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CAUSES AND CONSEQUENCES OF DOMINANCE AND DIVERSITY IN GRASSLANDS

By

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Abstract

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Understanding how species coexist and differ in abundance is central to ecology. Theory predicts competitively superior species should dominate systems and suppress diversity, yet many natural communities characterized by dominants are species rich. Understanding how shifts in dominance among species, and the inherent diversity of communities affect ecosystem function is a second central theme in ecology. For example, decreasing the number of species in local communities can reduce the ability of the community to respond to disturbance. These ideas have captured ecologists' attention because anthropogenic pressures are causing many systems to lose species. In my dissertation I focused on processes that determine dominance and diversity and the consequences of changes in dominance and diversity on the ability of communities to respond to exotic invasion and disturbance.

In chapter 1 I asked: does competitive ability correspond with large differences in plant species abundance found in field surveys of grasslands in western Montana? In a garden experiment I found that intraspecific competition appears to promote coexistence, but differences in abundance were not related to inherent interspecific competitive abilities in common garden experiments.

In chapter 2 I asked: how important is competition relative to other mechanisms of coexistence, such as dispersal limitation and seed predation? Experimental manipulations of natural grassland communities showed that dispersal limitation caused a greater constraint on local diversity than competition from a single dominant species or from several common species. Seed predation, in contrast, did not influence diversity two years after the treatments were applied.

In chapter 3 I asked: does invader impact on natives vary with disturbance and diversity? Burning a subset of experimentally invaded assemblages showed that the buffering effect of diversity on invader impact was lost after a form of disturbance that is commonly experienced by the native system.

An important historical focus in plant ecology was on how species could coexist *despite* competition for limiting and shared resources, and in this context I found that competition did not correspond well with the ability of species to coexist or with the relative abundance of species. I also found that increasing native species diversity did not buffer the relative responses of natives and invaders to disturbance. Overall I found that by studying ecological processes together instead of in isolation we can gain a better understanding of the complexity of ecosystems.

A child said What is the grass? *fetching it to me with full hands,*
How could I answer the child? I do not know what it is any more than he.

I guess it must be the flag of my disposition, out of hopeful green stuff woven.

Or I guess the grass itself a child, the produced babe of the vegetation.

Or I guess it is a uniform hieroglyphic;
And it means, Sprouting alike in broad zones and narrow zones,
Growing among black folds as among white,
Kanuck, Tuckahoe, Congressman, Cuff, I give them the same, I receive the same.

And now it seems to me the beautiful uncut hair of graves.

~Song of Myself, Walt Whitman

Chapter 1

Common species are poorer inter- and intraspecific competitors than rare species

Abstract

Theory predicts that species coexistence and relative abundances should be determined by the differences among species in the strength of intra- versus interspecific competitive abilities. While many greenhouse studies have compared the relative strengths of intra- and interspecific competition, few experiments have examined how this correlates with relative abundance of co-occurring species in natural systems. We compared competition among common and rare perennial plants that co-occur in grasslands in western Montana, USA. We designed a garden experiment where a focal individual was surrounded by four individuals from the same species (intraspecific) or another species (interspecific) to test the relative strengths of competition. We used the relative interaction index (Rii) to compare performance when grown alone to performance in competition. The interspecific treatment included 10 different combinations of groups based on abundance (common or rare) and functional (grass or forb) categories. As predicted by theory, intraspecific competition was stronger for common species than for rare species. Surprisingly, however, common species were also less tolerant (competitive response) to interspecific competition than rare species suggesting that other mechanisms besides variation in interspecific competitive responses likely influence the abundance of our focal species in nature. Furthermore, the mean competitive effect of common species was no different than that of rare species. Thus

while differences in the strength of intraspecific competition may facilitate coexistence, the similarity in competitive effects between common and rare species suggest that interspecific competition may boost diversity by preventing common species from competitively excluding the rare species.

Introduction

Competition can be intense among plants because they are sessile organisms that require the same potentially limiting resources, such as light, water, and nutrients. Given that competition among co-occurring species can be strong (Goldberg & Barton 1992; Gurevitch *et al*. 1992), a central ecological question is how such competing species coexist (Connell 1961; Tilman 1982; MacArthur 1958; Chesson 2000a; Chase & Leibold 2003; Silvertown 2004). Theory predicts that a superior competitor will rapidly drive an inferior competitor to extinction (Hutchinson 1961; Grime 1973; Tilman 1985). Species with varying competitive abilities, however, often coexist in natural communities (e.g. Connell 1961; Whittaker 1965; Pennings & Callaway 1992; Tilman 1994) although sometimes with large differences in abundance.

Interspecific competitive differences may lead to differences in abundance or contribute to coexistence. We know that there can be strong interspecific competitive hierarchies among co-occurring plant species (Keddy & Shipley 1989; Goldberg & Landa 1991) and in some cases strong competitors from greenhouse experiments are also highly abundant in the field (Mitchley & Grubb 1986; Miller & Werner 1987). These results suggest that strong interspecific competitors should be the most abundant species in the field. Alternatively, Rabinowitz *et al.* (1984) suggested that rare species are strong interspecific competitors and this is one reason why they can coexist with more abundant species.

One key to coexistence among competing species may lie in the strength of intraspecific competition (Tilman 1988; Chesson 2000a; Wright 2002). Theory predicts that intraspecific competition will typically be strong because individuals from the same species will have the same resource requirements (MacArthur 1958; Tilman 1985). Niche differences, also called stabilizing forces, can promote coexistence because species limit themselves more than others (Chesson 2000a; Adler *et al.* 2007). The common species, in particular, must experience stronger self-limitation than rare species (Chesson 2000a; Kylafis and Loreau 2011) in order to prevent competitive exclusion (Gurevitch *et al.* 1990; Stoll & Prati 2001). If a plant is rare it will be surrounded by species with different niches, allowing it to increase in abundance, whereas if a species is abundant it will be surrounded by individuals with similar niches and experience strong self-limitation (Adler *et al.* 2007; MacDougall *et al.* 2009). Relatively weak intraspecific competition for rare species may also contribute to coexistence (Fonteyn & Mahall 1978; Stoll & Prati 2001).

Despite clear theoretical predictions for differences in the relative strength of intra- and interspecific competition for common and rare species, empirical evidence is mixed. Reviews of competition have found neither intra- nor interspecific competition is consistently stronger (Goldberg & Barton 1992; Gurevitch *et al.* 1992), perhaps because experiments that quantify intra- and interspecific competitive abilities among species seldom relate these results to abundance in the field. There is some evidence that the most abundant species can decrease the performance of co-occurring species (Abulfatih & Bazzaz 1979; Emery & Gross 2007; Gilbert *et al.* 2009), supporting the idea that interspecific competitive abilities determine abundance. Other empirical work showed that, in contrast to coexistence theory, intraspecific competition is weak for the abundant species (e.g. Fonteyn & Mahall 1981; Hamerlynck *et al.* 2002) or that the strength of intraspecific competition for the dominant species depends on the size of the individuals competing (Haase *et al.* 1996). Although many studies have compared the relative strengths of intra- and interspecific competition, few compared naturally co-occurring species or examined whether variation in competitive strengths were related to different abundances in the field. Therefore, it remains unclear how species of different abundances can coexist because the strength intraspecific competition is rarely quantified in experiments of interspecific competitive hierarchies (Silvertown 2004). However, such stabilizing forces are important for coexistence (Chesson 2000a).

We compared the relative strengths of intra- and interspecific competition for common and rare species that co-occur in intermontane grasslands of western Montana. Past studies often examined competitive interactions between specific species (e.g. Goldberg 1987; Rees *et al.* 1996) or particular species from one abundance category (e.g. Fonteyn & Mahall 1981; Myers & Harms 2009). In the current study, randomly choosing species from different abundance categories, based on field data from natural grasslands, allowed us to test whether the strength of competition was related to abundance rather than the competitive strength of specific species. Specifically, we tested several hypotheses and assumptions related to how the intensity of competition should vary with plant abundance. In particular, we experimentally explored the following questions: (1) Are strong interspecific competitors more abundant in the field than weak competitors? (2) Is intraspecific competition stronger for common than rare species, as predicted by coexistence theory? (3) Is intraspecific competition consistently stronger than interspecific competition, as predicted by niche theory?

Methods

To determine whether relative competitive abilities among species were related to field abundance, we chose 17 focal species including grasses and forbs (Table 1) that co-occur in grasslands in western Montana. Preliminary observations in 2010, and qualitative descriptions of the species in the area provided in the species description and identification guidebook by Lackschewitz (1991), suggested that these species represented either common or rare groups of species. Although rarity can be defined based on local abundance or range size (e.g. Rabinowitz 1981; Gaston 1994) here we focus on local abundance since we are interested in competition, which is a local interaction.

To test whether species were assigned to the appropriate abundance category, we used data from plant community surveys in natural intermontane grasslands, dominated by native perennial bunchgrasses, to quantify local abundance of the selected species in 2011. These surveys were conducted at 16 1 ha sites across west-central Montana and each site was at least 5 km apart; sites ranged from UTM 11T 529115 N, 12T 351331 E, 12T 5116754 N, to 11T 666271 E (Pearson & Ortega, unpublished data). At each site we sampled vegetation using 20 randomly located 1 m^2 quadrats, which were at least 10 m apart. The quadrats were divided into 100 cells to reduce observer bias and to assist visual estimation of species percent cover to the nearest 5% for species with >10% cover and to the nearest 1% for species with <10% cover. These data will be used to test whether the selected species were assigned to the appropriate abundance category (i.e., rare or common).

Starting in April 2010, we grew locally collected seeds of our focal species in 125 ml pots containing a 50:50 sand:native soil mix. In May 2010, we transplanted these seedlings into 70 x 70 cm plots (Fig. 1) and arranged within rows in a tilled/fallow field at Fort Missoula, Montana, USA. Neighbors from separate plots were 40 cm apart. We watered the transplants for the four weeks to help them establish. To estimate performance without competition we grew an individual of each species alone at the center of the plot, with five replicates per species. For the competition treatments each plot contained one focal plant surrounded by four neighbors with each neighbor placed 10 cm away from the focal plant in a different cardinal direction (Fig. 1); the identity of neighbors varied by treatment. To estimate the strength of intraspecific competition we grew five replicates of each species surrounded with four conspecifics, with the same spatial configuration as the interspecific treatments.

To estimate the strength of interspecific competition between different abundance and functional groups we examined the competitive response of focal species against heterospecific neighbors. In total there were 10 interspecific treatments (Table 2), with each treatment replicated 10 times. For each replicate of a given treatment, a species was randomly chosen from the appropriate category (i.e. common vs. rare and grass vs. forb).

There were a total of 270 plots (17 species alone x 5 replicates, 17 species in intraspecific competition x 5 replicates, 10 interspecific competition combinations of the 17 species x 10 replicates), although due to transplant stress and herbivory a total of 259 plots were harvested. Treatment was randomly assigned to each plot. We weeded the plots throughout each growing season to ensure that only the assigned individuals were in the plots.

In July 2011, we measured the vegetative height (excluding flowering stems) of each individual. In July 2012, after two growing seasons, we counted the number of flowering stems and harvested the above ground biomass of all the plants. Each plant was bagged, dried at 60^{o}C (until a constant dry biomass was reached) and weighed. The effect of competition between adults on focal plant biomass and number of flowering stems provide measures of the effect of competition on abundance and the potential to reproduce respectively.

Data analysis

In order to compare the strengths of competition for different groups we first had to standardize performance given species differences in size. We calculated the strength of competition using the relative interaction index according to Armas *et al.* (2004); Rii = (Y*together* – Y*alone*)/(Y*alone* + Y*together*), where Y was either focal plant biomass or number of flowering stems. This index ranges from -1 to +1 and represents a range of interactions from competition to facilitation, respectively. We used the Rii to compare the relative response of individuals to intra- versus interspecific competition.

To compare the strength of intra- vs. interspecific competition for common vs. rare species we used the GLIMMIX procedure in SAS (version 9.3) to analyze differences in the relative interaction indices for biomass and flowering stems separately. We treated abundance group (i.e. rare or common), type of competition (intra- or interspecific), and focal species identity as fixed factors. Although species identity was not a focus to our questions, we included it as a fixed factor to ensure that the patterns we attribute to the other fixed factors were not driven by particular species. Since each species only occurred in one abundance category, species identity was nested within the abundance factor. A few species (*Artemisia frigida, Geranium viscosissimum,* *Symphyotrichum ericoides,* and *Bouteloua gracilis*) did not flower and thus were excluded from the analysis of Rii's for flowering stems.

In addition to examining whether there was an overall competitive effect, we also compared the strength of intraspecific competition to competition between specific neighbor and focal groups (from Table 2). We performed separate one-way ANOVAs for each of the four focal groups (common grasses, common forbs, rare grasses, and rare forbs) with neighboring group as a fixed factor. We included species identity as a fixed factor in this analysis to test if patterns were driven by particular species. We present the least squares means and SEs throughout.

Results

The field survey data confirmed our initial qualitative classification of grasses and forbs into abundance categories. The grass (Fig. 2a) and forb (Fig. 2b) species we classified as common had high average percent cover in the surveys of natural grasslands. The species we classified as rare did not occur in any of the 320 plots across all the sites; however they do occur in this area (Lackschewitz 1991). The data show that the selected species are rare at a regional scale, although this does not necessarily mean they are rare at a local scale (Lesica *et al.* 2006). These species would always have a low average local abundance because they are encountered so infrequently across the region.

