



Evenness–invasibility relationships differ between two extinction scenarios in tallgrass prairie

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Experiments that have manipulated species richness with random draws of species from a larger species pool have usually found that invasibility declines as richness increases. These results have usually been attributed to niche complementarity, and interpreted to mean that communities will become less resistant to invaders as species go locally extinct. However, it is not clear how relevant these studies are to real-world situations where species extinctions are non-random, and where species diversity declines due to increased rarity (i.e. reduced evenness) without having local extinctions. We experimentally varied species richness from 1 to 4, and evenness from 0.44 to 0.97 with two different extinction scenarios in two-year old plantings using seedling transplants in western Iowa. In both scenarios, evenness was varied by changing the level of dominance of the tall grass *Andropogon gerardii*. In one scenario, which simulated a loss of short species from *Andropogon* communities, we directly tested for complementarity in light capture due to having species in mixtures with dissimilar heights. We contrasted this scenario with a second set of mixtures that contained all tall species. In both cases, we controlled for factors such as rooting depth and planting density. Mean invader biomass was higher in monocultures ($5.4 \text{ g m}^{-2} \text{ week}^{-1}$) than in 4-species mixtures ($3.2 \text{ g m}^{-2} \text{ week}^{-1}$). Reduced evenness did not affect invader biomass in mixtures with dissimilar heights. However, the amount of invader biomass decreased by 60% as evenness increased across mixtures with all tall species. This difference was most pronounced early in the growing season when high evenness plots had greater light capture than low evenness plots. These results suggest that the effect of reduced species diversity on invasibility are 1) not related to complementarity through height dissimilarity, and 2) variable depending on the phenological traits of the species that are becoming rare or going locally extinct.

Several neighborhood scale experiments have found that increased species richness increases invasion resistance (Tilman 1997, Knops et al. 1999, Hector et al. 2001, Kennedy et al. 2002, but see Lavorel et al. 1999). However, the interpretation of these experiments and their relevance to real-world situations have been questioned (Lonsdale 1999, Crawley et al. 1999, Wardle 2001, Stohlgren et al. 2003, Brown and Peet 2003, Zavaleta and Hulvey 2004). One interpretation is that the greater resistance to invasion observed in more diverse plots results from niche complementarity (Knops et al. 1999, Naeem et al. 2000, Kennedy et al. 2002). Plots with more species are said to more efficiently utilize resources such as light and nutrients, leaving fewer potential opportunities for invaders

(Fargione et al. 2003, Fargione and Tilman 2005). In contrast, Crawley et al. (1999) and Wardle (2001) have argued that the observed pattern is actually the result of the sampling effect, or the greater likelihood of more diverse plots containing one of the few aggressive species that actually drive a community's ability to resist invasion. It is now generally accepted that these interpretations are not mutually exclusive, as both niche complementarity and the sampling effect could be acting at the same time (Hooper et al. 2005).

To understand the relationship between diversity and invasibility, as it might exist in a natural setting, it is necessary to design experiments that move beyond random manipulations and consider more ecologically

realistic extinction and rarity scenarios (Zavaleta and Hulvey 2004). Kennedy et al. (2002) and others have argued that the increased resistance to invasion observed with increasing species richness in experimental plots means that natural systems will become more invulnerable as species become extinct (i.e. richness declines). However, the relevance of many neighborhood-scale studies of diversity and invasibility to natural systems can be questioned on the grounds that species richness in the experiments is usually manipulated by seeding plots with differing numbers of species randomly selected from a species pool. Therefore, these studies are only directly relevant to situations where species are randomly going extinct (Zavaleta and Hulvey 2004, Bunker et al. 2005). It is not clear if results from such experiments are applicable to natural systems, as extinctions are unlikely to be random events (Leach and Givnish 1996, Fischer and Stocklin 1997, Wardle 1999, Duncan and Young 2000, Chapin et al. 2000, Wilsey and Polley 2004, Zavaleta and Hulvey 2004). Leach and Givnish (1996) found that short forbs and legumes went locally extinct more frequently than tall and non-leguminous forbs in small isolated prairie remnants in Wisconsin. Current grassland management practices also tend to favor warm season (C_4) grasses over forbs and cool season (C_3) grasses (Collins et al. 1998, Martin et al. 2005), which leads to low diversity grasslands with many forbs being extremely rare. Lyons and Schwartz (2001) removed rare species from grassland plots in California and found that this increased the ability of the invader *Lolium multiflorum* Lam. to establish when it was seeded into the plots. In another California grassland experiment, Zavaleta and Hulvey (2004) manipulated grassland species richness in a manner designed to mimic changes that might be observed in long-term data. When the invader *Centaurea solstitialis* L. was seeded into the plots, increased species richness reduced *Centaurea* biomass much more than had been predicted based on previous trials that manipulated richness levels with random species losses. Recent modeling work has also shown that different extinction scenarios can be expected to have dramatically divergent effects on ecosystem processes (Bunker et al. 2005). A more ecologically realistic approach to biodiversity–ecosystem function research has been advocated as a means to make the results of basic ecological research more relevant to conservation (Schwartz et al. 2000, Srivastava and Vellend 2005).

Another question about the interpretation of these experiments arises from the use of species richness as a surrogate for diversity (Stirling and Wilsey 2001). Richness alone does not completely account for the diversity of a system, as it does not include relative abundance or rarity and in many cases is only weakly correlated with them (Stirling and Wilsey 2001, Wilsey et al. 2005a). Diversity has both richness and evenness

components. However, very few studies of diversity and invasibility have considered evenness, dominance or other measures that incorporate relative abundance. In one of the few studies that manipulated evenness, Wilsey and Polley (2002) used four grassland species and found that plots with higher evenness tended to be less invaded. Additionally, Smith et al. (2004) found that invasibility increased with dominance by warm season grasses, and that there was no relationship between invasibility and richness. Examining the effects of evenness upon invasibility may be more directly applicable to natural systems than studies that look at richness alone, because species often become rare but not extinct (Wilsey and Potvin 2000, Chapin et al. 2000). Manipulating evenness as opposed to richness also has the benefit of removing the sampling effect because diversity can be changed while still including the same species in mixtures (Wilsey and Potvin 2000, Loreau et al. 2001, Wilsey and Polley 2002).

