan State University's W. K. Kellogg Biological Station (KBS) in southwest Michigan USA (Kalamazoo County; 42°24'N, 85°24'W). The three sites had similar soils (Kalamazoo sandy loam) and had been abandoned from agriculture 25 (sites 1,2) and 40+ (site 3) years prior to establishment of this experiment. Sites 1 and 2 had been mowed occasionally following abandonment; site 3 had been unmanaged.

All sites had similar assemblages of perennial forbs and grasses, and within each site there were vegetation patches dominated by different species. These patches ranged in size from 5–50 m<sup>2</sup>, and were separated from other patch types by at least 5 m. We selected four species that were common in all sites—*Andropogon virginicus*, *Bromus inermis*, *Centaurea maculosa* or *Solidago canadensis*—and laid out the 1 × 1 m plots within patches dominated by each of these four species (hereafter referred to by genus name). For each of the four dominant species, we haphazardly laid out eight plots in each site.

The four dominant species represented a range in functional types and nativity. *Bromus inermis* is a non-native C<sub>3</sub> clonal grass, *Centaurea maculosa* is a non-native forb, *Solidago canadensis* is a native clonal forb, and *Andropogon virginicus* is a native C<sub>4</sub> bunch grass. We defined dominance as ≥40% relative cover of the dominant species in the plot based on visual estimates in August 2003 using a cardboard square that represented 2% cover for reference. This was an arbitrary, but relatively effective, distinction of dominant species within the field. Due to haphazard animal disturbances and shifts in community composition from 2003 to the spring of 2004, ten of the 96 plots were dropped from later analyses.

In 2004, we added 50 seeds of 19 different plant species to a 0.25 × 0.5 m subsection of each plot in early spring (March) to take advantage of possible freeze/thaw requirements needed for germination. The species added were all common to old-fields and grasslands of SW Michigan (Rabeler 2001) and represented a variety of functional types and nativity (Table 1). These species were chosen based on seed availability, seed size (no very large or very small seeds), and plant family (Poaceae, Asteraceae, or Fabaceae only as some control for phylogenetic relationships). In August 2004, we censused the plots to determine which species had seedlings established in the seed-added plots. While most species we added as seed were not present in our experimental sites, we censused seedlings in 0.25 × 0.5 m paired adjacent control subplots in

Table 1. Species added as seed to experimental plots.

Species	Life form	Plant family	Origin
<i>Achillea millefolium</i>	forb	Asteraceae	native
<i>Andropogon gerardii</i>	C <sub>4</sub> bunchgrass	Poaceae	native
<i>Bromus inermis</i>	C <sub>3</sub> clonal grass	Poaceae	non-native
<i>Bromus kalmii</i>	C <sub>3</sub> bunchgrass	Poaceae	native
<i>Calamagrostis canadensis</i>	C <sub>3</sub> clonal grass	Poaceae	native
<i>Centaurea maculosa</i>	forb	Asteraceae	non-native
<i>Coreopsis lanceolata</i>	forb	Asteraceae	native
<i>Dactylis glomerata</i>	C <sub>3</sub> bunchgrass	Poaceae	non-native
<i>Desmodium canadensis</i>	legume	Fabaceae	native
<i>Echinacea pallida</i>	forb	Asteraceae	native
<i>Elymus canadensis</i>	C <sub>3</sub> clonal grass	Poaceae	native
<i>Lespedeza capitata</i>	legume	Fabaceae	native
<i>Liatris aspera</i>	forb	Asteraceae	native
<i>Muhlenbergia racemosa</i>	C <sub>4</sub> clonal grass	Poaceae	native
<i>Panicum virgatum</i>	C <sub>4</sub> clonal grass	Poaceae	native
<i>Poa pratensis</i>	C <sub>3</sub> clonal grass	Poaceae	non-native
<i>Ratibida pinnata</i>	forb	Asteraceae	native
<i>Schizachyrium scoparium</i>	C <sub>4</sub> bunchgrass	Poaceae	native
<i>Solidago nemoralis</i>	forb	Asteraceae	native

order to quantify any seedling establishment from the seedbank and local dispersal. To remove any confounding effects of the seedbank or natural dispersal on our measure of invasibility, we subtracted the number of seedlings of each species in the control subplots from the number of seedlings in the seed-addition plots. To compare our results with other studies, we used three measures of invasibility: 1) the net total number of *native* seedlings established in the seed-added subplot, 2) the net total number of *non-native* seedlings established, and 3) total number of species (maximum of 19) established in these plots.