Common species did worse than rare species in competition (Fig. 3; $F_{1,129}$=14.0, $p<0.001$) and this occurred regardless of whether we examined intra- or interspecific competition (competition type x abundance: $F_{1,129}$=0.1, P=0.100). Thus, common species suffered greater declines in biomass as a result of both intra- and interspecific competition than did rare species. The relative strength of intra- versus interspecific competition did not vary across the two abundance groups ($F_{1,129}<0.1$, $P=0.989$). Species identity ($F_{14,129}=1.6$, $P=0.080$) and the interaction between species identity and type of competition ($F_{14,129}=1.6$, $P=0.092$) did not have a significant effect on the Rii for biomass (Appendix 1a).

The Rii for flowering stems (Fig. 4) also showed that common species performed worse in competition than rare species ($F_{1,114}=7.0$, $P=0.009$), regardless of whether we examined intra- or inter-specific competition (competition type x abundance: $F_{1,114}=0.4$, $p=0.508$). There was no difference between intra- and inter-specific competition across abundance groups ($F_{1,114}=1.2$, $P=0.279$). In contrast to the Rii for biomass, the response of flowering stems to competition depended on species identity (Appendix 1b; $F_{11,114}=3.7$, $P<0.001$) and the relative strength of intra- vs. interspecific competition depended on species identity (competition type x species(abundance); $F_{11,114}=2.3$, $P=0.016$). The number of flowering stems for *F. idahoensis* and *S. ericoides* were strongly affected by interspecific competition, whereas *A. millefolium*, *P. secunda*, and *L. cinereus* were not (Appendix 1b). *F. idahoensis* was also strongly affected by intraspecific competition, whereas *H. villosa*, *K. macrantha*, and *L. cinereus* were not (Appendix 1b).

In general there was no difference between categories of neighbor species on the Rii for biomass of the focal species (Fig. 5). There was no significant difference between the competitive effect of neighboring groups on common grasses (Fig. 5a; $F_{3,42}=1.7$, $P=0.193$) and the response of the common grasses did not depend on the identity of the focal species ($F_{3,42}=0.2$, $P=0.931$). There was no significant difference between the competitive effect of neighboring groups on common forbs (Fig. 5b; $F_{3,39}=1.7$, $P=0.188$)

and the response of the common forbs did not depend on focal species identity ($F_{4,39}$=2.2, *P*=0.093). There was no significant difference between the competitive effect of neighboring groups on rare grasses (Fig. 5c; $F_{2,31}$=2.1, *P*=0.146) and the response of the rare grasses did not depend on species identity ($F_{3,31}$=1.1, *P*=0.364). There was no significant difference between the competitive effect of neighboring groups on rare forbs (Fig. 5d; $F_{2,21}$=2.0, *P*=0.158) and the response of the rare forbs did not depend on species identity ($F_{2,21}$=1.4, *P*=0.272).

There were minor differences between categories of neighbor species on the Rii for flowering stems of the focal species (Fig. 6). There was no significant difference between the competitive effect of neighboring groups on common grasses (Fig. 6a; $F_{3,42}$=2.2, *P*=0.105), however the response of the common grasses depended on species identity ($F_{3,42}$=4.6, *P*=0.008) where *P. spicata* (Rii = -0.72 ± 0.09) and *F. idahoensis* (Rii = -0.86 ± 0.11) tended to be more negatively affected than *K. macrantha* (Rii = -0.40 ± 0.10) and *P. secunda* (Rii = -0.35 ± 0.16). When common forbs were the focal species, heterospecific common forbs had less of an effect (Rii closer to 0) than intraspecific competition (Fig. 6b; $F_{3,25}$=3.9, *P*=0.020). The response of the common forbs also depended on focal species identity ($F_{2,25}$=4.9, *P*=0.016) where *H. villosa* (Rii = -0.24 ± 0.09) was not strongly affected by competition, whereas *A. millefolium* (Rii = -0.51 ± 0.09) and *G. aristata* (Rii = -0.62 ± 0.09) were more strongly affected. There was no significant difference between the competitive effect of neighboring groups on rare grasses (Fig. 6c; $F_{2,25}$=2.9, *P*=0.074), however the response of the rare grasses depended on species identity ($F_{2,25}$=4.5, *P*=0.021) where the number of flowering stems for *L. cinereus* showed little response to competition (Rii = 0.04 ± 0.12) whereas *E. elimoidies*

(Rii = -0.43 ± 0.11) and *N. viridula* (Rii = -0.40 ± 0.14) were more strongly affected by competition. There was no significant difference between the competitive effect of neighboring groups on rare forbs (Fig. 6d; $F_{2,22}$=2.5, *P*=0.102) and the response of the rare forbs did not depend on species identity ($F_{2,22}$=3.1, *P*=0.064).

Discussion

We found little support for the hypothesis that common species are competitive dominants and rare species are weak competitors (Whittaker 1965; McNaughton & Wolf 1970). Instead we found that species that were abundant in field surveys performed poorly in competition, whereas the biomass and number of flowering stems for rare species were much more tolerant to competition from other species (Figs. 3 and 4). Contrary to what might be expected by theory (Hutchinson 1961; Tilman 1985), grasses that occur at the highest abundance in the field did not have stronger competitive effects than other groups on the focal species (Fig. 5 and 6). Although the competitive response of biomass did not depend on the identity of the focal species, in some instances the response of flowering stems to competition depended on species identity (Appendix 1).

(1) Are strong interspecific competitors more abundant in the field than weak competitors?

We found that competitive ability did not match abundance in the field as predicted. Our results are similar to those of Rabinowitz *et al.* (1984), for example, who found that rare grasses were surprisingly strong response competitors. Likewise, studies of a small number of common and rare shrubs found that competitive ability did not explain differences in field abundance (Aplet & Laven 1993). Similar to our study using many different species, these results contradict the idea that rare species have a low abundance because of strong competition from common species. In many of these studies a few specific species were examined, whereas in our study we examined several species from each abundance category and found that the response of focal species biomass to competition did not depend on species identity; common species were always less tolerant to interspecific competition than rare species. However, focal species identity did influence the response of the number of flowering stems to interspecific competition where some common species were less tolerant (*F. idahoensis* and *S. ericoides*) to competition than others (*A. millefolium* and *P. secunda*).

In contrast, other studies found strong interspecific competitors had high field abundance (Howard & Goldberg 2001; Farrer & Goldberg 2011), but only examined a few specific species rather than several species from different abundance categories. Another reason for the difference may be that we examined competition at the adult life-stage, whereas the studies that found competitive rankings were correlated with field abundance were conducted amongst seedlings. Although competition between seedlings, or between seedlings and adults, can influence abundance via survival and establishment (Goldberg 1996), we focused on the cover of adult/established individuals because it is one of the main measures of local abundance. Furthermore, the number of flowering stems represents potential for future reproduction and is therefore also important to local abundance.

Despite the general lack of correlation between competitive ability and relative abundance, our results indicate that response to competition may be important for coexistence. We found that rare species were relatively tolerant of competition from common species, which may be key to allowing them to persist at low abundances and coexist with common species in field settings (Rabinowitz *et al.* 1984). The rare grasses are taller than the common species (Table 1) and thus may be particularly good competitors for light (Grime 1977; Wildova *et al*. 2007). The response of biomass and flowering stems for rare forbs did not depend on focal species identity or neighbor group identity, indicating that various groups had similar competitive effects on rare forbs. In particular, rare forbs showed a weak response to competition from common species (Fig. 5), perhaps because rare forbs started growing and flowering earlier in the spring allowing them to get a head-start on competition.

(2) Is intraspecific competition stronger for common than rare species, as predicted by coexistence theory?

As predicted by coexistence theory, we found that intraspecific competition is stronger for common than rare species. Low levels of intraspecific competition for rare species may contribute to coexistence, by allowing rare species to increase in abundance (Stoll & Prati 2001). Intense intraspecific competition for common species would also contribute to coexistence, because this decreases their chance of excluding weaker competitors (Chesson 2000b; Chase & Leibold 2003; Silvertown 2004; Kylafis & Loreau 2011). Another study found that the dominant species had strong intraspecific competition, whereas for the subdominant species intra- and interspecific competition were similar (Gurevitch *et al*. 1990). However, few other studies have made the intra- vs. interspecific comparison based on natural abundances using several species from each abundance group.

(3) Is intraspecific competition consistently stronger than interspecific competition, as predicted by niche theory?

In contrast to the niche hypothesis, we found that intra- and interspecific competition had similar strengths across abundance groups. One reason may be that intra- and interspecific competition were always stronger for the common species, so across all levels of abundance intra- and interspecific competition levels would be comparable. Competition levels may also be driven by lower than expected intraspecific competition for rare species. That is, the rare species often grow in patches and so need low levels of intraspecific competition in order to persist and not outcompete themselves (Stoll & Prati 2001; Lenssen *et al.* 2005; Monzeglio & Stoll 2008; Raventos *et al.* 2010; Vogt *et al.* 2010). Competition levels may also be similar due to higher than expected interspecific competition. That is, species growing in the same system will have similar environmental limitations and may show strong competition because of overlaps in resource requirements.

Competitive response of biomass vs. flowering stems

In general, the number of flowering stems showed a similar pattern in response to competition as biomass, where common species were less tolerant of intra- and interspecific competition than rare species. Such a pattern suggests that groups experiencing less growth are not compensating through increased reproduction. Our results suggest that flowering in rare species is less sensitive to interspecific competition than common species. Similarly, at a local scale, Rabinowitz *et al.* (1989) found that reproductive performance in rare grasses was more consistent over time than common grasses. In contrast, a meta-analysis examining causes for rarity and commonness at large scales found that rare species produced fewer seeds (Murray *et al.* 2002).

Although species identity never had a significant effect on the Rii for biomass, the response of the number of flowering stems to competition was occasionally dependent on focal species identity. Overall, the number of flowering stems for many common species was susceptible to intraspecific competition whereas *H. villosa* and *K. macrantha* were less tolerant (Appendix 1). In contrast, the number of flowering stems for many of the rare species was tolerant to intraspecific competition but *E. elymoides* had a higher Rii indicating that it produced far fewer flowering stems in intraspecific competition than when grown alone.

In comparison to studies that examine only a few species, the competitive responses of biomass here can be more broadly generalized to common and rare species, since we did not find an effect of species identity and because we used several species for within each group. However, this does not always apply to the number of flowering stems as the identity of the focal species sometimes influenced the competitive response.

Constraints and conclusions

Although we focused on competition, other interactions may also influence species relative abundances. One hypothesis is that dominance may be promoted if common species experience weak feedbacks relative to rare species. In a study of old-field plants in Canada, Klironomos (2002) found that rare species experienced stronger negative feedbacks than common species. Alternatively, dominant competitors may experience strong negative plant-soil feedbacks that limit its performance and promote coexistence (Vanderputten *et al.* 1993; Olff *et al.* 2000; Casper & Castelli 2007). More recently, in a grassland system similar to ours, Reinhart (2012) found no correlation between the strength of plant-soil feedbacks and plant abundance. High abundance of a species may also reflect patterns of consumer preference and defense rather than competitive ability. For example, excluding generalist herbivores (Belsky 1992) or seed predators (Howe & Brown 2000) changed relative abundances and shifted dominant species identity. Alternatively, herbivores often reduce the abundance of the competitive dominant, to the benefit of less common competitively subordinate species (e.g. Dayton *et al.* 1992; Carson & Root 2000; Duffy & Hay 2000). Thus consumer preference, and not differences in competitive ability, may explain species' natural abundances.

Our experimental design overcomes limitations of many competition experiments because we had a focal plant embedded in a competitive neighborhood, rather than only two individuals in competition (Weigelt *et al*. 2007). However, this experiment was still conducted in a garden rather than completely natural conditions and our results only apply to competition between individuals at the same life-stage. Although it is informative to examine competition in natural settings between different life stages (see Farrer & Goldberg 2011), this approach also limits the number of species manipulated. In our study, using a pool of species to represent common and rare abundance categories allowed us to generalize beyond the specific species studied and make conclusions about the relationship between the strength of intra- vs. interspecific competition and abundance in the field.

Historically, ecologists focused on the importance of competition in structuring plant communities and ways in which variation in competitive abilities among species could promote or deter coexistence. There is some experimental support for the notion that competitive ability based on plant size, seed size, or seedling survival determine abundance in natural communities (Mitchley & Grubb 1986; Miller & Werner 1987;

Aplet & Laven 1993; Rees *et al.* 1996; Howard & Goldberg 2001), but it is less clear whether intraspecific levels promote coexistence. In our experiment, the competitive effects of common species were not any stronger than those of rare species and common species had a poor response to competition. This suggests that other factors, such as plant-soil feedbacks or consumer preference, cause dominance in our system. Competition may still be important, because in the field the common grasses are often in intraspecific situations and rare species are often in interspecific competition with the common grasses. Thus strong competitive effects for common species and weak effects for rare species may counter intuitively suggest that competition promotes, rather than inhibits, diversity.

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Table 1. Focal species used in the competition experiment. Mean (+/- SEM) height for each species when grown alone, measured at the end of the first growing season.