Our study used experimental plots to test the hypothesis that increased diversity leads to increased resistance to invasion at the neighborhood scale due to greater niche complementarity. We experimentally manipulated species evenness within mixtures in a manner designed to mimic two rarity/extinction scenarios known to occur in prairies. By varying evenness through changes in the dominance of *Andropogon gerardii* (big bluestem), we were able to fill varying proportions of total niche space. In the first scenario, short species become rare and then are lost from communities dominated by *Andropogon gerardii*, as has been observed in small isolated remnant prairies (Leach and Givnish 1996). This may have impacts on invasibility due to a reduction in species richness and dissimilarity (Nijs and Roy 2000). Greater dissimilarity in height can be related to increased net primary productivity (Naeem et al. 1994, Wilsey and Potvin 2000). By varying dissimilarity in height, we were able to directly test the role of one form of niche complementarity in determining the degree of resistance to invasion. In the second scenario, only tall species were included in the mixture, and tall subordinate species abundance was reduced as *Andropogon gerardii* increased in dominance across treatments. This follows a pattern often observed in prairies, where management (e.g. frequent spring fire) can cause one or a few tall warm season grasses to become extremely dominant (Collins et al. 1998, Howe 2000, Martin et al. 2005).

In both scenarios, forbs decreased in abundance with increased grass dominance, which is known to happen in many prairies under management regimes with frequent spring fires and no grazing (Towne and Owensby 1984, Collins et al. 1998, Howe 2000). Both scenarios were designed so that *Andropogon gerardii* became more dominant as evenness decreased.

This is ecologically realistic, as *Andropogon* is often a dominant species in tallgrass prairies, and it has been observed to become especially dominant in reconstructed prairies (Sluis 1999, Howe 2000, Martin et al. 2005). The evenness levels used bracketed the differences typically observed between restored prairies, which generally have low evenness and high dominance by C_4 grasses, and remnant prairies, which tend to have a more even mix of grasses and forbs (Martin et al. 2005, Table 2).

We predicted that plots with higher diversity, either richness (monocultures versus mixtures) or evenness, would be less invaded than plots with lower diversity. We also predicted, due to greater niche complementarity, that plots containing more height dissimilarity (i.e. those plots with both tall and short species present, Fig. 1) would be less invaded than plots containing more similar heights among species.

Methods

Study site and species used

The experiment was conducted on a hill in an abandoned pasture at Iowa State University's Western Research Farm, which is located in Monona County in the loess hills region of Iowa. The pasture had not been grazed for several years and had not been fertilized in at least a decade. The dominant species in the pasture prior to the establishment of our plots was the exotic grass smooth brome (*Bromus inermis*).

We used six species native to the loess hills in our plots: the tall, deeply rooting C_4 grass *Andropogon gerardii* and the tall, shallowly rooting, C_4 grass *Schizachyrium scoparium*, the short, shallowly rooting C_4 grass *Bouteloua gracilis*, the tall, shallowly rooting forb *Heterotheca villosa*, the tall, deeply rooting forb *Salvia azurea*, and the short, shallowly rooting forb

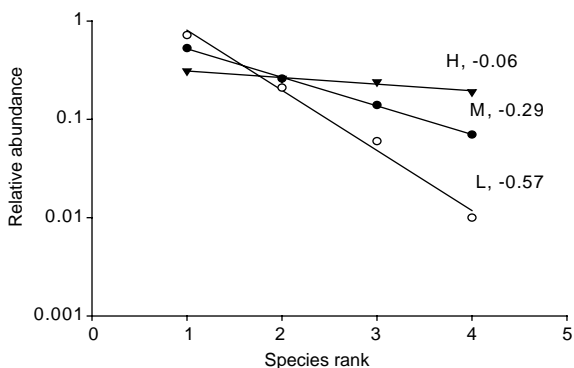


Fig. 1. Planted log rank–relative abundance slopes in the high (H), medium (M), and low (L) evenness treatments in a field experiment in Western Iowa.

Liatriis punctata. Relative heights and rooting depths were available from plant keys and published papers for all of these species (Sun et al. 1997, Craine et al. 2002) (Table 1). It was especially important to control rooting depth so that height dissimilarity could be tested without this confounding variable. Thus, we were limited to species with published rooting depths. We verified that species we considered tall were actually taller than our short species by measuring the heights of at least three plants in each plot in August of each sampling year (Table 1).

Experimental plots

All plots were 1 m² and were established by removing the smooth brome with shallow tillage and then planting small, equal-size transplants at a density of 72 plants m⁻². This density was chosen based on average densities that we sampled in a nearby loess hills prairie remnant (42.10° N, 95.97° W). We surveyed eight 1 m² plots 1.5 months after a spring fire, when individuals could be differentiated, and found an average density of 68.5 plants m⁻² (range of 45–94). A random sample of transplants at the time of planting in 2003 averaged 0.6 g plant⁻¹ and did not vary among species ($F_{5,30} = 1.7$ p = 0.17). All transplants were grown in potting soil in 4-inch pots, with several plants per pot, in an ISU greenhouse. Once planted in the field, the transplants were watered once to facilitate survival, but remained un-watered thereafter. The plots were kept weeded and allowed to establish for one growing season, with data collection occurring in the second season. Corridors between plots were seeded with the grass *Bouteloua curtipendula*.

Each of the six species used was planted in monoculture plots. Our two rarity/extinction scenarios were set up in two sets of mixture plots (Table 1). One set of mixtures contained all tall species (T-plots), and the other set contained both tall and short species (D-, or dissimilar plots). Species richness (4) was constant across all mixtures, but there were high, medium and low evenness treatments. T-plots contained *Andropogon*, *Salvia*, *Schizachyrium* and *Heterotheca*. D-plots contained the tall species *Andropogon* and *Salvia*, and the short species *Bouteloua* and *Liatriis* (Table 1).