### Environmental correlates

To assess whether plots dominated by different species or located in different sites differed in other variables that might affect invasibility, we measured light levels below the vegetation (photosynthetic photon flux density, PPFD, intercepted by the canopy), soil moisture, available inorganic nitrogen, aboveground plant biomass, and plant community species richness and evenness in or near each plot. We determined PPFD in each plot late in the growing season (August) using a Sunfleck Ceptometer (Decagon Devices, Inc.). Within each plot we took three PPFD measures within  $\pm 2$  h of solar noon in full sun (1 m above the plots) and at three points at ground level (under the vegetation and litter). We averaged these three measures to obtain an estimate of the percentage of full sunlight intercepted by the vegetation for each plot.

We measured available soil inorganic nitrogen and soil moisture in each plot in May 2004. Two soil cores (10 cm depth, 1.9 cm diameter) were taken from areas immediately adjacent to the plots. Samples were placed on ice in the field and then processed in the lab within 24 h of sampling. Soils were sieved (2 mm sieve) to remove vegetation, roots, and rocks, and sub-sampled for gravimetric soil moisture and inorganic nitrogen content within 24 h of sampling. Gravimetric soil moisture was determined by weight loss after drying 10–15 g soil at 105°C for 24 h. For the nitrogen assays, we extracted 20 g fresh soil in 50 ml 1M KCl. These samples were shaken for 1 min, settled for 24 h at room temperature, and filtered through a 1- $\mu$ m Gelman glass filter. The  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations of the extracts were determined using an Alpkem auto-analyzer (Robertson et al. 1999).

In August, we quantified composition in each plot from visual estimates of relative cover of all plant species using a reference square of 2% cover. Rare species that we missed in the initial visual estimate were later recorded as <1% cover. Because of slight variations in estimates, percent cover data were standardized to add to 100%. Species richness and evenness of all vascular plant species were calculated from these visual estimates of community composition. Evenness was calculated as  $E = 1/DS$  where  $S$  is species richness and  $D$  is Simpson's dominance (Simpson 1949) where  $x_s$  is the abundance of the  $s$ th species:

$$D = \sum_{s=1}^s (x_s / \Sigma x)^2$$

This metric is independent of species richness and more responsive to changes in dominant than rare species abundance (Smith and Wilson 1996), and so served as a measure of relative dominance. Also in mid-August (peak biomass), we estimated aboveground productivity from harvests of biomass and litter taken from a 0.25  $\times$  0.50 m area immediately adjacent to each plot in order to minimize disturbance to the plots for future experiments. Samples were dried (48 h at 65°C) and then weighed.

### Data analyses

To examine effects of dominant species identity on invasibility in these communities, as well as understand potential mechanisms by which dominant species may affect invasibility, we used mixed-model ANOVA and ANCOVA with patch type as the main (fixed) effect and site as a random block. As we had no a priori expectations that response patterns would differ across the sites, we did not specify the interaction term in the model (see Newman et al. 1997 for justification of this choice). For the ANCOVA, we used aboveground

biomass, litter biomass, light levels (%PPFD intercepted), total soil inorganic nitrogen, soil moisture, intact community species richness, and community evenness as covariates. These variables showed no evidence of multicollinearity, with variance inflation factors (VIF) all less than 1.7 in preliminary analyses. Count data were log transformed ( $\ln(x+1)$ ) in order to meet normality assumptions for analyses. All analyses were performed using the PROC MIXED statement in SAS 9.1 (SAS Institute 1999–2001).

## Results

### Dominant species identity and invasibility

We used ANOVA to examine effects of dominant species on invasibility. Invasibility differed among plots with different dominant species (Table 2), with *Andropogon* plots having lower numbers of invading non-native seedlings than *Bromus* or *Centaurea* plots and lower numbers of native seedlings than *Centaurea* plots. *Andropogon* and *Solidago* plots had fewer invading species than *Centaurea* plots (Fig. 1). The site block was not significant (Table 2).

To examine possible mechanisms by which these dominant species alter invasibility, we used an ANCOVA with aboveground biomass, litter biomass, light levels (% PPFD intercepted), total soil inorganic nitrogen, soil moisture, intact community species richness, and community evenness as covariates. Dominant species identity was still a significant predictor of invasion even after accounting for these other variables (Table 2). *Andropogon* plots still had lower numbers of invading non-native seedlings than *Bromus* or *Centaurea* plots and fewer native seedlings than *Centaurea* plots. *Andropogon* plots also had fewer invading species than *Centaurea* plots (Fig. 1).