Species	**Abundance group**	**Mean height alone (cm)**
GRASSES		
Poa secunda	Common	6.2 ± 0.6
Pseudoroegneria spicata	Common	20.8 ± 1.3
Koeleria macrantha	Common	8.6 ± 0.5
Festuca idahoensis	Common	6.8 ± 0.5
Hesperostipa comata	Common	12.6 ± 1.3
Nassella viridula	Rare	19.4 ± 1.1
Elymus elymoides	Rare	21.5 ± 1.0
Leymus cinereus	Rare	60.4 ± 0.7
Bouteloua gracilis	Rare	37.6 ± 2.6
FORBS		
Achillea millefolium	Common	18.6 ± 0.8
Heterotheca villosa	Common	9.6 ± 1.4
Artemisia frigida	Common	13 ± 1.2
Gaillardia aristata	Common	14.4 ± 0.4
Geranium viscosissimum	Common	13.8 ± 0.6
Symphyotrichum ericoides	Rare	8.8 ± 0.4
Ipomopsis aggregata	Rare	10 ± 2.3

Linum perenne	Rare	23 ± 0.9

Table 2. Interspecific competition treatments. To examine the strength of interspecific competition amongst common species we competed: 1) common forbs against heterospecific common forbs, and 2) common grasses against heterospecific common grasses. To test whether common species had a strong competitive effect on rare species we competed: rare species against common species (3-6). To test whether common species showed a low competitive response to rare species we competed: common species against rare species (7-10).

	Focal species	**Neighbor species**
1)	Common forb	Common forb
2)	Common grass	Common grass
3)	Rare forb	Common forb
4)	Rare forb	Common grass
5)	Rare grass	Common forb
6)	Rare grass	Common grass
7)	Common forb	Rare forb
8)	Common forb	Rare grass
9)	Common grass	Rare grass
10)	Common grass	Rare forb

Figure 1. Diagram showing how plants were arranged within experimental plots. The four neighbors (1-4) were each 10 cm away from the focal individual. Neighbors from separate plots were 40 cm apart. The focal individual was in the plot without any neighbors for the control where each species was grown alone. The four neighbors always had the same species identity. For intraspecific treatments the four neighbors were conspecifics of the focal individual. For the interspecific treatments focal and neighbor species identity was randomly chosen to represent the one of the 10 treatments (Table 2).

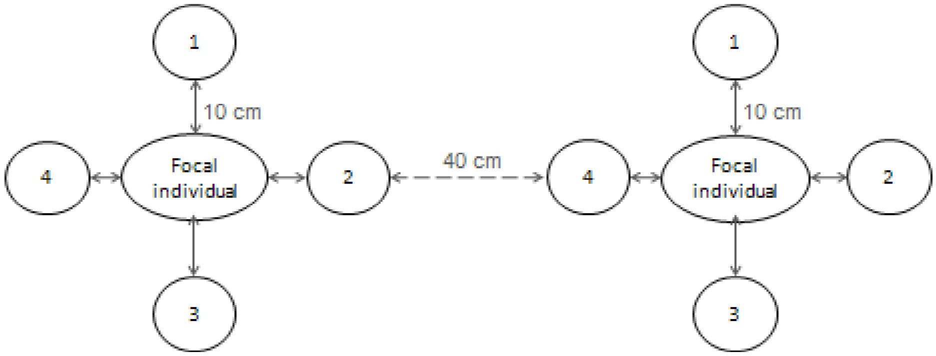

Figure 2. Relative abundance curves for the species used in our experiment. Surveys were conducted at 16 sites across Western Montana (see Methods). The x-axis indicates species identity for a) grasses: KOMA *Koeleria macrantha*, FEID *Festuca idahoensis*, HECO *Hesperostipa comata*, POSE *Poa secunda*, AGSP *Pseudoroegneria spicata*, NAVI *Nasella viridula*, ELEL *Elymus elymoides*, LECI *Leymus cinereus*, BOGR *Bouteloua gracilis*; and b) forbs: ARFR *Artemisia frigida*, HEVI *Heterotheca villosa*, GEVI *Geranium viscosissimum*, GAAR *Gaillardia aristata*, ACMI *Achillea millefolium*, SYER *Symphyotrichum ericoides*, IPAG *Ipomopsis aggregata*, and LIPE *Linum perenne*.

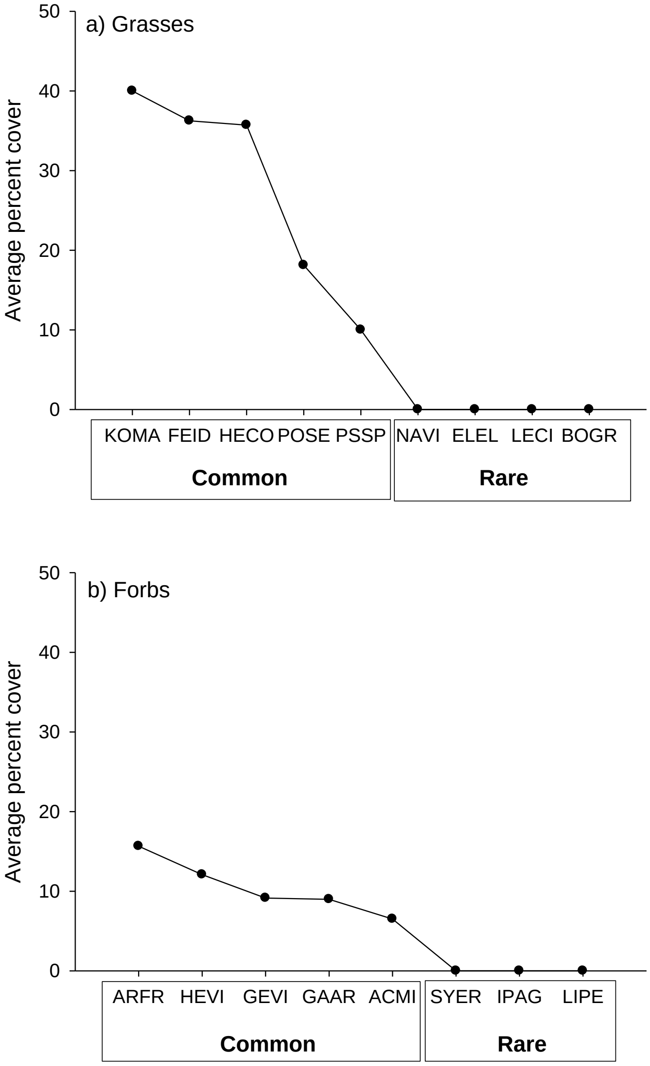

Figure 3. The relative interaction index (Rii) for focal individual biomass for common and rare species in inter- and intraspecific competition. The closer the Rii value is to -1 the greater the negative competitive effect was on the focal plant. The bars represent LS means of the Rii and the error bars represent standard error.

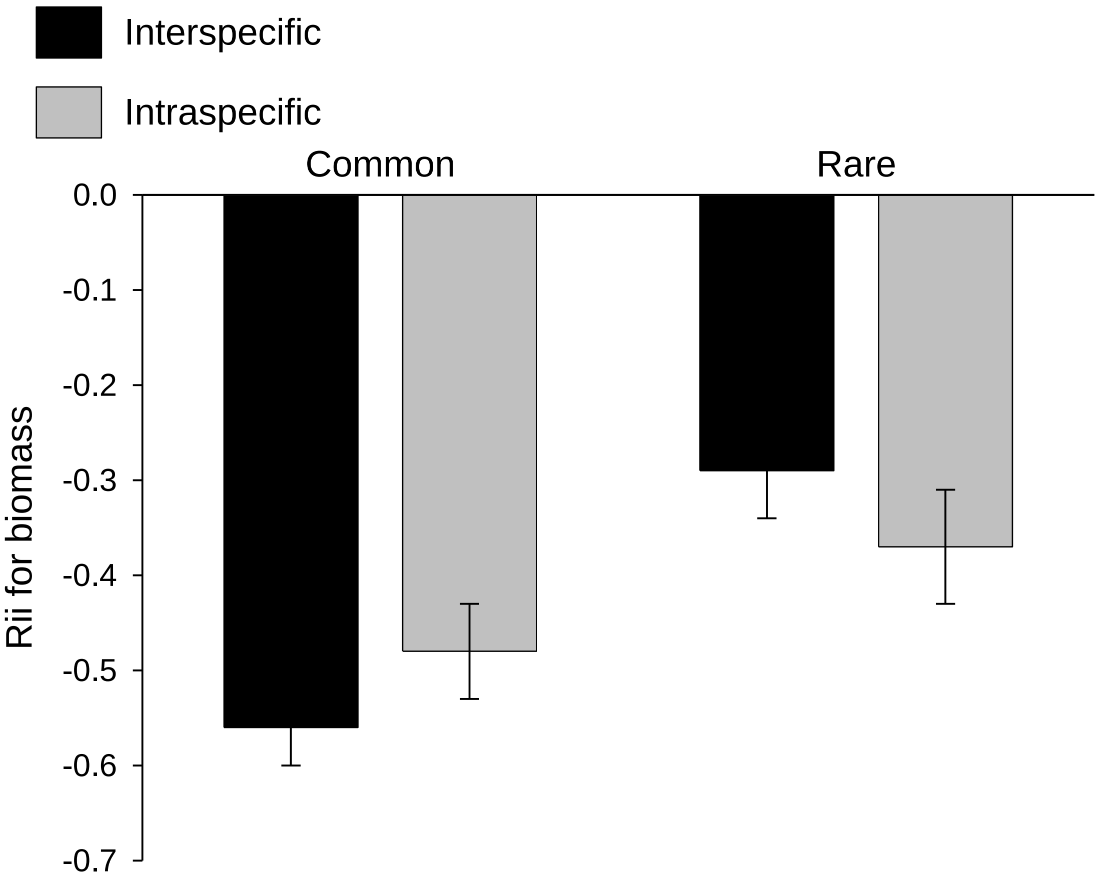

Figure 4. The relative interaction index (Rii) for the number of flowering stems of the focal individual for common and rare species in inter- and intraspecific competition. The closer the Rii value is to -1 the greater the negative competitive effect was on the focal plant. The bars represent LS means of the Rii and the error bars represent standard error.

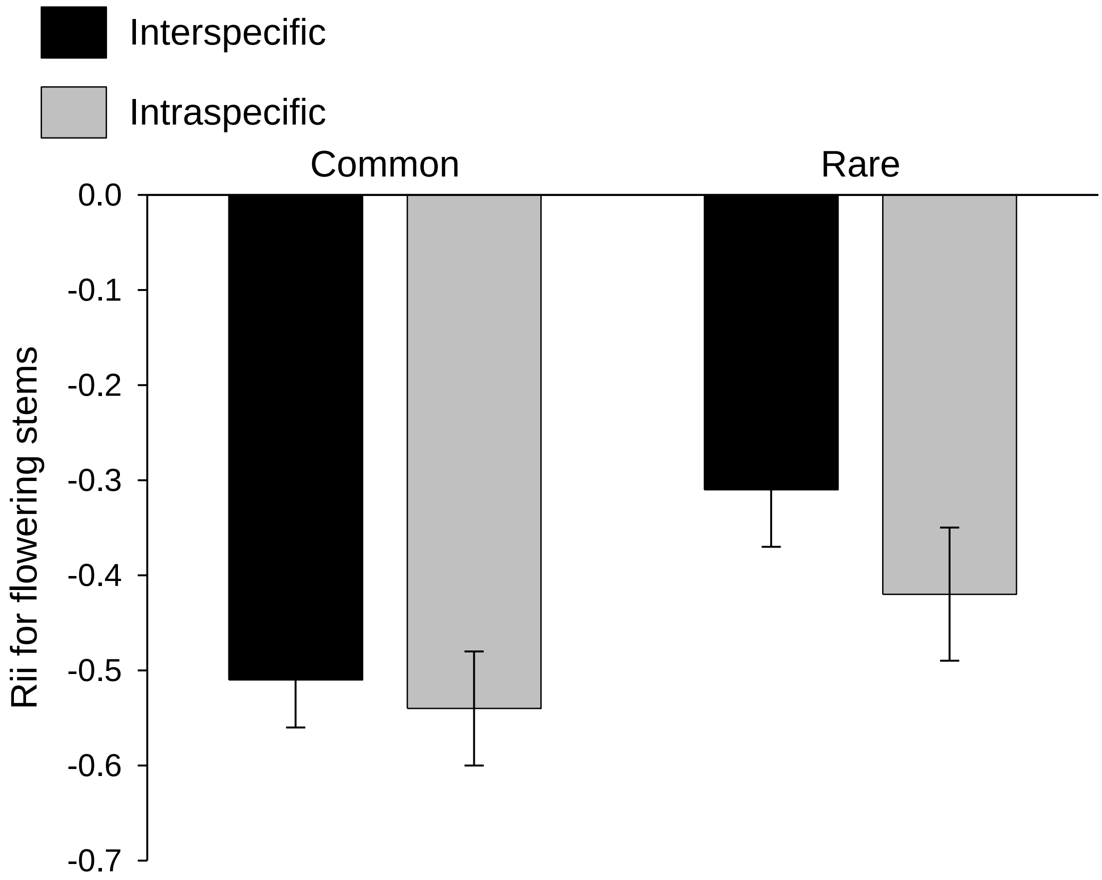

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Figure 5. Inter- and intraspecific competitive effects on focal group biomass for (a) common grasses, (b) common forbs, (c) rare grasses, and (d) rare forbs. The bars represent LS means of the relative interaction indices (Rii) and the error bars represent standard error.