Evenness treatments

Species evenness of mixtures was varied by planting species with relative abundances in a way that would change the slope of species rank–abundance relationships (Fig. 1; Wilsey and Polley 2004). Rank–abundance slopes are often used as a diversity measure that encompasses both richness and evenness (Tokeshi

Table 1. Number of individuals transplanted into experimental plots in a field experiment that varied species richness (1 or 4 species), and evenness (high or 'H', medium 'M', or low 'L', quantified with Simpson's evenness or $[(1/\sum p_i^2)]/S$), with evenness being varied by changing the dominance of *Andropogon gerardii* (i.e. number of *Andropogon* individuals/total individuals). The height column shows the measured mean height (cm) reached by each species in the experiment (the standard deviation is in parentheses). The rooting depth column gives the rooting depth classification.

Species	Height	Root depth	Plot Type						
			All tall			Dissimilar heights			<i>Andropogon</i> Monoculture
			H	M	L	H	M	L	
<i>Andropogon</i>	133.2 (18.0)	deep ^{1,2}	22	38	52	22	38	52	72
<i>Salvia</i>	94.5 (17.3)	deep ²	19	19	15	19	19	15	
<i>Bouteloua</i>	44.6 (8.8)	shallow ^{1,2}				17	10	4	
<i>Liatris</i>	42.0 (10.5)	shallow ²				14	5	1	
<i>Schizachyrium</i>	84.1 (14.8)	shallow ^{1,2}	17	10	4				
<i>Heterotheca</i>	96.9 (12.0)	shallow ²	14	5	1	–	–	–	–
Total			72	72	72	72	72	72	72
Dominance			0.31	0.53	0.72	0.31	0.53	0.72	1
Evenness			0.97	0.67	0.44	0.97	0.67	0.44	undefined

¹Craine et al. 2002

²Sun et al. 1997

1993), but when species richness is held constant, as it was in our mixtures, slopes of rank–abundance relationships measure evenness alone. Our D-plots were planted so that the short species *Bouteloua* and *Liatris* decreased in abundance as evenness declined. In T-plots *Heterotheca* and *Schizachyrium* decreased in abundance as evenness declined. In both T and D-plots *Andropogon* abundance increased as evenness declined (Fig. 1, Table 1).

We based slopes of the rank–abundance relationships on a new analysis of data collected by Martin et al. (2005) (Table 2). Our treatments bracketed the observed differences between restored and remnant prairies, with the observed rank–abundance slopes in restored prairie falling between our low and medium evenness plots and the observed values in remnants falling between our medium and high evenness plots (Fig. 1, Table 2). All plots were inventoried during June of the year they were sampled, and observed rank–abundance relationships and *Andropogon* dominance did not differ significantly from planted levels ($p > 0.15$).

Table 2. Mean slopes for rank–abundance (\log_{10} [relative biomass] \times species rank) relationships among three remnant (Wilsey et al. 2005b) and one restored tallgrass prairie (Neal Smith National Wildlife Refuge) in southern Iowa. Letters denote differences (a priori contrasts from Anova, $P < 0.001$) between the three remnants ($n = 8$ per remnant) and the restoration ($n = 8$) within dates. These are new results based on data collected by Martin et al. (2005).

Sampling time	Morris	Rolling	Sheeder	Neal Smith
June 2003	–0.14 ^a	–0.18 ^a	–0.17 ^a	–0.33 ^b
August 2003	–0.16 ^a	–0.22 ^a	–0.18 ^a	–0.41 ^b

Trial and block design

The experiment was conducted in two separate trials, with 36 plots per trial. Each trial consisted of three complete blocks, one each on the north, east and southwest slopes of the hill where the experiment took place. Each block contained each evenness treatment of both sets of mixtures, as well as each species in monoculture, for a total of twelve plots per block. The first trial was planted in late spring 2003, with data collection occurring throughout the 2004 growing season; the second trial was planted in spring 2004 with data collection occurring throughout the 2005 growing season.

Invasion rate

We quantified invasion rate by sampling plants that recruited into the plots as volunteers. In this study system, volunteers mainly consist of exotic species (*Bromus inermis*, *Setaria* spp., *Chenopodium album*, *Cirsium arvense*, *Medicago lupulina*, *Taraxacum officinale*, *Melilotus* spp.) and cosmopolitan weeds (e.g. *Ambrosia* spp., *Conyza canadensis*). Sampling the natural recruitment of these plants is a more realistic estimate of invasion than sampling one or a few planted species (Wilsey and Polley 2002). All volunteer plants were removed in mid-April, early June, early July and mid-October of both sampling years, sorted by species, dried and weighed. These weeding dates were chosen during the first trial by observing the plots and weeding as needed, in order to remove weed seedlings with minimal disturbance to the soil surface. The amount of biomass removed from each plot was divided by the

number of weeks since the previous weeding to obtain a rate ($\text{g m}^{-2} \text{ week}^{-1}$) of species invasion for each plot. In the case of the April weeding, the amount of biomass removed was divided by the number of weeks since March 1, which was approximately the date of the beginning of spring green-up at the site in both years of the experiment. Invader biomass values were a tiny fraction of total plot biomass (unpubl.).

We separated total invader biomass by taxon into grasses, forbs and legumes in order to test the hypothesis that treatments will differentially affect different taxa, and to examine the question of whether diversity-invasibility relationships are taxon specific.

Light at soil surface

We measured the proportion of photosynthetically active radiation (PAR) reaching ground level in each plot with a Decagon Accupar light meter in June, July and September of both sampling years (Fig. 4). Because our weeding dates were timed to prevent invaders from becoming very large, measuring the amount of light at ground level was an accurate method of determining light capture by the planted canopy.

Monoculture comparisons

We compared invasion rates and light levels among monocultures in order to look for potential species effects caused by individual species being particularly vulnerable or resistant to invasion.

Statistical analyses

We used SAS repeated measures ANOVA to test for treatment differences in invasion rate over the course of the growing season. Invasion rate data were ln-transformed due to non-constant variance. When invasion rate data were broken into separate taxa we did not include either the April or October weeding dates in the analyses because too many plots were not invaded by all taxa at these dates, leaving too many zeroes in the data set (Fig. 3).