Most of the covariates included in the ANCOVA, including community evenness, were not significant predictors of invasion. However, litter biomass, community species richness, and soil nitrogen, along with dominant species identity, were significant predictors of at least one measure of invasibility (Table 2). Community species richness was a predictor of numbers of non-native invading seedlings, while litter was an important predictor of invading seedling species richness and numbers of native seedlings. Soil nitrogen was also a predictor of native seedling invasion (Table 2). Least-squares fit lines indicated that invasion generally decreased as litter biomass increased and as community species richness decreased. The effect of soil nitrogen depended on the identity of the dominant species: plots dominated by *Solidago* had lower invasion at higher nitrogen levels while all other plots had higher invasion at higher nitrogen levels (Fig. 2).

Table 2. Results for ANCOVA of effects of community dominance type on three measures of invasibility. Values for the random block factor 'site' are from covariance parameter estimates (Z-estimates). Significant variables ( $p < 0.05$ ) are in bold.

	DF	Seedling species richness				In (non-native seedlings)				In (native seedlings)			
		MS	F	p	MS	F	p	MS	F	MS	F	p	p
Simple ANOVA													
Patch type	3	14.65	3.60	<b>0.017</b>	2.88	4.70	<b>0.005</b>	1.81	3.60	1.81	3.60	0.079	
Site	2	1.06	0.86	0.389	0.07	0.77	0.442	0.23	0.88	0.23	0.88	0.378	
Residual	81	3.96			0.61			0.67					
ANCOVA													
Patch type	3	8.45	2.35	0.079	2.50	4.27	<b>0.008</b>	1.78	2.96	1.78	2.96	<b>0.038</b>	
Site	2	1.43	0.91	0.362	0.07	0.74	0.457	0.30	0.93	0.30	0.93	0.354	
Abvgd biomass	1	0.43	0.08	0.782	0.06	0.22	0.644	0.01	0.01	0.01	0.01	0.934	
Litter	1	20.9	5.69	<b>0.020</b>	1.09	1.69	0.198	3.93	6.48	3.93	6.48	<b>0.013</b>	
Species richness	1	6.86	2.34	0.131	2.31	5.15	<b>0.026</b>	0.45	0.98	0.45	0.98	0.327	
Evenness	1	11.8	3.08	0.084	1.26	1.88	0.175	0.70	1.03	0.70	1.03	0.314	
Soil moisture	1	0.57	0.17	0.685	0.17	0.32	0.574	1.38	2.38	1.38	2.38	0.127	
Light avail.	1	3.11	0.62	0.434	0.02	0.21	0.649	0.11	0.08	0.11	0.08	0.776	
Soil nitrogen	1	0.84	0.16	0.692	0.09	0.07	0.795	2.93	4.69	2.93	4.69	<b>0.034</b>	
Residual	73	3.48			0.55			0.58					