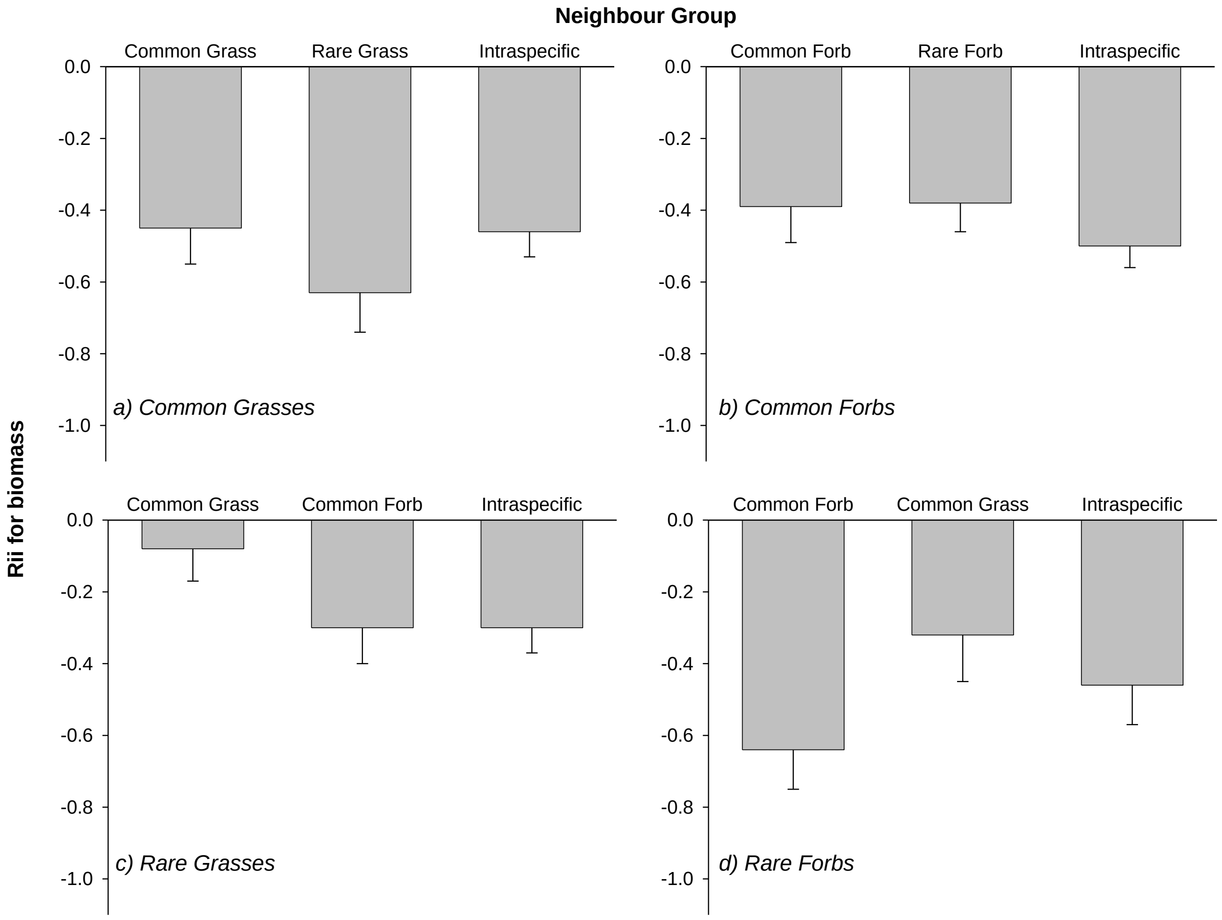
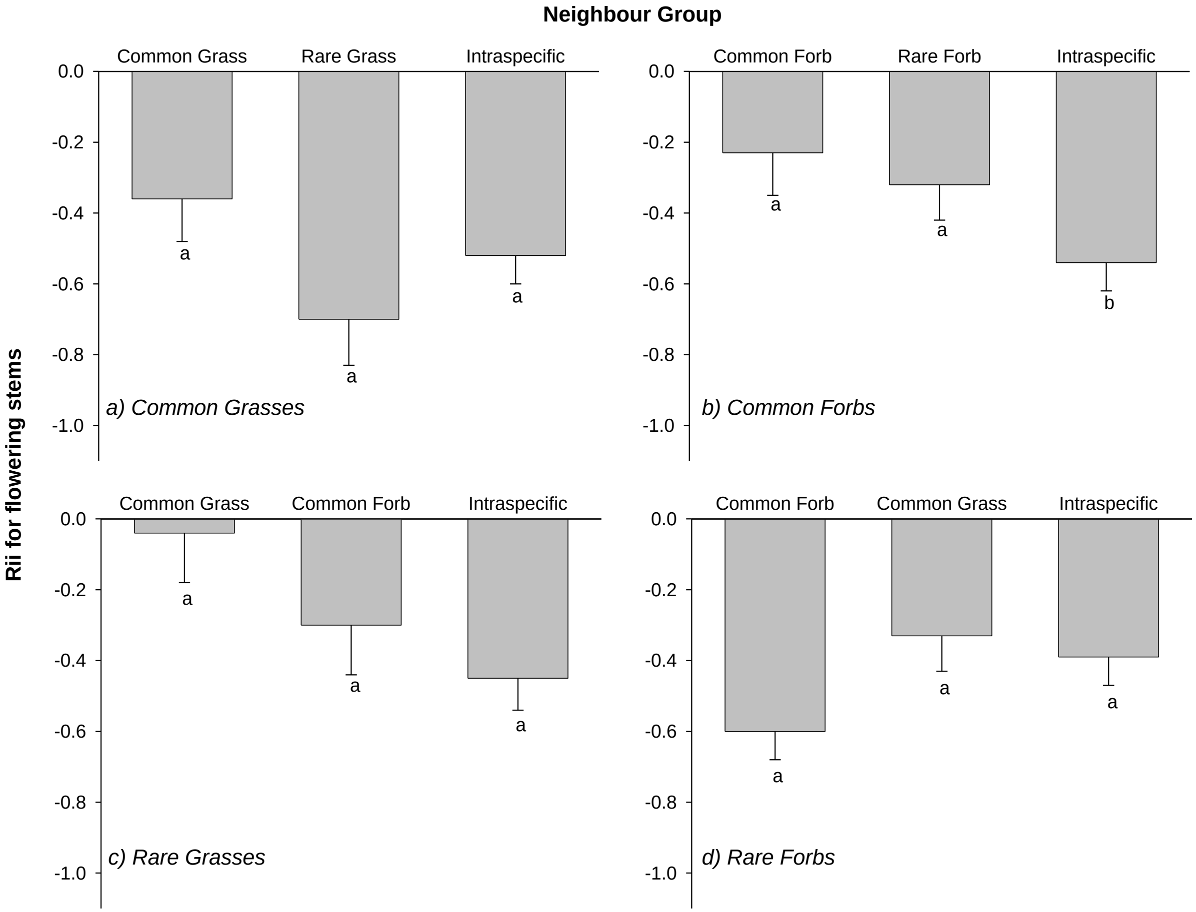
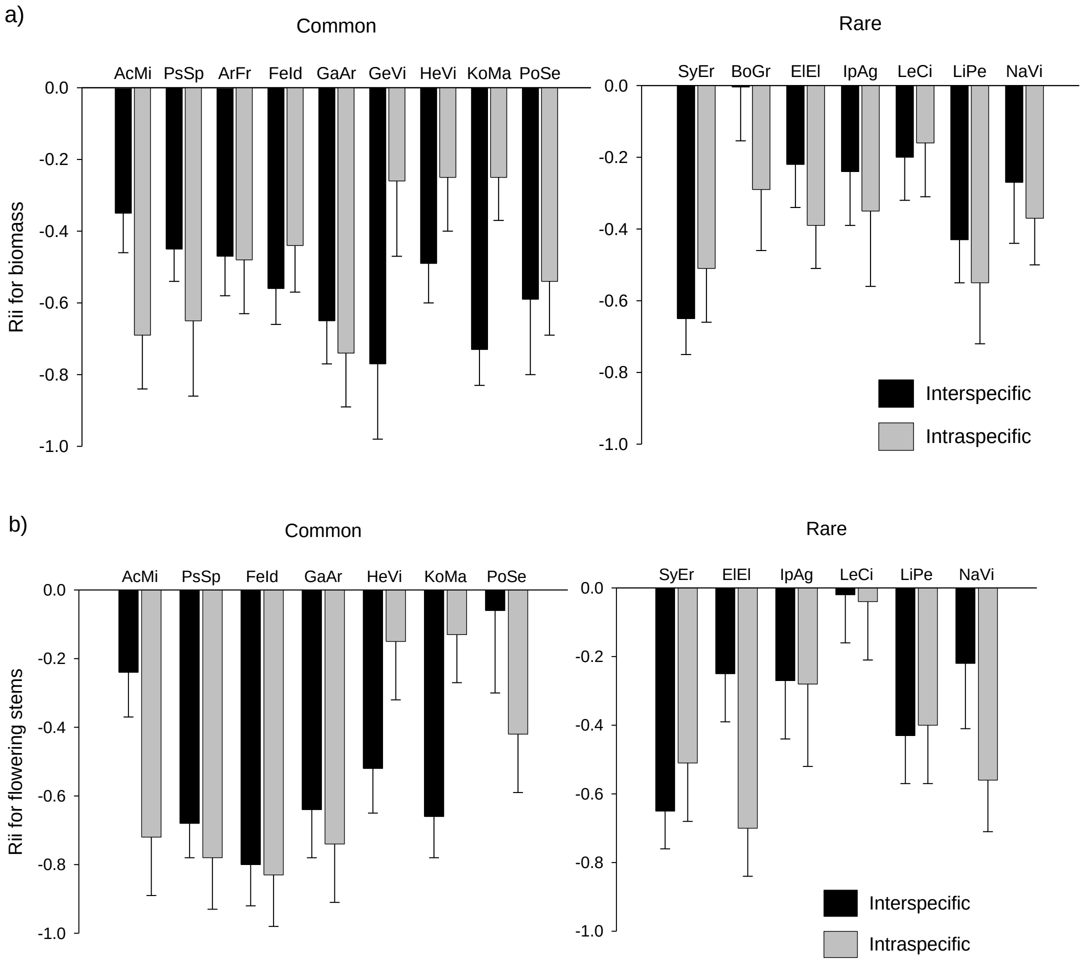


Figure 6. Inter- and intraspecific competitive effects on focal group number of flowering stems for (a) common grasses, (b) common forbs, (c) rare grasses, and (d) rare forbs. The bars represent LS means of the relative interaction indices (Rii) and the error bars represent standard error



Appendix 1

The relative interaction index (Rii) for a) biomass and b) number of flowering stems for focal species from the common abundance group: ACMI *Achillea millefolium*, PSSP *Pseudoroegneria spicata*, ARFR *Artemisia frigida*, FEID *Festuca idahoensis*, GAAR *Gaillardia aristata*, GEVI *Geranium viscosissimum*, HEVI *Heterotheca villosa*, KOMA *Koeleria macrantha*, HECO *Hesperostipa comata*, POSE *Poa secunda*, and the rare abundance group: SYER *Symphyotrichum ericoides*, BOGR *Bouteloua gracilis*, ELEL *Elymus elymoides*, IPAG *Ipomopsis aggregata*, LECI *Leymus cinereus*, LIPE *Linum perenne*, NAVI *Nassella viridula*. For average values for each group see Fig. 3 (biomass) and Fig. 4 (flowering stems).



Chapter 2

Seed dispersal is more limiting to grassland diversity than competition or seed predation

Abstract

Although competition has historically been viewed as the predominant process affecting plant communities, it is increasingly recognized that a variety of other processes such as dispersal limitation and seed consumption can influence community structure. The relative strength of these processes, however, remains unclear. We examined how interspecific competition, dispersal limitation, and post-dispersal seed predation by mice individually and interactively influenced plant species richness, evenness, and seedling establishment in grasslands in western Montana. We added seeds of 20 species of mostly locally uncommon species to plots where we manipulated competition from resident dominant or common plants in and out of larger rodent exclosure plots. Competition was manipulated by removing the same amount of cover of an individual dominant species or several common species in the smaller subplots. Seed addition and competitor removal increased the richness and evenness of local assemblages. Across all levels of the other treatments, average richness for the control subplots without competitor removal was 12.0 ± 0.9 species whereas the removals provided some competitive release and averaged 15.5 ± 1.1 for the dominant removal and 16.0 ± 1.1 when common species were removed. We detected no difference between the dominant and common removal treatments on diversity, suggesting that one dominant species had similar competitive effects as several common species. In contrast, preventing seed predation by mice did not have significant effects on richness or evenness. Our results suggest that regional dispersal limitation prevents relatively uncommon species from reaching appropriate environments, and this is a greater constraint on local community diversity compared to local interactions, such as competition and seed predation. Although competition was important in this system, it was not the most important process determining diversity, nor did the most abundant species provide the most intense competition.