Seven a priori linear contrasts were used to test for differences among treatments in invasion rate data sets. These contrasts were as follows: (1) the mean of all monoculture plots was compared to the mean of all mixtures based on the hypothesis that increased species richness would lead to lower rates of invasion in mixtures; (2) T-plots were compared to D-plots to test the hypothesis that the greater dissimilarity in height present in D-plots would lead to lower rates of invasion and light penetration through niche complementarity; (3) the effect of evenness treatments was

tested across all mixtures to test the general hypothesis that increased evenness would lead to lower rates of invasion. The effect of evenness treatments was tested in (4) T-plots alone and (5) D-plots alone in order to determine the effect of evenness in each specific rarity/extinction scenario and see if these effects differed from the general trend tested in contrast no. 3. The effect of *Andropogon* dominance was tested in (6) T-plots and (7) D-plots in contrasts that included the *Andropogon* monocultures to test the hypothesis that increased C_4 grass dominance would lead to greater invasion (Smith et al. 2004).

All contrast coefficients were based on planted rank-abundance slopes and *Andropogon* dominance and calculated using PROC IML (SAS Institute). In evenness contrasts the coefficient values were 0.73, -0.06 , and -0.68 for H, M and L plots. In *Andropogon* dominance contrasts the coefficient values were 0.71 in the *Andropogon* monocultures and 0.16, -0.21 and -0.65 in the L, M, and H plots. With each a priori linear contrast we tested for lack of fit by adding a quadratic term (Petersen 1985), and then removed it if lack of fit was not significant. This was necessary in order to detect any possible non-linear relationships in the data, as these would not be found with linear contrasts alone. All analyses used type IV sums of squares because one *Liatis* monoculture was not planted during the first trial due to a shortage of transplants and this caused a missing cell.

We regressed trends in invasion rate data to ln-transformed light data in order to see if canopy light penetration was correlated with invasion rate. All comparisons among monocultures were made using Tukey-adjusted comparisons of least squares means.

Results

Invasion rate

The mean rate of invasion was 69% higher in monocultures ($5.4 \text{ g m}^{-2} \text{ week}^{-1}$) than in mixtures ($3.2 \text{ g m}^{-2} \text{ week}^{-1}$) (Table 3, Fig. 2). The magnitude of the difference between monocultures and mixtures varied across time ($F_{3,168} = 3.27$, $p = 0.02$), but the mean rate of invasion for monocultures was always higher than for mixtures and this difference was significant for all weeding dates except April (Fig. 2).

Invasion rate was not consistent throughout the growing season. In both years, there was an order of magnitude greater biomass of invaders between April and early July (means: 8.2 from April to early June and $7.8 \text{ g m}^{-2} \text{ week}^{-1}$ from early June to early July) than either before April ($0.5 \text{ g m}^{-2} \text{ week}^{-1}$) or after early July ($0.7 \text{ g m}^{-2} \text{ week}^{-1}$) (Fig. 2, Table 3, time main effect $p < 0.001$).

Table 3. Results from ANOVAs of invader biomass and canopy light penetration as a function of planted species evenness and richness in a field experiment in Iowa. Total biomass shows analysis of all invader biomass over all weeding dates, while the other columns separate this biomass by taxon and include only the June and July weeding dates. In the a priori contrasts, *Andropogon* dominance T and *Andropogon* dominance D include the *Andropogon* monocultures and only the tall (T) or dissimilar (D) plots.

Source	DF	Biomass F	Grasses F	Forbs F	Legumes F	Light F		
Year	1	17.7***	157.6***	29.62***	134.9***	4.7*		
Block	2	15.3***	0.4	9.6***	24.7***	0.01		
Plot	11	4.4***	7.1***	3.83***	1.3	13.8***		
A priori linear contrasts								
monocultures vs mixtures	1	7.7**	12.2***	5.29*	2.3	57.3***		
Dissimilar (D) vs Tall (T) plots	1	1.6	3.6	0.55	1.1	0.9		
overall evenness	1	0.8	0.3	0.25	0.5	0.04		
evenness within T plots	1	4.05*	4.05*	1.08	1.13	0.4		
evenness within D plots	1	0.57	1.4	0.11	0.01	0.1		
<i>Andropogon</i> dominance (T)	1	8.2**	10.6**	3.17	3.8	4.5*		
<i>Andropogon</i> dominance (D)	1	0.3	0.1	0.3	0.5	0.9		
error	56							
			d.f.			d.f.		
Time	3	381.1***	1	35***	25.2***	2.4	2	67.8***
Time × year	3	30.9***	1	3.4 +	7.3**	3.9	2	5.5**
Time × block	6	5.8***	2	1.7	1.6	5.8*	4	2.9*
Time × plot	33	1.8**	11	2.7**	1.5	1.2	22	5.6***
error	168	56		112				

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Interestingly, and contrary to our hypotheses, there was no significant effect of overall evenness on invasion rate in mixtures (Table 3) and the effect of evenness was actually less important in plots with dissimilar heights (Table 3). There was no overall difference in invasion rate between T and D -plots (Table 3). We had hypothesized that D-plots would be less invaded due to niche complementarity resulting from the inclusion of both tall and short species in these mixtures, but found no support for this hypothesis. In the D-plots, where the abundance of short species decreased and *Andropogon* increased as evenness declined, there was no relationship between evenness and invasion rate (Table 3). However, in the T-plots there was a significant, negative linear relationship between invasion rate and evenness (Table 3, Fig. 2). During the two time periods with high rates of invasion, invasion rates declined from 7.7 to 3.4 $\text{g m}^{-2} \text{week}^{-1}$ (April to early June) and from 8.9 to 3.6 $\text{g m}^{-2} \text{week}^{-1}$ (early June to early July) from low to high evenness (declines of 56 and 60%).

Taking into account *Andropogon* monocultures and testing for dominance effects yielded results consistent with those for evenness effects in mixtures (Table 3, Fig. 2). Linear contrasts that included the *Andropogon* monocultures and compared *Andropogon* dominance to invasion rate were not significant in the D plots, but showed a significant, linear decrease in invasion rate in the T plots as *Andropogon* dominance decreased (i.e. evenness increased) (Fig. 2). Mean invasion rates

declined from 14.0 and 9.2 in *Andropogon* monocultures to 3.4 and 3.6 $\text{g m}^{-2} \text{week}^{-1}$ in low dominance (high evenness) plots during the two time periods with high invasion (i.e. from April to early July). Although the direction of this relationship was the same in all months, the contrast had a significant interaction with time ($F_{3,168} = 3.7$, $p = 0.013$). It was steeper and significant in April and June ($F_{1,56} = 6.61$, $p = 0.0128$ and $F_{1,56} = 11.93$, $p = 0.001$) and became more shallow and lost significance in July and October ($F_{1,56} = 3.82$ $p = 0.056$ and $F_{1,56} = 0.67$ $p = 0.42$) (Fig. 2). None of the quadratic contrast terms added to test for lack of fit were significant.