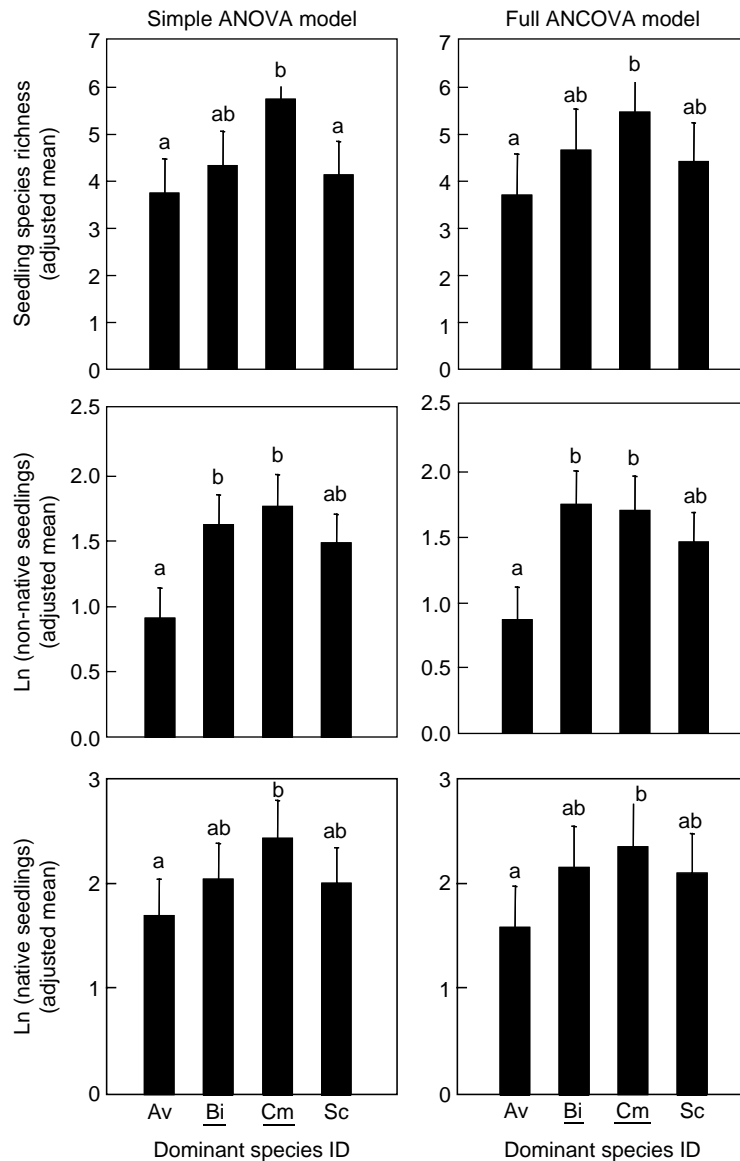


Fig. 1. Comparative invasion success following seed addition (19 species added) into plots dominated by the four different herbaceous perennial species. Data shown are adjusted means from the ANOVA and ANCOVA models for all three measures of invasibility. Letters indicate significant differences at the  $p < 0.05$  level (except for the ANOVA with native seedlings and the ANCOVA with seedling species richness, which have  $p < 0.08$ ), using Tukey multiple comparisons tests. Dominant species are abbreviated *Andropogon virginicus* (Av), *Bromus inermis* (Bi), *Centaurea maculosa* (Cm), and *Solidago canadensis* (Sc). The non-native dominant species are underlined. Error bars indicate one SE of the mean.

## Discussion

### Dominant species effects

In this experiment we found that identity of dominant species affected local invasibility, with *Andropogon*-dominated plots being the least invasible, and *Centaurea* and *Bromus* plots tending to be the most highly invaded. Native and non-native species had similar

patterns of invasion success. The difference among dominant species was evident even after accounting for other variables, such as aboveground biomass, soil nitrogen, and litter, which can also affect invasibility. This indicates that dominant species are influencing invasion through mechanisms that were not measured in this study. While it is difficult to separate cause-and-effect of environment and plant community in this study (only an experiment manipulating these variables