Keywords: competition, dispersal limitation, diversity, grasslands, *Peromyscus maniculatus*, relative abundance, seed predation, seedling establishment

Introduction

One way to understand ecological processes that determine local plant community structure is to think of them as a series of filters, at regional and local scales, which species must sequentially pass through before establishing in a community (Ricklefs 1987; Keddy 1992). For plants, competition has been traditionally viewed as the primary driver determining local plant diversity (Tilman 1982; Chase & Leibold 2003). However, whether regional processes or other local interactions, such as dispersal limitation or consumers, respectively, have stronger effects on local community structure compared to competition is unclear because these processes are often studied in isolation (e.g. Abulfatih & Bazzaz 1979; Foster & Tilman 2003; Heske *et al.* 1993).

A widely held assumption is that the strength of competition in plant communities is directly correlated to the relative abundance of species, i.e., the most abundant species may be the strongest competitor and can often decrease the abundance of weaker competitors (Weiner 1990; Schwinning & Fox 1995; Pennings & Callaway 1992; Facelli & Temby 2002). Although we know competition can change community composition (Johnson & Mann 1988) and decrease richness (Abulfatih & Bazzaz 1979; Wardle *et al.* 1999), whether the most abundant species have more limiting effects on the establishment of potentially colonizing species compared to less abundant species is unclear. On the one hand, the most abundant species may be competitively superior and potentially exclude colonizing species. On the other hand, less abundant resident species may together create a strong competitive environment, because in sum they occupy more niche space than a single dominant species (e.g. Tilman 1982; Chase & Leibold 2003). Results from previous studies have found evidence that both dominant species (Emery &

Gross 2006; Gilbert *et al.* 2009) as well as many rarer ones (Lyons & Schwartz 2001; Zavaleta & Hulvey 2004) can competitively exclude colonizing species from establishing. However, it is not clear whether response to removals in many of these studies is actually due to differences in abundance in the field or if the competitive release is due to the specific identity of the species being removed.

In addition to competition, post-dispersal seed predation by rodents can also strongly influence colonization and might interact with competition from resident species. Past studies demonstrated that rodent seed predation can change the density of dispersed seeds (Reichman 1979; Hulme 1994; Moles *et al.* 2003), which can in turn change the relative abundances of recruiting species (Brown & Heske 1990; Edwards & Crawley 1999; Bricker *et al.* 2010; Pearson *et al.* 2011). Of the few studies that have concurrently examined seed predation and competition, two found that seed predation decreased the abundance of the strongest competitor (Samson *et al.* 1992; Howe & Brown 2001). Yet whether seed predation changes the establishment of potential colonist species in the face of competition from residents remains unclear.

Finally, the diversity and relative abundance of species in local communities may be less influenced by local processes and more affected by regional scale “neutral” influences, such as seed dispersal. In many communities, dispersal limitation constrains local species richness (Tilman 1997; Turnbull *et al.* 2000; Brown & Fridley 2003; Foster & Tilman 2003; Wilsey & Polley 2003). Dispersal limitation may influence seed predation and competition; certainly without seeds arriving at a site there is no template for processes that act at the local scale (Schupp & Fuentes 1995; Harms *et al.* 2000; Clark *et al.* 2007). Furthermore, the importance of dispersal limitation for community assembly may depend on the competitive effect of the dominant species (Myers & Harms 2009a).

The relative importance of dispersal limitation, competition, and seed predation in affecting the structure of local communities is unknown. In our system the most abundant species tend to be large bunchgrasses and there is a wide variation in the species abundance, but the causes for these differences are unclear. Previous work in these grasslands revealed that rodent seed predation can influence the establishment of large seeded species (Bricker *et al.* 2010; Pearson *et al.* 2011; Pearson *et al.* 2012) and can interact with disturbance to influence recruitment into local sites (Maron *et al.* 2012). Here we experimentally test how dispersal limitation, competition from dominant and common species, and post-dispersal seed predation by mice individually and interactively influence local plant community diversity in grasslands in western Montana.

Methods

Study system

Our study was conducted at eight widely separated sites that spanned ~50 km across the grasslands in the Blackfoot Valley in western Montana. Across the region, plant communities are dominated by rough fescue (*Festuca capestris*), but several other graminoids can be locally dominant. Most of the rare species in the region tend to be annual or perennial forbs (Appendix 1). The main rodent seed predator at our sites is the deer mouse (*Peromyscus maniculatus*). Montane voles (*Microtus montanus*) and Columbian ground squirrels (*Spermophilus columbianus*) also occur at all our sites, but voles occur at low densities and both species are mainly herbivorous (as opposed to granivorous; Maron *et al.* 2010).

Experimental design

We performed a factorial experiment that crossed seed addition, mice exclusion, and competitor removals (Fig. 1). The seed addition treatment had two levels: with or without 20 added species. The seed predation treatment had two levels: inside or outside a fence that prevented access by mice. The competitor removal treatment had three levels: removal of the dominant species only, removal of several common species, and no removal. Competition and seed addition treatments were placed in 10 m x 10 m mice exclosures and nearby (10-20 m away) paired mice exclosure control plots at each site (three sites in 2006 and five sites in 2009). Mice exclosures were constructed using a 60 cm high welded wire fence (mesh size = 0.625 × 0.625 cm) fence topped with 20 cm of aluminum flashing to prevent mice from climbing over. Fences were buried 40-50 cm underground to prevent mice from tunneling into plots. We maintained snap traps within exclosures to ensure plots were free from mice. Two exclosures were constructed in 2002, one in 2004, and five in 2008. Mice exclosure control plots were located adjacent to each rodent exclosure. We randomly located and marked six 50 cm x 50 cm subplots within each mice exclosure and exclosure-control and randomly assigned subplots to seed addition and removal treatments (Fig. 1; 3 removals x 2 seed addition x 2 mice exclosure x 8 sites = 96 subplots).

To test how dispersal limitation might influence local species richness and differences in species abundance we added a mixture of seeds from 20 native species (Table 1) in August 2010. Although these 20 species are present in the system, they are rarely present in our plots (Maron & Pearson, unpublished data). Adding relatively uncommon species allowed us to examine how dispersal limitation, seed predation, and competition contributed to the low abundance of these species. Two species were included in the additions despite their higher regional abundance: *L. sericeus* because it has a large seed and *C. parviflora* because it is a spring-annual, allowing us to examine a larger variation in seed size and phenology. Seeds were collected from multiple sites across the Blackfoot Valley in 2010. We added 50 seeds per subplot for species with large seeds > 0.006 g, 100 seeds per subplot for species with medium seeds ≤ 0.006 g and > 0.001g, and 175 seeds per subplot for species with small seeds ≤ 0.001 g. We chose these seed numbers to represent variation among species due to trade-offs between seed size vs. seed number. That is, there is a continuum between species that produce lots of small seeds or a few big seeds (Moles & Westoby 2004). We added a quarter of the amount for *C. parviflora* seeds, since we did not have enough, but it has the highest natural establishment of the 20 added species (Pinto *et al.*, unpublished data).

We performed two types of removals to test for competitive effects of dominant and common species. The removals were based on local rank-abundance curves we constructed for each subplot and thus were “species-blind” because removal was not based on species identity (see Appendix 2 for the various species included in these treatments). One advantage to this approach is that we can make conclusions about competitive release from groups that differ in local abundance, rather than competition from specific species. The species-blind approach is also appropriate given that most of our dependent variables are too, that is neither richness or evenness account for differences in species identity.

We used a 50 cm x 50 cm quadrat with string marking 25 equal sized squares, each square represented 4% of the plot, to estimate cover of the species targeted for removal. Next we removed vegetation representing 40% of the area in the subplot for each competition treatment. For the dominant removal we removed the locally dominant species, that is the species with rank 1 in the 50 cm x 50 cm subplot. For the common species treatment we consecutively removed 3-6 species, starting at rank 2, until 40% cover was removed. Hence, locally abundant and common species were defined by relative abundance measured within a plot and species identity within these categories varied across plots. We removed 40% cover so that the treatment created a consistent amount of bare ground, which is important for seedling establishment. However, because the dominant species tended to be large bunchgrasses, we removed a larger amount of biomass in the dominant treatment (111 ± 31 g) than the common species treatment (42 ± 18 g). For the removals we diluted an herbicide (Round-Up, glyphosate 5% concentration) and painted it on the targeted species. We painted the targeted species in late June 2010 and returned in late July 2010 to clip the dead vegetation. The biomass was dried in ovens at 70^{o}C and weighed.

To test how our treatments influenced species establishment, in June 2011 we counted the number of seedlings of each added species in each subplot. To test how our treatments influenced community structure, in June 2012, we used a 50cm x 50cm quadrat divided into 25 squares and counted the number of squares in which each species occurred.

Statistical analyses

We first tested whether our removal treatments effectively decreased the abundance of the targeted species. To do this we performed repeated measures ANOVAs, using a negative binomial distribution, to compare the number of squares (out of a total of

25) in which the targeted dominant or common species, separately, occurred over the three years of our experiment.

The year after the seed addition, in 2011, we examined how many of the added species had established as seedlings. We did this only for the first year because two years after the seed addition, in 2012, it was difficult to distinguish between new seedlings and small plants that had established in the previous year. To further test whether the treatments had lasting effects on community structure, in 2012 we examined changes in local species richness, diversity as measured by the inverse Simpson’s index, and composition. The inverse Simpson’s index is the reciprocal of the dominance measure (where 1 would indicate complete dominance) and thus the inverse Simpson’s index measures how many species would be represented in the community if they all had equal abundances. We pooled the mice exclosure and control plots when calculating the inverse Simpson’s index, since there was no significant difference in richness between the exclosure and control (see Results).

For species richness of seedlings of added species in 2011, local community richness in 2012, and the inverse Simpson’s index in 2012, we conducted separate split-plot three-way ANOVAs using SAS (version 9.3). We used these analyses to examine the effects of seed addition, competitor removals, and mice exclusion. We used a split-plot analysis because mice exclusion was applied at the whole plot level whereas the other treatments were applied at the subplot level. Site was included as a random factor.

Results

Removal treatments successfully reduced the abundance (as estimated by the number of squares per quadrat) of both the targeted local dominant species ($F_{2,81}$=121.08,

$P<0.001$) and the targeted common species in ($F_{2,93}=35.36$, $P<0.001$) for both years after the removal (Fig 2). Across the replicates of the removal treatments, there were six different species that were removed as local dominants and 34 removed as locally common (Appendix 2).

Seed addition resulted in a significant increase in the number of added species establishing in 2011 ($F_{1,70}=110.8$, $P<0.001$). However, the magnitude of these effects were contingent upon local competition (seed addition x competition: $F_{2,70}=3.4$, $P=0.040$). Least-squares means contrasts showed that there was greater natural recruitment of the focal 20 species in no-seeds-added and no-removal control plots than in the subplots where no seeds were added and common species were removed ($t_{70}=-2.49$, $P=0.015$; Fig. 3). Neither the main effects of competition ($F_{2,70}=2.2$, $P>0.1$) nor mice exclusion ($F_{1,7}=0.08$, $P>0.8$) significantly affected the number of added species that established. Moreover, there were no significant interactions between competitor removal, mice exclusion, and seed addition (mice exclusion x removals: $F_{2,70}=0.4$, $P>0.6$; mice exclusion x seed addition: $F_{1,70}=2.7$, $P>0.1$; mice exclusion x seed addition x removal: $F_{2,70}=1.1$, $P>0.4$). Of the 20 species we added, 16 established in at least one plot in 2011 (Table 1).

Two years post seed addition, there was a sustained increase in overall local community richness ($F_{1,70}=23.5$, $P<0.001$; Fig. 4). Community richness was not affected by mice exclusion ($F_{1,7}=0.7$, $P>0.4$) and this relationship was unaffected by the seed addition (mice exclusion x seed addition: $F_{1,70}=0.5$, $P>0.5$). Overall richness was higher in competitor removal subplots ($F_{2,70}=10.2$, $P=0.001$) with contrasts revealing higher richness in the common and dominant removal treatment plots relative to the controls (common vs. control: $t_{70}=4.19$, $P<0.001$; dominant vs. control: $t_{70}=3.77$, $P<0.001$), but the common and dominant treatments did not differ in richness ($t_{70}=0.44$, $P>0.7$). Overall richness was not affected by interactions between seed addition, seed predation, and competition (seed addition x removal: $F_{2,70}=1.7$, $P>0.2$; mice exclusion x removal: $F_{2,70}=0.5$, $P>0.6$; mice exclusion x seed addition x removal: $F_{2,70}=0.5$, $P>0.6$).

Evenness (as measured by the inverse Simpson's index) increased with the seed addition ($F_{2,26}=5.19$, $P=0.031$) and with the removals ($F_{2,26}=3.94$, $P=0.032$). Although removals increased evenness relative to the control (common vs. control: $t_{26}=2.2$, $P=0.037$, dominant vs. control: $t_{26}=2.69$, $P=0.012$), there was no difference in evenness between common or dominant removal treatments ($t_{26}=-0.5$, $P=0.620$; Fig. 5).

Discussion

Dispersal limitation, competition, and seed predation can be important in structuring plant communities, but we know little about how these filters interact to affect community structure because prior work has treated these processes independently. We show that the broad-scale filter of dispersal limitation had very strong effects on seedling species richness in our system, thereby potentially influencing other local filters. We found that the seed addition treatment had a larger effect on the number of species establishing as seedlings, community richness, and species evenness than competitive release or the mouse exclusion. Surprisingly, we found very few interactions between dispersal limitation, seed predation, and competition. This was partly due to the overriding importance of the seed addition treatment of species that had low abundance in the region, which suggests that dispersal limitation can limit the abundance of certain species at a regional scale and thus limit local richness and evenness.