The invading species were exotic species and cosmopolitan weeds that are problematic in our area. Breaking down invader biomass by taxon and analyzing grasses, non-leguminous forbs and legumes separately showed that treatment effects observed in the total biomass analysis were driven by the responses of grasses and forbs. The legumes recruiting into our plots, mainly the exotics *Medicago lupulina* and *Trifolium pratense*, were not significantly affected by our experimental treatments (Table 3, Fig. 3). Grasses, including *Bromus inermis*, *Poa* spp., and *Setaria* spp., and forbs, such as *Conyza canadensis*, *Cirsium* spp., *Taraxacum officinale*, *Chenopodium album* and *Ambrosia* spp., generally followed the same trends as total invader biomass data (Table 3, Fig. 3.)

In the analysis of grass biomass, one of the quadratic terms added to linear contrasts to test for lack of fit

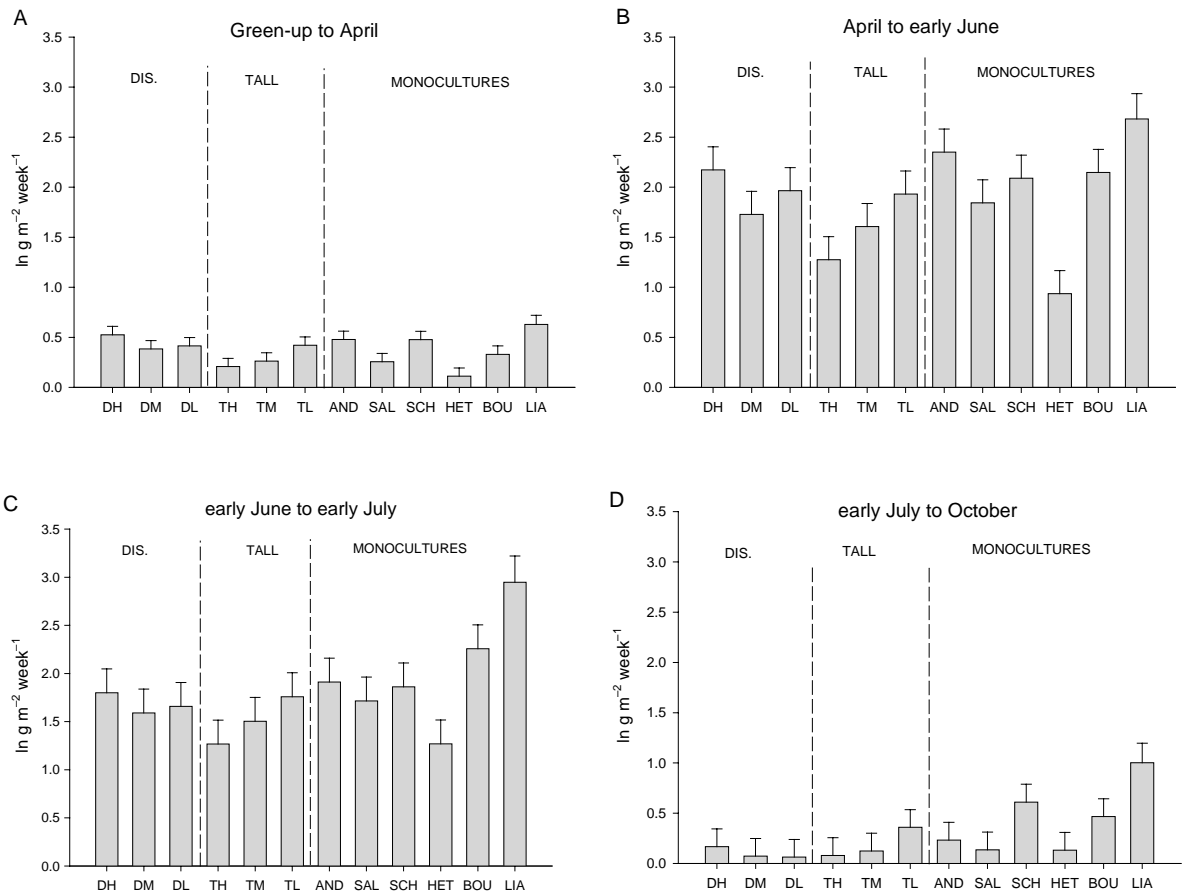


Fig. 2. Mean (Lsmeans + standard error) rate of invader biomass accumulation across 2004 and 2005 in four species mixtures planted at three levels of evenness (H, M, L) with species of dissimilar heights (D) or with all tall species (T), or monocultures in a field experiment in Western Iowa. Abbreviations for the monocultures are: AND – *Andropogon gerardii*, SAL – *Salvia azurea*, SCH – *Schizachyrium scoparium*, HET – *Heterotheca villosa*, BOU – *Bouteloua gracilis*, and LIA – *Liatris punctata*.

was significant. Adding a quadratic term made the contrast for the effect of *Andropogon* dominance in D plots significant ($F_{1,56} = 4.5$, $p = 0.04$). This contrast was not significant without the quadratic term (Table 3), suggesting that grass invasion initially declined with *Andropogon* dominance in D plots but then increased as *Andropogon* dominance decreased further (Fig. 3).

Light at soil surface

Proportion of light reaching the soil surface varied among treatments and was a significant predictor of invasion rate (Fig. 4, 5). Invasion rate was strongly related to light levels at the soil surface (Fig. 4), with significant log-linear relationships in June ($r^2 = 0.48$, slope = 0.62, SE = 0.08), July ($r^2 = 0.52$, slope = 0.49, SE = 0.06), and September ($r^2 = 0.20$, slope = 0.28, SE = 0.07). Furthermore, differences in treatments were

no longer significant after taking into account ln-light availability in an ANCOVA (all contrasts $p > 0.05$), which suggests that light was driving evenness-invasion relationships.