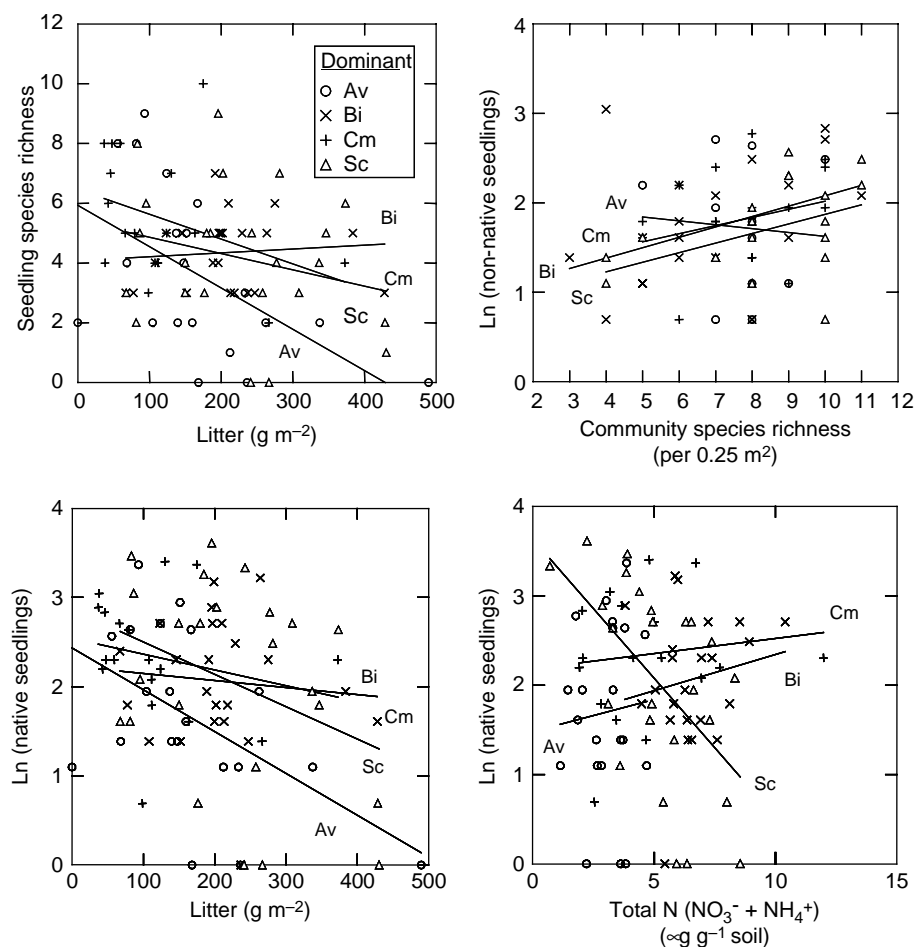


Fig. 2. Relationships between the different measures of invasibility and their significant covariates from the full ANCOVA models. Least-squares linear smoothers are shown to indicate the direction of relationships for each dominant species patch type.

would directly demonstrate this), our study does point to several possible mechanisms regulating community invasibility in natural field conditions.

### Possible mechanisms

We specifically measured aboveground biomass, litter, light levels, soil inorganic nitrogen, soil moisture, and intact community species richness in this experiment because we expected that they would be important mechanisms that could alter invasibility based on findings from other studies (Foster 1999, Franzen 2001). For example, native C4 grasses such as *Andropogon* are known to draw down soil nitrogen levels, which can prevent establishment by less competitive invaders (Fargione et al. 2003). Though interestingly, in our study effects of soil nitrogen varied with dominant species identity. It is also been demonstrated that certain dominant species regulate aboveground

productivity in grassland systems (Smith and Knapp 2003), and productivity has been shown to regulate invasion in several studies (Foster and Gross 1998, Suding and Goldberg 1999, Hector et al. 2001). A review of invasion studies by Hector et al. (2001), as well as several more recent studies, (Foster et al. 2002, Prieur-Richard et al. 2002, Hofmann and Isslstein 2004) indicate that light, soil nitrate, and water availability are all important factors regulating invasibility of terrestrial plant communities. However, only litter biomass, soil nitrogen, and community species richness were significant predictors of invasion in our experiment. Further, no one factor was a significant predictor of all three measures of invasion and the direction of the relationships varied with dominant species identity.

This result is supported to some extent in other studies. For example, litter abundance is often a related to invasibility, but not necessarily in predictable directions (Facelli and Pickett 1991, Xiong and Nilsson

1999). Litter can inhibit seedling establishment by reducing light levels and creating a physical barrier to seedling emergence and growth (Maret and Wilson 2005) or by harboring seed predators (Reader 1991). However, litter can also promote seedling establishment by retaining soil moisture (Eckstein and Donath 2005) or protecting seeds from extreme environmental conditions. Our observations that litter biomass reduced seedling establishment agrees with results from Foster (1999), who manipulated litter amounts in similar southwest Michigan old-fields and found that it decreased seedling emergence of two native grasses.

It is possible that factors not measured in this study, particularly those that operate belowground, are causing the differences in invasibility we observed among plots dominated by different species in these fields. For example, *Andropogon* is known to be a strong competitor for belowground resources and is strongly mycorrhizal (Hartnett et al. 1993). If soil phosphorus levels are greatly reduced in *Andropogon* patches, the greater competitive ability of *Andropogon* in the presence of mycorrhizae may explain why areas dominated by this species had low invasibility. Other studies have reported that individual species effects on invasion may be due to allelopathy (Callaway et al. 2004) or feedbacks between plant species and associated soil biota, microbes, or soil invertebrates (Klironomos 2002, van Ruijven et al. 2003). In this study, we did not test for these types of species-specific effects, and there is a definite need for further in-depth studies of plant–soil interactions and how these may impact invasibility.