The seed addition significantly affected all measures of community structure, indicating dispersal limitation is important in this system. The seed addition caused an increase in overall richness (Fig. 4) and caused many of the added species to reach higher levels of abundance across our sites, leading to an increase in evenness (Fig. 5). The increase in richness of the added species (Fig. 3) indicates that many of these species are dispersal limited and that local environmental factors are not preventing these species from establishing or increasing in abundance. Although 16 of 20 species we added were able to establish at least once in a subplot, many of them did not reach high abundances. This could arise from competition for microsites between seedlings (Turnbull *et al.* 2004).

Our results lend further support to the many studies in grassland systems that found evidence for dispersal limitation (Ehrlen & Eriksson 2000; Munzbergova & Herben 2005; Nathan & Muller-Landau 2000; Fargione *et al.* 2003; Brown & Fridley 2003). Although these studies demonstrate that dispersal limitation is widespread, when added species do not establish in seed addition experiments it is not always clear whether abiotic or biotic factors are responsible for the lack of recruitment by particular species (Turnbull *et al.* 2000), and the role of seed predation is generally ignored in such studies (Maron *et al.* 2012). In our experiment we did not find a significant interaction between the seed addition and the removals, indicating establishment was not limited by competition from the species we removed. We also concurrently excluded seed predators and so know that the species that were not able to establish from the added seeds were likely limited by environmental factors and not by seed predators; at least at the species level although other work shows that populations are limited by seed predation (Pearson *et al*. 2011; Maron *et al*. 2012).

In our study, although the removal of dominant and common species did not cause an increase in species establishment as seedlings, the removals did cause an increase in local community richness two years after removals. The increase in richness may seem surprising at first because establishment of added species was not higher after the removal of potential competitors. However, the higher richness in competitor removal subplots may have been driven by natural recruitment of disturbance-mediated species, such as *Achillea millefolium, Hieracium cynoglossoides*, and *Danthonia unispicata*, in removal subplots. This demonstrates one mechanism for coexistence, where removal of the strong competitors led to the establishment of good colonizers. Moreover, certain species may be dormant and only reappear aboveground under certain conditions, such as reduced competition after the removals. Lastly, plants surrounding the subplots may have grown bigger when their neighbors were removed due to competitive release. Although our method of removing species does not allow us to examine competitive release from specific species, we can conclude that the abundant species (both locally dominant and common species) created a competitive environment that limited local richness.

We found that removing dominant or common species had similar effects on several measures of community structure. This was surprising since the treatments caused differences in richness, where several species were removed for the common treatment versus just one for the dominant treatment. We predicted that removing several species would cause a greater increase in diversity, because more niches would become available and there would therefore be more species establishing than when only one species was removed. Alternatively, early work on competition led to the assumption that the most abundant species must be the strongest competitor (Grime 1973; McNaughton & Wolf 1970) and so we also wanted to test whether its removal would provide the greatest competitive release and lead to greater establishment of added species. We did not find support for either of these hypotheses.

The similarity between the common and dominant removal treatments is somewhat surprising since the strength of competition between plants is often more intense from species with high biomass. Although the method for implementing our treatments ensured that we created the same amount of bare ground with the removals, the dominant species had a much higher biomass than the common species combined. Competition from the common species may have been high, despite their lower biomass, because several species will together use a greater variety of resources. The locally common species removed comprised many different life history strategies including bunchgrasses, sedges, annual and perennial forbs. Since removing several of these species had a similar effect to removing one dominant graminoid, this suggests that there is strong competition for similar resources between plant species in this system.

Other studies have found contrasting results for the effect of competitor removals on seedling establishment, which may be explained by differences in species identity. Some studies have found that dominant species control the establishment of native seedlings (Gilbert *et al.* 2009; Myers & Harms 2009a) whereas others found that the rare species in a community resist invasion by exotics (Lyons & Schwartz 2001; Zavaleta & Hulvey 2004). A few studies found that whether or not the dominant influences establishment and overall richness depends on the functional identity of the dominant (Gilbert *et al.* 2009; Myers & Harms 2009a; Emery & Gross 2006). Another study constructed communities varying in evenness, but with the same species, and found that less abundant species did not influence seedling establishment (Emery & Gross 2007), which is potentially different from our study because in our case removals caused a change in richness.

The importance of functional identity in previous studies illustrates that the results may be based on specific species responses. In contrast, removals in our study were species-blind and so the competitive release was more likely due to the local abundance of the species rather than their specific identity, especially for the common species removal treatment that included 34 different species. A caveat is that the dominant species removal only included six species and *F. campestris* was often the locally dominant species, so results from this particular treatment may depend on the response to removal of *F. campestris* rather than dominant species in general. In contrast to previous studies that removed species based on regional differences in abundance, the removal treatment in our study was done based on abundance at a local scale, where the individual plants are actually interacting, and so is a more accurate description of how competitive effects may differ for species of varying abundance.

Previous work that manipulated disturbance and seed addition in this system found that removing all the vegetation from subplots lead to an increase in recruitment of added species (Maron *et al.* 2012), contrary to what we found when we manipulated only the cover of specific groups of species. Perhaps turning over of soil during the disturbance treatment in work by Maron *et al.* (2012) caused enhanced recruitment compared to our results, since disturbance can aid seedling establishment (Turnbull *et al.* 2000; Myers & Harms 2009b; Zobel *et al.* 2000). Another potential reason for this discrepancy is that the current study used a partial removal of the vegetation, so it is possible that the remaining species in the plots created a competitive environment in which it was more difficult to establish.

We did not find that seed predation influenced broad measures of plant community structure. Previous work in this system revealed that mice limited population-level establishment and abundance of specific species, particularly large seeded species (Pearson *et al.* 2011; Maron *et al.* 2012) like *Lupinus sericeus* and *Lithospermum ruderale* (Bricker *et al.* 2010) and *Tragopogon dubius* (Pearson *et al.* 2012). However, in the current study we did not find that seed predation affected local richness or evenness. Another study in this system, using the same seed addition treatment, found that in seed addition subplots seed predator exclusion led to a higher seedling abundance of the added species, especially after a disturbance (Maron *et al.* 2012). The similarity in richness and evenness with and without mice in the current study differs from work in other systems that found shifts in species relative abundances when rodents were excluded (Howe & Brown 2001; Brown & Heske 1990; Heske *et al.* 1993). These studies were much longer term (e.g. 12 years) and it is possible that a longer time frame is necessary to see shifts for many of the perennial plants in our system as well. Another potential reason for the difference between studies may be because our community measures included several smaller seeded species, which masked any changes in abundance of the large seeded species due to mice exclusion. More likely, it results from individual plants of a species recruiting even though fewer members of that species recruit. If so, then seed predation may take longer to limit plants at the species level than at the population level.

Overall we found evidence for strong dispersal limitation in this system. The seed addition significantly influenced richness, evenness. Our results suggest that competition can be important in grassland systems and limit community diversity. Competitive release may have been strong from the dominant species due to high biomass of the bunchgrasses and it may have been equally strong from the common species because of a greater niche breadth covered by several species. Our approach of examining many species provides results that are more broadly generalized for two main reasons: 1) we removed species based on local abundance, rather than removing specific species, and 2) we added a large number of species as seeds that varied in life history strategies, rather than a few species that were likely to respond to the treatments (for instance because of seed size). We found little evidence for the effect of seed predators, or any interactions between these processes, on plant species richness and evenness in contrast to other work showing strong effects of seed limitation at the population level. Since many plants in our system are long-lived perennials, it may be that interactions will become more apparent over time. For example, the effect of the seed addition may decrease over time while the effect of the removals increases; although species may germinate after seed additions, as they grow competitive interactions may become stronger and prevent establishment (Turnbull *et al.* 2000). Our results demonstrate that although competition is important in grasslands, it is not only competition from the most abundant species that creates the most intense competitive environment.

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Table 1. Species used in the seed addition treatment. The number of seeds added to each subplot for each species depended on their seed size; small seeded species had more seeds added than did larger seeded species (see Methods for details). In 2011, 16/20 species occurred in at least one subplot, shown in the "established in 2011" column.

Species	**Seed size category**	**Seed size (g)**	**Established in 2011**
Anemone multifida	small	0.00133	Y
Astragalus drummondii	medium	0.00340	Y
Balsamorhiza sagittata	medium	0.00908	Y
Collinsia parviflora	small	0.00060	Y
Collomia linearis	small	0.00091	Y
Delphinium bicolor	small	0.00045	N
Dodecatheon conjugens	small	0.00024	Y
Erigeron pumilus	small	0.00010	Y
Fritillaria pudica	small	0.00158	Y
Gaillardia aristata	medium	0.00246	Y
Geum triflorum	medium	0.00124	Y
Heterotheca villosa	small	0.00063	Y
Lithophragma glabrum	small	0.00005	N
Lithospermum ruderale	large	0.02037	Y
Lomatium macrocarpum	medium	0.00806	Y
Lupinus sericeus	large	0.02360	Y
Potentilla arguta	small	0.00009	Y

Saxifraga oregana	small	0.00012	N
Achnatherum richardsonii	medium	0.00160	N
Zigadenus venenosus	medium	0.00023	Y

Figure 1. Experimental design. The large squares represent the mice exclusion plots (10 m x 10 m) and exclusion controls (10 m x 10 m) that were 10-20 m away. The small squares represent subplots that were 50cm x 50cm on a side and nested within the larger mice exclusion plots. Within these larger plots we performed a factorial cross of seed additions and competitor removals, to test for dispersal limitation and competitive effects respectively. There were 20 species added to each seed addition subplot. There were three levels of removals: 1) control (nothing removed), 2) removal of several common species, or 3) removal of one dominant species. Treatments were randomly assigned to subplots in and out of mice exclosure plots. The design was replicated at 8 sites in the Blackfoot Valley, Montana (see Methods for details).

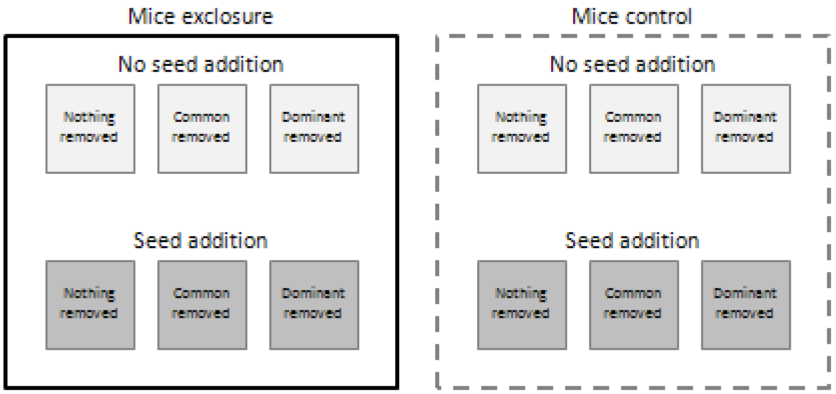


Figure 2. Abundance of the targeted species in the dominant (a) and common (b) species removal treatments, across the seed addition and seed predator exclusion treatments, estimated by the number of squares for each species in a subplot (for a potential total 25 squares for each species per quadrat). As described in the Methods, we removed species in 2010 based on a visual estimation of 40% cover to be more consistent between subplots. In panel (a), "dominant species cover" is the least-squares mean of the number of squares for the local dominant in the subplot before the treatment, in 2010, and after the treatment, in 2011/2012. In panel (b), "common species cover" is the least-squares mean of the summed number of squares of the species removed in that subplot before the treatment, in 2010, and after the treatment, in 2011/2012.

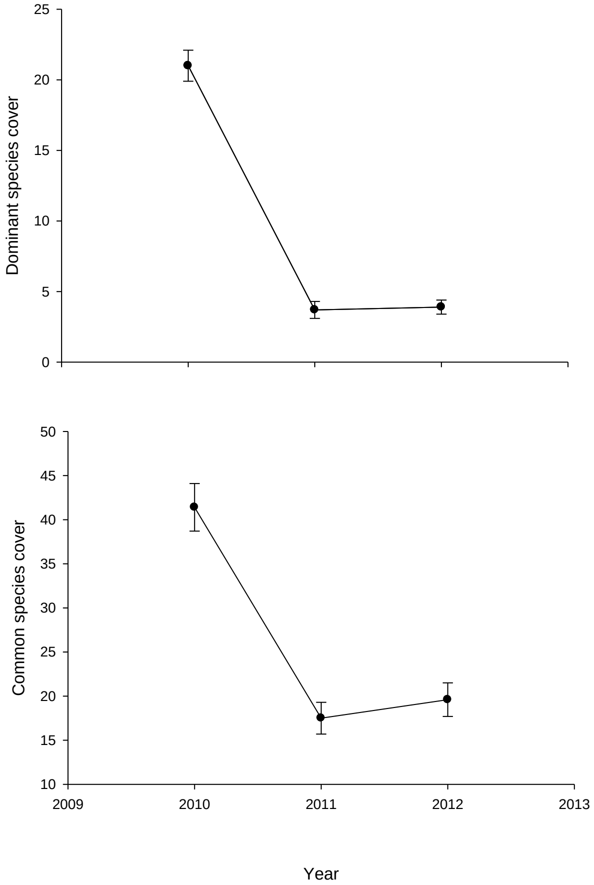


Figure 3. Effect of seed addition, seed predation, and plant removal on seedling recruitment of the focal species. Mean (+/- SEM) number of added species that established as seedlings was higher in seed addition subplots than in the subplots where they established naturally. Seedling richness of the added species was similar between control (left panel, mice access to the seeds) and seed predator exclusion (right panel, no mice access to the seeds) plots. Removal treatments did not significantly affect richness of the added species in seed addition plots, but seedling species richness was higher in control plots where when nothing was removed than when the common species were removed under conditions of natural recruitment.