The mean amount of light reaching the soil surface over the growing season was significantly higher in monocultures (34.5% of PAR) than in mixtures (15.1%). This contrast had a significant interaction with time ($F_{2,112} = 5.76$, $p = 0.004$), but was significant at all sampling dates and did not change direction (Fig. 5). There was no significant relationship between evenness and mean light penetration, either overall or within the T or D plots. Surprisingly, given the presence of short species in D plots, there was no significant difference in the amount of light reaching the ground surface between T and D plots (Table 3). The effect of *Andropogon* dominance upon light penetration was significant in the T plots (Table 3). This contrast had a significant interaction with time ($F_{2,112} = 3.89$, $p = 0.02$). As was the case with the

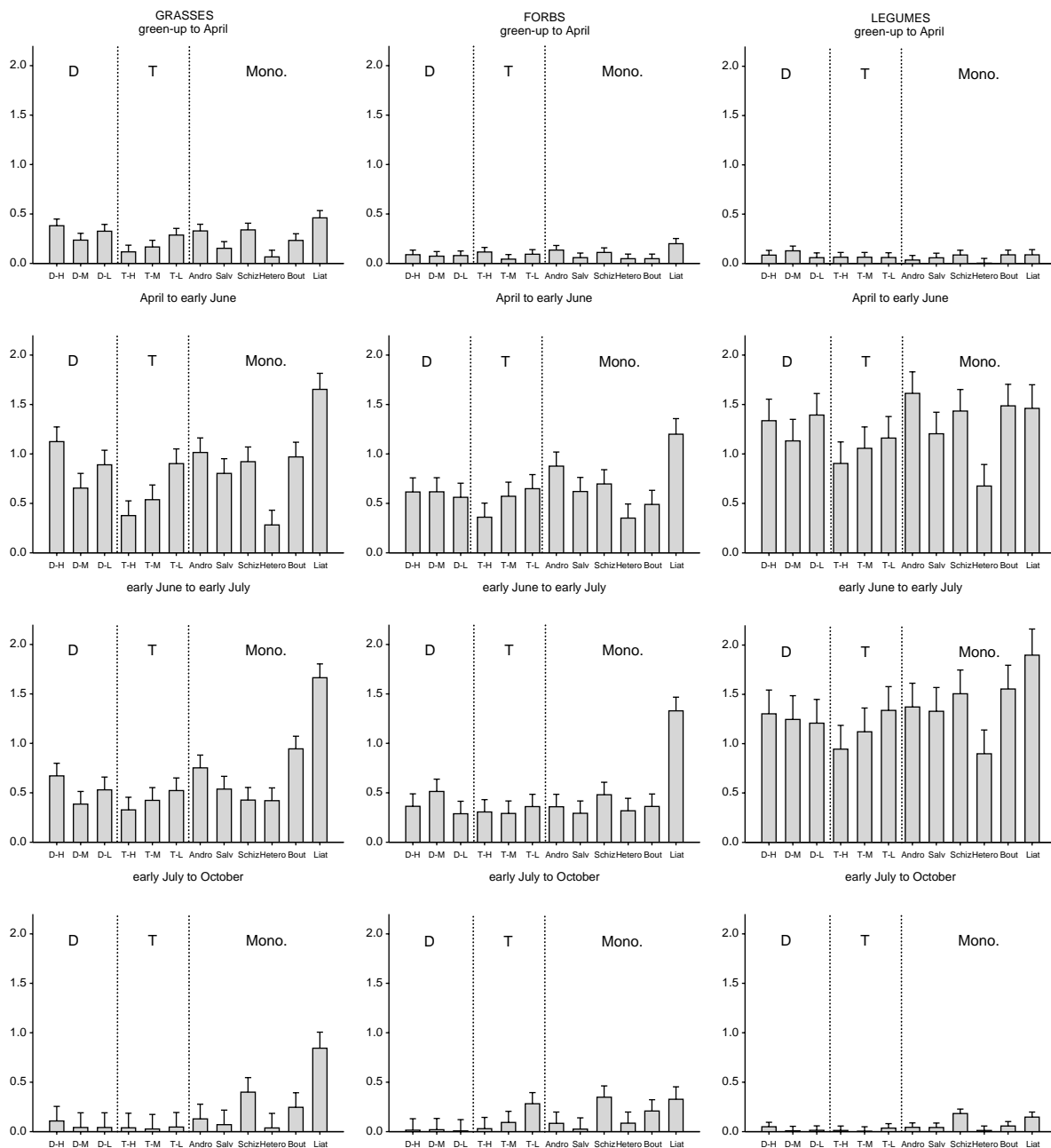


Fig. 3. Mean rate of invasion by taxon at each weeding date across 2004 and 2005 in a planted field experiment in western Iowa. The y-axes are $\ln \text{ g m}^{-2} \text{ week}^{-1}$ invader biomass. Abbreviations for the are D: dissimilar mixtures, T: all tall mixtures, and Andro – *Andropogon gerardii*, Salv – *Salvia azurea*, Sch – *Schizachyrium scoparium*, Hetero – *Heterotheca villosa*, Bout – *Bouteloua gracilis*, and Lia – *Liatis punctata* monocultures.

relationship between invasion rate and *Andropogon* dominance in the T-plots, light penetration increased with *Andropogon* dominance earlier in the growing season (June $F_{1,56} = 6.34$ $p = 0.015$), but there was no significant relationship later on (July $F_{1,56} = 2.18$ $p = 0.15$, September $F_{1,56} = 1.35$ $p = 0.25$).