It is also possible that other species that consistently co-occur with the dominant species in these communities are driving the species-correlated differences in invasibility that we observed in this study. Lindig-Cisneros and Zedler (2002) found that it was the abundance of particular subordinate species that reduced invasion by reed canary grass more than the identity of the dominant species in fen habitats. Other studies have reported that rare species are important in reducing invasibility of plant communities (Lyons and Schwartz 2001, Zavaleta and Hulvey 2004). While all sites in our study had similar species compositions overall, there were detectable differences in species composition among the four patch types. For example, in all sites two  $C_3$  grasses, *Danthonia spicata* and *Phleum pratense*, only occurred in *Andropogon*-dominated patches, whereas *Stellaria media* and *Chrysanthemum leucanthemum*, both dicots, occurred most often in *Solidago*-dominated plots. However, no particular subordinate species was consistently detected in all plots for a given dominant species, so it is unlikely that subordinate species were important in determining the species-specific differences in invasibility that we detected in these fields.

## Species richness

We expected to find that species rich plots would be less invulnerable than species poor plots due to competitive interactions (niche complementarity, Tilman 1997); negative relationships between species richness and invasion have been reported in many experimental studies (Knight and Reich 2005), though not in all (Robinson et al. 1995, Stohlgren et al. 1999). However, we found that local species richness was positively related to invasion by non-native species in our plots (Table 2, Fig. 2). Most studies that have reported positive relationships between community species richness and invasion (or abundance of non-native species) have focused on large spatial scales, which reinforced the hypothesis that landscape-level environmental variability drives the relationship between diversity and invasion. Because our study plots were similar in size to those used in other experimental studies and were distributed across a relatively small area (2–3 ha), it seems unlikely that landscape level variability in environmental factors (e.g. precipitation, soil type) is causing these patterns. It may be that the 'diversity begets diversity' hypothesis that is commonly invoked to explain positive relationships at larger spatial scales (Stohlgren et al. 1999) may also operate at smaller spatial scales. For example, Palmer and Maurer (1997) have proposed that a high diversity of interacting subordinate species may create increased micro-heterogeneity, allowing even more species to invade. More work examining other possible mechanisms that might promote diversity at small and large spatial scale is needed.

## Relative abundance of dominants

Although we detected significant effects of dominant species identity on invasibility, the relative abundance (evenness) of these species in a plot did not generally affect invasibility (Table 2). The lack of a relationship between species abundance and invasibility in this study is surprising, given results from other experimental studies that find that dominance (relative abundance of the dominant species) to be an important predictor of invasion (Robinson et al. 1995, Prieur-Richard et al. 2002, Smith et al. 2004). Also, some recent theory predicts that community evenness has an important role in ecosystem functioning (Nijs and Roy 2000) and so would be expected to influence invasion. Our results do not negate the importance of abundance, but do suggest that beyond a certain threshold (e.g. 40% cover), relative cover aboveground of the dominant species may not have a detectable effect on community functioning. It is possible that at the plot size we used in this study (0.25 m<sup>2</sup>), belowground effects from the

dominant species were similar regardless of whether they had 40% or 90% cover. Belowground competitive neighborhoods may be much larger than above-ground neighborhoods (Hawkes and Casper 2002), and at least one study has shown that belowground competition may be independent of aboveground diversity (Cahill 2003).

## Conclusion

Understanding the factors influencing dynamics of species invasion or colonization is essential for habitat protection and restoration. Our work has shown that the identity of dominant species can be an important regulator of invasion, even beyond the dominant species' relationship with environmental factors such as productivity and soil resource availability that are usually linked with invasibility of communities. Although we only examined the first-year seedling establishment of invading species in a perennial old-field system, these results are still important as they show the potential for individual species to have strong effects on community processes. Also, several studies of invasive species and of plants in general have shown that seedling recruitment can be a key life stage in population growth (Silvertown et al. 1993, Shea and Kelly 1998, Parker 2000). Knowing whether dominant species will have different effects as initial environmental 'filters' (Booth and Swanton 2002) on invasion may help managers and practitioners select effective species to use in restoration efforts to reduce or limit further invasions by non-natives or promote establishment of native species (Seabloom et al. 2003, Suding et al. 2003). For example, in our study plots dominated by the non-native species *Bromus* and *Centaurea* had high invasibility by both native and non-native species. This suggests that restoration of sites dominated by these species could be facilitated by reverse "invasions" of native species; however high invasibility may also be a mechanism whereby positive feedbacks facilitate further invasions by exotics (e.g. "invasional meltdown", Simberloff and Von Holle 1999). While ecologists continue to search for generalities regarding community invasibility, it is important to remember that species identity, as well as diversity, can play a large role in community dynamics.

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