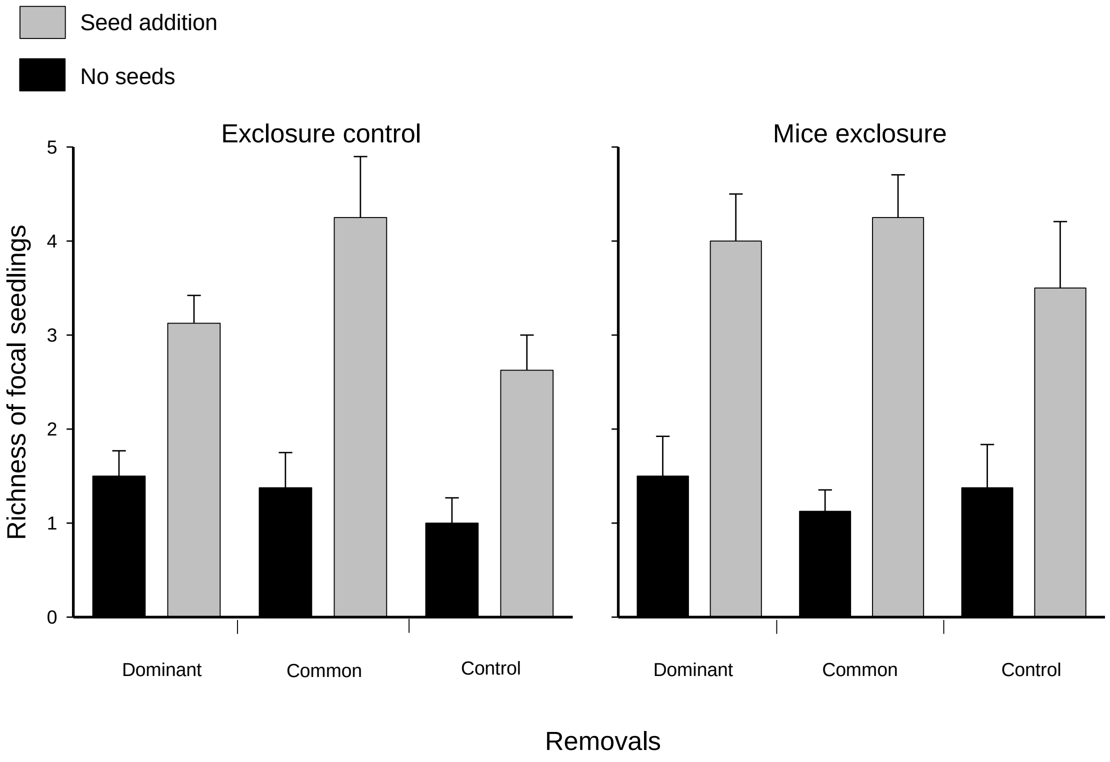


Figure 4. Effect of seed addition, seed predation, and plant removal on local species richness. Local community richness, including resident and added species, was higher in the seed addition plots than in control subplots. Richness of the added species was similar between control (left panel, mice access to the seeds) and seed predator exclusion (right panel, no mice access to the seeds) plots. The common and dominant removals did not differ in richness, but both had a higher richness than the controls without removals.

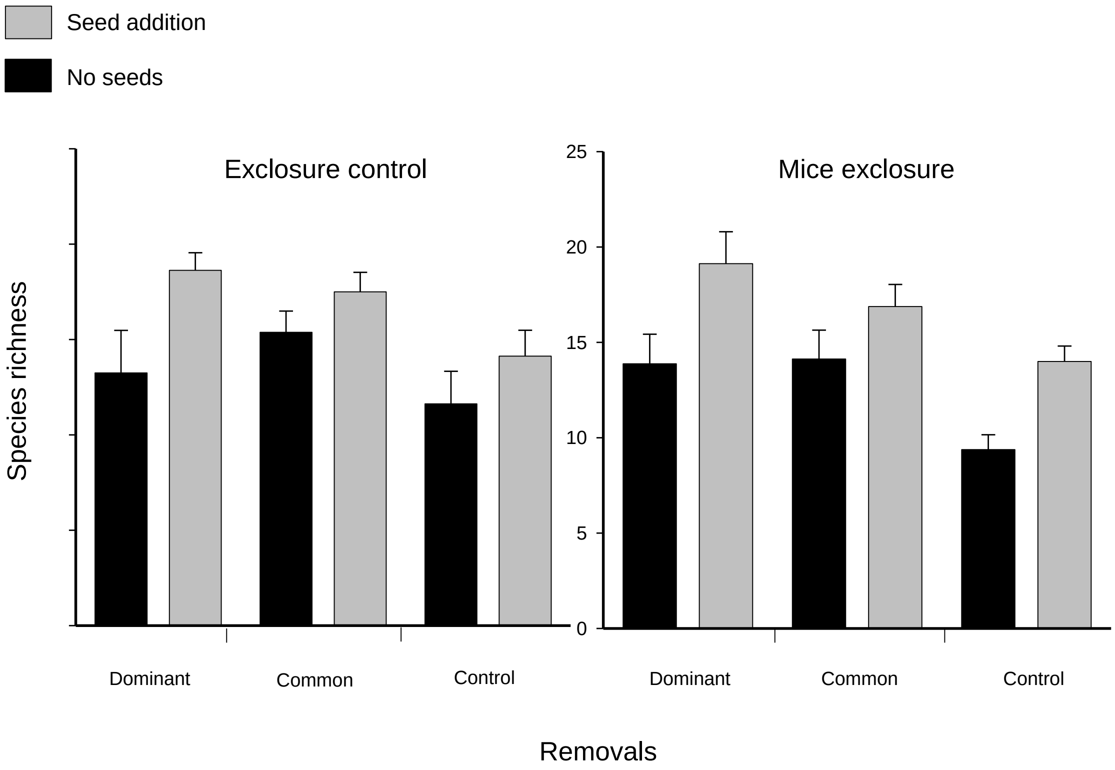
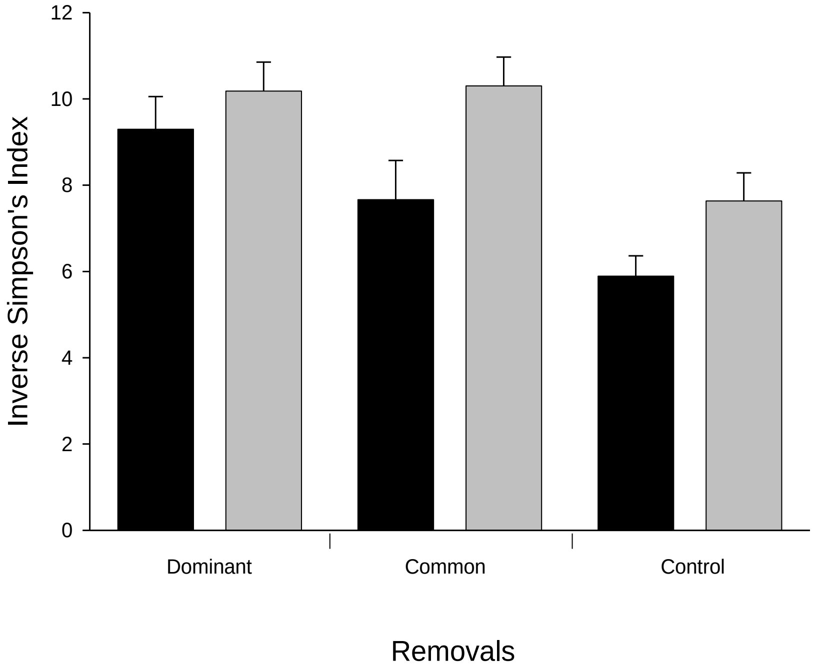


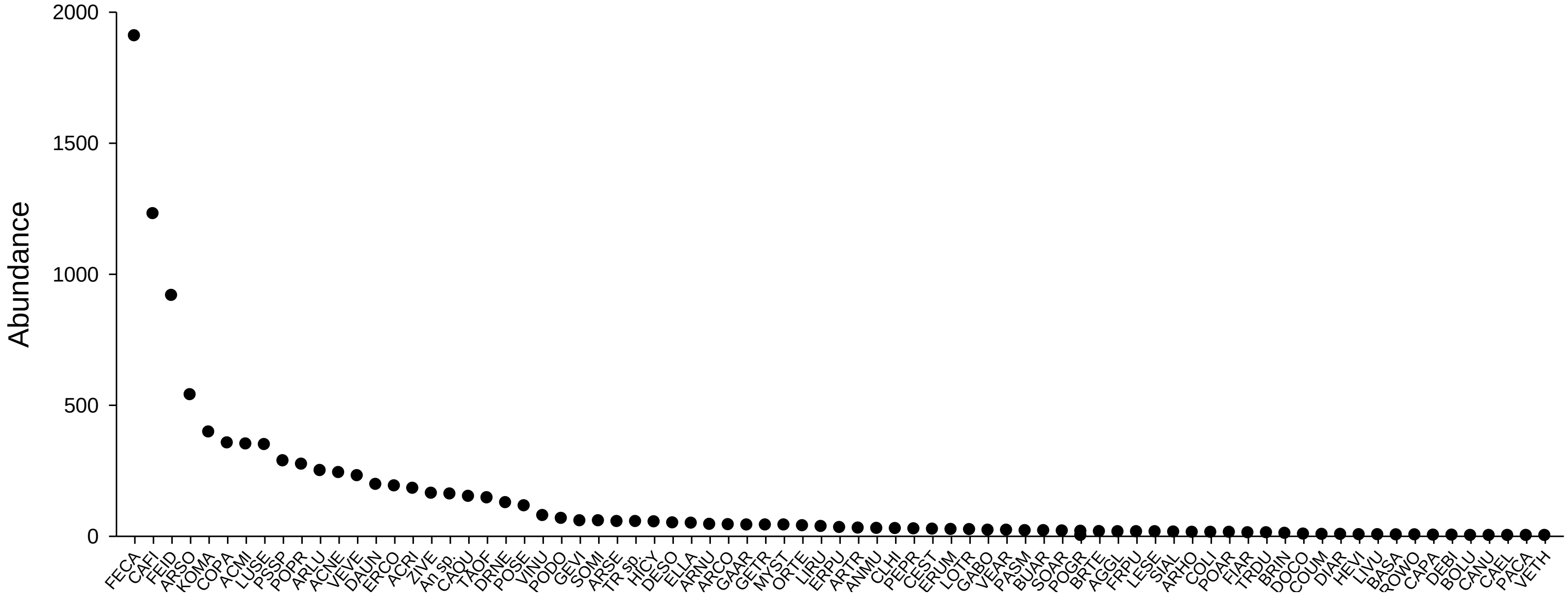
Figure 5. The seed addition (light bars) increased evenness, measured by the Inverse Simpson's index, relative to the controls (dark bars) pooled across the mice exclosure and exclosure-control plots. The common and dominant removals were similar in evenness, but both had a higher evenness than the no removal controls.



Appendix 1

Rank-abundance curve of plant species in the Blackfoot Valley before treatments were applied in 2010. Sampling quadrats were 50 cm x 50 cm on a side and divided into 25 squares with string. For each subplot we counted the number of squares in which each species occurred and then summed the total number of squares for regional species abundance on the y-axis. The symbols on the x-axis represent the following species: FECA *Festuca campestris*, CAFI *Carex filifolia*, FEID *F. idahoensis*, ARSO *Arnica sororia*, KOMA *Koeleria macrantha*, COPA *Collinsia parviflora*, ACMI *Achillea millefolium*, LUSE *Lupinus sericeus*, PSSP *Pseudoroegneria spicata*, POPR *Poa pratensis*, ARLU *Artemisia ludoviciana*, ACNE *Achnatherum nelsonii*, VEVE *Veronica verna*, DAUN *Danthonia unispicata*, ERCO *Erigeron corymbosus*, ACRI *Achnatherum richardsonii*, ZIVE *Zigadenus venenosus*, AN sp. *Antennaria species*, CAQU *Camassia quamash*, TAOF *Taraxacum officinale*, DRNE *Draba nemorosa*, POSE *Poa secunda*, VINU *Viola nuttallii*, PODO *Polygonum douglasii*, GEVI *Geranium viscosissimum*, SOMI *Solidago missouriensis*, ARSE *Arenaria serpyllifolia*, TR sp. *Trifolium spp.*, HICY *Hieracium cynoglossoides*, DESO *Descurainia sophia*, ELLA *Elymus lanceolatus*, ARNU *Arabis nuttallii*, ARCO *Arenaria congesta*, GAAR *Gaillardia aristata*, GETR *Geum triflorum*, MYST *Myosotis stricta*, ORTE *Orthocarpus tenuifolius*, LIRU *Lithospermum ruderale*, ERPU *Erigeron pumilus*, ARTR *Artemisia tridentata*, ANMU *Anemone multifida*, CLHI *Clematis hirsuta*, PEPR *Penstemon procerus*, CEST *Centaurea stoebe*, ERUM *Eriogonum umbellatum*, LOTR *Lomatium triternatum*, GABO *Galium boreale*, VEAR *Veronica arvensis*, PASM *Pascopyrum smithii*, BUAR *Buglossoides arvensis*, SAOR *Saxifraga oreganum*, POGR *Potentilla gracilis*, BRTE

Bromus tectorum, AGGL *Agoseris glauca*, FRPU *Fritillaria pudica*, LESE *Leptosiphon septentrionalis*, SIAL *Sisymbrium altissimum*, ARHO *Arabis holboellii*, COLI *Collinsia linearis*, POAR *Potentilla arguta*, LOAR *Logfia arvensis*, TRDU *Tragopogon dubius*, BRIN *Bromus inermis*, DOCO *Dodecatheon conjugens*, COUM *Comandra umbellata*, DIAR *Dianthus armeria*, HEVI *Heterotheca villosa*, LIVU *Linaria vulgaris*, BASA *Balsamorhiza sagittata*, POWO *Poa wolfii*, CAPA *Castilleja parviflora*, DEBI *Delphinium bicolor*, BOLU *Botrychium lunaria*, CANU *Carduus nutans*, CAEL *Calochortus elegans*, POGR *Potentilla gracilis*, PACA *Packera cana*, VETH *Verbascum thapsus*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Appendix 2.