Monocultures

Liatis, the short forb species, had both the greatest amount of light penetration and highest rate of invasion in monoculture at all sampling dates (Fig. 2, 4, 5). *Heterotheca*, a tall forb species, generally had

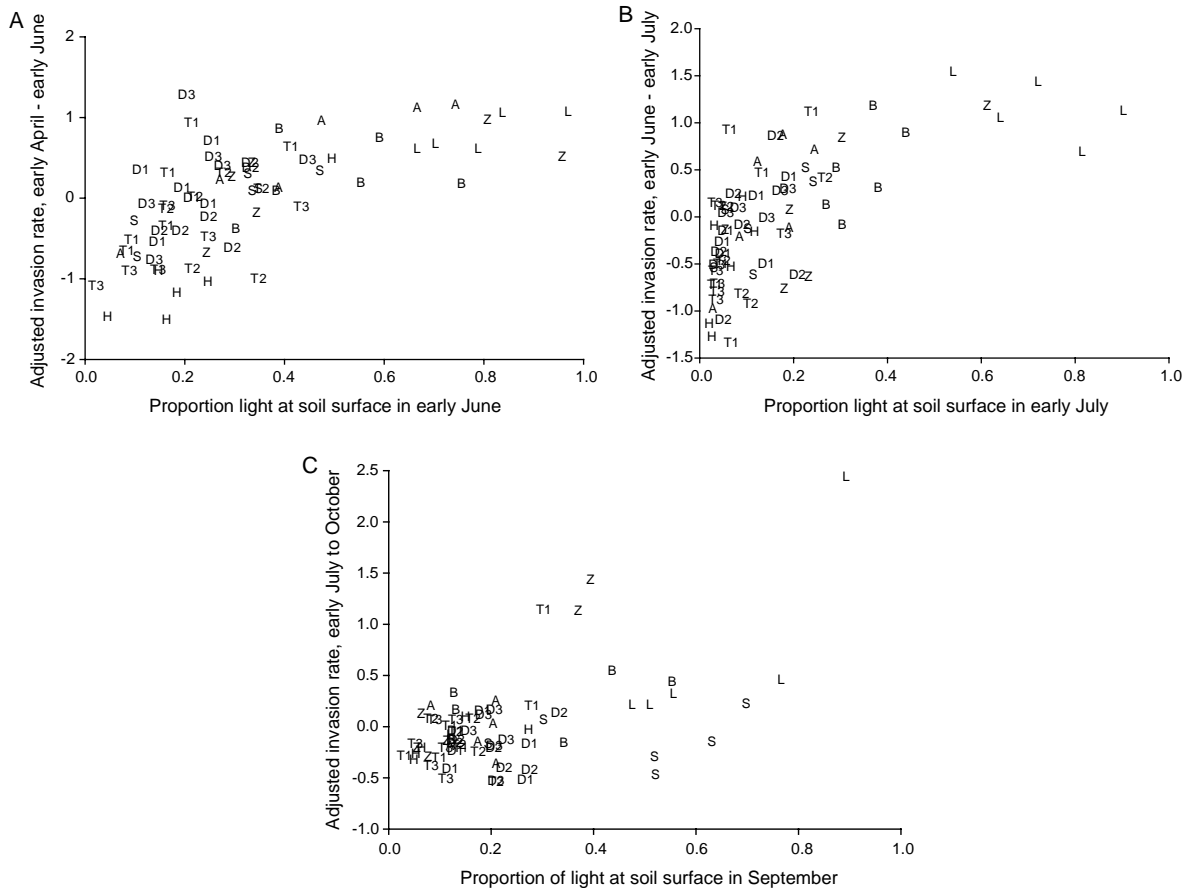


Fig. 4. Relationships between proportion of light at soil surface and invasion rate (adjusted for differences among blocks and trials) in monoculture and four species mixture plots that differed in species evenness in June (A), July (B) and September (C). Abbreviations are: A – *Andropogon gerardii*, S – *Salvia azurea*, Z – *Schizachyrium scoparium*, H – *Heterotheca villosa*, B – *Bouteloua gracilis*, and L – *Liatris punctata* (monocultures), and D1 – dissimilar height, low evenness, D2 – dissimilar height, medium evenness, D3 – dissimilar height, high evenness, T1 – tall, low evenness, T2 – tall, medium evenness, T3 – tall, high evenness (mixtures).

the lowest rate of invasion and least light penetration (Fig. 2, 4, 5). Early in the growing season, when there was a positive, linear relationship between both light penetration (June $F_{1,56} = 6.34$, $p = 0.015$) and invasion rate (June $F_{1,56} = 6.61$, $p = 0.001$) and *Andropogon* dominance in the T-plots, *Heterotheca* monocultures had less than half the mean amount of canopy light penetration of *Andropogon* monocultures (21% vs 43%) and also had a significantly lower rate of invasion (Tukey adjusted comparison $\alpha < 0.05$). The differences in light penetration and invasion rate between *Andropogon* and *Heterotheca* monocultures became insignificant later in the growing season, as did the effects of *Andropogon* dominance in the T-plots on both light penetration and invasion rate.

Discussion

We used two ecologically realistic rarity/extinction scenarios to experimentally test the hypothesis that less diverse plant communities are easier to invade than more diverse communities at the plant neighborhood scale. We found that changing rank-abundance relationships in *Andropogon gerardii* dominated communities by decreasing the abundance of short species, which has been documented to occur in small, isolated remnant prairies (Leach and Givnish 1996), had no significant effect on invasibility. However, lowering the abundance of other tall species in *Andropogon gerardii* dominated communities, which is frequently the observed difference between remnant and restored prairies with restorations having lower abundance of

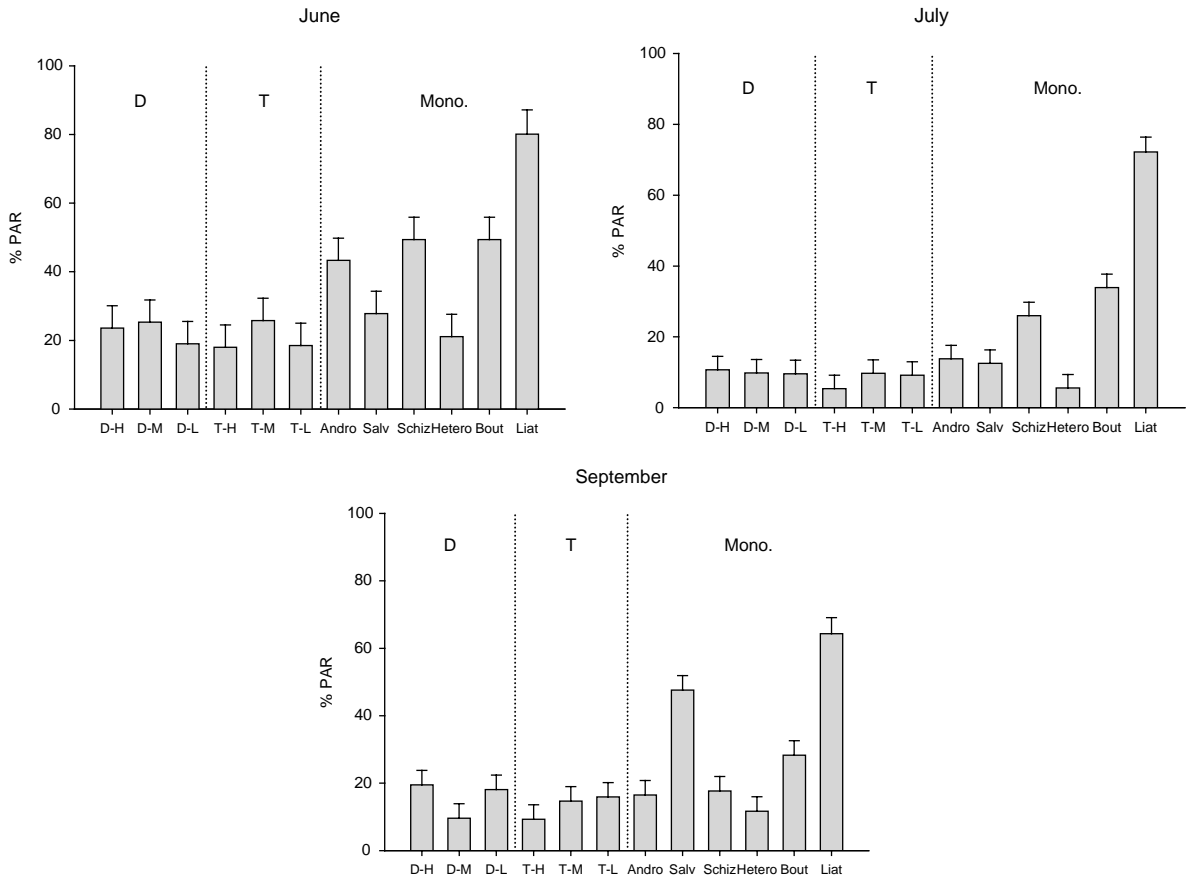


Fig. 5. Light at the soil surface (least square means + SE), as a percentage of total photosynthetically active radiation, in each plot type at each sampling time in a planted field experiment in Western Iowa. Abbreviations are as in Fig. 3.

other tall species (Martin et al. 2005), led to a linear increase in invasibility. This may have been caused, at least in part, by the effect of decreased canopy light capture early in the growing season, which was correlated with increased *Andropogon* dominance and decreased abundance of other tall species. Light was positively correlated with invasion rate, especially early in the growing season, and these correlations weakened over time. These results suggest that the effects of increased rarity and extinction on the invasibility of plant communities will vary greatly depending upon which species are becoming rare or going extinct, and supports modeling work by Bunker et al. (2005) showing highly variable effects of different extinction scenarios upon ecosystem functioning.

When we broke down the invader biomass by taxon, we found that taxa responded differently to our treatments. Grasses and non-leguminous forbs responded similarly and drove the trends seen in the total biomass data, but legumes were not significantly different. If we had only collected data on legumes that invaded our plots, we would have incorrectly concluded

that our treatments had no effect on invasion. This supports the conclusion of Wilsey and Polley (2002), that it may be inappropriate to make general statements about the invasibility or resistance of a community based on experiments that use only one or a few seeded invader species.

The mechanism by which diversity is most often hypothesized to influence invasibility is niche complementarity – a more diverse assemblage of species is thought to be better able to monopolize available resources and exclude invaders more than a less diverse assemblage (Knops et al 1999, Hector et al. 2001, Kennedy et al. 2002). If this mechanism is working, it should be possible to quantify and describe functional diversity more accurately than just by species number (Symstad 2000). A four species assemblage in which all four species are highly similar to one another should be easier to invade than a four species mixture containing more dissimilar species. In this experiment we controlled for rooting depth and taxonomic group, but varied height. This was the first direct test of the effect of species height dissimilarity on

invasion. We hypothesized that height complementarity would cause mixtures containing both tall and short species to be less invaded than mixtures containing only tall species due to greater canopy light capture, but found no support for this hypothesis. However, we did find some evidence of niche complementarity based on phenology within the tall species mixtures. Differences across time periods had important effects in our experiment. We found heavy invasion pressure from mid-spring to very early summer, with many fewer invaders appearing in any plots either very early in the growing season or from early-summer on. Monocultures of *Heterotheca*, a cool season forb that begins using resources very early in the spring, were more resistant to invasion than monocultures of *Andropogon*, a warm season grass. In our tall plots, invasion resistance increased as *Andropogon* dominance declined and *Heterotheca* abundance increased. This may have been driven by *Heterotheca*'s ability to capture light early in the growing season, when invasion pressure was heaviest. Other studies of diversity effects on ecosystem processes have found phenology to be as or more important than other measures of functional similarity (Hooper and Vitousek 1997, Hooper 1998). This has not usually been addressed in studies of the diversity-invasibility relationship. However, authors of these studies have usually reported only seasonal totals for invaders, commonly sampling only once during the growing season (Symstad 2000), perhaps on the implicit assumption that invasion pressures will be more or less consistent over the course of a growing season. In our system at least, this was not the case. In one experiment that did consider phenology, Zavaleta and Hulvey (2004) found that more diverse communities were more likely to contain species that competed for resources later in the growing season. These communities were better at resisting invasion by star thistle (*Centaurea solstitialis*) because more members of these communities were actively using resources at the same time as this seeded invader.

Our results have practical implications for managing prairies. We included all volunteers appearing in our plots as invaders in our study, and found that the great majority of them appear in the spring and the first two weeks of summer. This suggests that another negative effect of overly frequent fires, or other management regimes that favor warm season grasses, beyond loss of diversity (Towne and Owensby 1984, Collins et al. 1998, Martin et al. 2005), may be reduced resistance to invasion by cool season forbs and grasses, which make up a substantial portion of the weed flora.

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