Species removed, based on local abundance, for the dominant and common species competition treatments. See Methods section for details on removals.

Dominant treatment	**Common treatment**
Achnatherum nelsonii	*Achillea millefolium*
Achnatherum richardsonii	*Achnatherum nelsonii*
Carex filifolia	*Achnatherum richardsonii*
Festuca campestris	*Antennaria rosea*
Poa pratensis	*Arenaria congesta*
Pseudoroegneria spicata	*Artemisia frigida*
	Artemisia ludoviciana
	Arnica sororia
	Artemisia tridentata
	Bromus inermis
	Carex filifolia
	Carex siccata
	Collinsia parviflora
	Danthonia unispicata
	Erigeron corymbosus
	Eriogonum umbellatum
	Festuca idahoensis
	Festuca campestris
	Hieracium cynoglossoides

Heterotheca villosa

Koeleria macrantha

Lithospermum ruderale

Lupinus sericeus

Myosotis stricta

Orthocarpus tenuifolius

Penstemon procerus

Poa pratensis

Poa secunda

Pseudoroegneria spicata

Solidago missouriensis

Taraxacum officinale

Veronica verna

Zigadenus venenosus

Chapter 3

Native species richness buffers invader impact in undisturbed but not disturbed grassland assemblages

Abstract

At local levels, invader abundance and impact on native assemblages depends on variation in plant diversity and the identity of the exotic species. However, many systems are prone to frequent natural disturbances and whether native diversity provides substantial resistance against invader impact in the face of disturbance has seldom been explored. We examined the influence of experimental burning on invader abundance and impact using previously constructed grassland assemblages that varied in native plant richness and that had been experimentally invaded with either *Centaurea stoebe*, *Linaria dalmatica,* or *Potentilla recta,* or left uninvaded. Using these assemblages allowed us to examine whether natives or invasives were favored by a disturbance that is common to the native system that has now been invaded to varying degrees by various exotic species based on the local diversity. Of particular interest was whether fire exacerbated or reduced invader abundance and impact, and how these effects might be mediated by background native species richness or by different exotic species. We found that invaders had higher cover in experimentally burned plots than in control plots across all levels of native species richness. In unburned plots there was no impact of invaders on natives at higher richness levels, however in burned plots the invaders had a strong impact on natives across all richness levels. *C. stoebe* had the highest cover, followed by *L. dalmatica* and lastly *P. recta*, but regardless of these differences in abundance the invaders all had a significant impact on native cover after the fire. These results indicate

that seven years after experimental invasion the native species richness still suppresses invader cover, however after a disturbance the invaders had a negative impact on the natives regardless of the species richness levels.

Introduction

Many systems are already invaded to varying degrees depending on their diversity and continue to experience natural disturbance regimes, but it is unclear how invaded communities will respond to natural disturbances. Declines in local plant species richness can often facilitate invader establishment and increase subsequent invader abundance (Tilman 1997; Naeem *et al*. 2000; Dukes 2002; Fargione & Tilman 2005; Maron & Marler 2007) and decrease resilience to a disturbance (Tilman & Downing 1994; Hector *et al*. 2010; Richardson *et al*. 2010; van Ruijven & Berendse 2010). However, the interplay between species loss and disturbance in affecting invader abundance is less clear because these processes are often studied in isolation. Given that low diversity communities are more heavily invaded, is there a legacy of this pattern post-disturbance? Or, given that disturbance encourages invasion (Burke & Grime 1996; Davis *et al*. 2000; Hierro *et al*. 2006), does disturbance “wipe the slate clean” and essentially open the door to invader success regardless of past influences of diversity on invasibility? In systems with a natural fire regime, invasibility is higher after a fire (Harrison *et al*. 2003) especially in low diversity communities (MacDougall 2005). Yet it is unclear whether there is a legacy of invasion that differs based on levels of diversity and influences subsequent patterns of invader abundance after a fire.

In addition to the question of how the relationship between native diversity and invader abundance is affected by fire, it is of interest to understand how this could affect the subsequent impact of invaders on natives. On the one hand, invader impact could decrease after fire because natives that are adapted to the fire regime may benefit, whereas non-adapted exotics may not (Levine *et al*. 2003). Alternatively, after fire the impact of invaders on natives might increase since disturbance may promote invader success more than it does that of natives (DiTomaso *et al.* 2006). Furthermore, the identity of the exotic species may also influence invader impact since exotics differ in their strength of invasion (Ortega & Pearson 2005) and their competitive abilities (Maron & Marler 2008b). Although previous studies have examined the interactions between invasion and the fire regime (Sheley *et al.* 1998; Jacobs & Sheley 2003; Lesica & Martin 2003; Emery & Gross 2005), few have examined how conditions before the disturbance, including native diversity, invader identity and abundance, may influence the impact of invaders on native species post-fire. Understanding these interactions could have important ramifications for how systems are managed, particularly as it relates to how fire might be used as a management tool to influence both native and exotic abundance (Hobbs & Huenneke 1992).

In this study, we tested how experimentally invaded plant assemblages that varied in native species diversity responded to fire. Previous work with these assemblages demonstrated that: 1) less diverse assemblages were more invaded, 2) *Centaurea stoebe* was a more potent invader than *Potentilla recta* and *Linaria dalmatica*, and 3) invader impact scaled linearly with invader abundance (Maron & Marler 2007, 2008a, 2008b). Thus in the current study we were able to examine how these differential conditions affected community response to a fire. To test whether conditions, such as diversity levels or exotic identity, had a legacy and influenced community response to disturbance we examined changes in invader and native cover with and without a disturbance. These measures also allowed us to examine whether natives or exotics were favored by an historic disturbance. Furthermore, by comparing native cover in uninvaded vs. invaded subplots we could examine the impact of the three different invaders on native cover.

Methods

Study System

We originally created experimental plant assemblages to mimic natural bunchgrass communities that vary in species richness in the Missoula Valley, USA. The three exotic species used in our study, *Centaurea stoebe* (spotted knapweed), *Linaria dalmatica* (Dalmatian toadflax) and *Potentilla recta* (sulphur cinquefoil), are all recognized as noxious weeds in the Mountain West (Montana Department of Agriculture 2003). Previous experimental work has shown that *C. stoebe* is the strongest of these invaders (Maron & Marler 2008b).

Experimental design

In the spring of 2003, we constructed experimental native plant assemblages in 3 x 3 m plots. Plots contained assemblages that ranged in native species richness from 1 to 16 species (Appendix 1), which were created by transplanting greenhouse-reared seedlings (from locally collected seed). Each plot was divided into four 1.3 x 1.3 m subplots separated by a 40 cm buffer and planted with identical mixes of species at the same initial densities (Fig. 1). Plots were arranged in three blocks and weeded throughout the summers to maintain the assigned species composition (see Maron & Marler 2007, 2008a). After two growing seasons, in the fall of 2004 subplots within the plots were randomly assigned to be invaded by sowing seeds of one of the three exotic species or remain as an uninvaded control (see Maron & Marler 2007 for details). The fourth subplot was left uninvaded. Subplots were invaded with either 10.71 g of knapweed seeds, 0.76 g of toadflax seeds, or 0.85 g of cinquefoil seeds, which represented the same number of seeds of each invader. In September 2005, subplots were reinvaded with half as many seeds of each invader as added in 2004. From 2004 to 2007, half of the plots received a water treatment during the growing season. For two of the three exotics there was no significant effect of this treatment on invasibility or competitive impact on the natives (Maron & Marler 2008a, 2008b) although watering did increase knapweed invasion (Maron & Marler 2007). In the present study we assigned former un-watered and watered plots equally between disturbance treatments (Table 1), but did not include water addition as a factor in our analyses.

At the beginning of the current study, in 2009 we randomly assigned a subset of 30 plots to an experimental disturbance treatment and 22 plots to a no-disturbance control. We randomly assigned formerly un-watered and watered plots equally between disturbance treatments. Control and treatment plots ranged in native species richness from 2 to 10 species, as measured in the uninvaded subplot in 2009. The disturbance treatment, for the current study, was then applied at the plot level and consisted of a drought followed by a burn. Fire is a disturbance common to grasslands in the dry intermountain west (Old 1969; Kozlowski & Ahlgren 1974; Axelrod 1985) and often occurs late in summer when lightning strikes ignite dry and senesced vegetation.

To impose the drought portion of the disturbance treatment, each time it rained during April-June 2009, we covered plots with 4.5 x 4.5 m clear plastic tarps (>80% light transmittance) that were suspended above plots with bungee cords connected to metal fence posts. Plots were typically covered for less than 24 hours. Rain gauges in three control plots and three drought-disturbance plots showed that the tarps significantly reduced total rainfall from an average of 60 ml to 19 ml (t_2=-18.44, p = 0.001). To impose the fire portion of the disturbance treatment, we applied a low intensity prescribed burn to the treatment plots in August 2009.

Data collection

We used a $1m^2$ quadrat placed at the center of each plot to estimate the cover of: native grasses, native forbs, focal invader, litter, and bare ground. Quadrats were divided into 25 equally sized cells to help estimate the percent canopy cover for any given element, to the nearest percent. We took these percent cover estimates during the peak growing season in 2009 before the prescribed burn and in the summer of 2011, two years after the burn. Since a potential mechanism for change in native cover is an increase in recruitment if fire creates more bare ground, we also counted the number of native seedlings in the quadrat in 2010.

Data analysis

We used ANOVA (SAS version 9.3 using the GLIMMIX procedure) to test the effects of fire on the following response variables in uninvaded and invaded subplots two years after the fire: 1) invader cover, 2) native cover in uninvaded subplots only, calculated as a sum of forb and grass cover per subplot, 3) native cover across uninvaded and invaded subplots, and 4) native seedling abundance. For invader cover, we also included “exotic species” as a fixed factor. We also included “exotic species” as a fixed factor for native response variables in order to contrast subplots invaded by each focal exotic to those that were uninvaded. Native species richness in 2009 was used as a covariate. Block and plot were random factors. We used a beta distribution for invader and native cover, using the transformation (y*(n-1)+ 0.5)/n where y is cover, divided by

100, and n is the total sample size (Cribari-Neto & Zeileis 2010). For native seedling abundance, we used a negative binomial distribution. Initial models included all possible interactions among fixed factors. For invasive cover, we progressively dropped non-significant interactions to obtain the final model. For native cover and seedling abundance, the three-way interaction was marginally significant so we did not drop any interactions.

In order to understand the patterns causing the statistical significance of certain interactions (see Results) we compared least squares means to examine the effects of fire, invasion, and their interaction at three levels of the richness-covariate: four, six, and eight species. These levels represent a range of species richness with more than three replicates per level. We first tested whether invader cover differed for the three exotics by comparing LS means of invasive cover at each of the three levels of richness, in burned and unburned plots separately. To test whether invaders impacted natives at each of level of species richness, we compared the LS means native cover or native seedling abundance in invaded vs. uninvaded subplots, in burned and unburned plots, respectively. We adjusted our p-values for all these comparisons: $p_{adjusted} = p*n$; where "n" is the number of comparisons. We present least squares means and associated SEs in Results.

Results

We tested whether there was a pre-treatment difference in cover between disturbed and undisturbed plots and found no difference for invader cover before the fire ($F_{1,45}$=0.58, *P* =0.450), nor were any of the interactions with fire significant (fire x exotic species: $F_{1,91}$=0.6, *P*=0.574; richness x fire: $F_{1,45}$<0.1, *P*=0.916; richness x exotic species x fire: $F_{1,91}$=0.7, *P*=0.513). There was also no difference in native cover between disturbed and undisturbed plots before the fire ($F_{1,45}$=0.03, *P*=0.862), nor were any of the interactions significant (fire x exotic species: $F_{1,138}$=1.3, *P*=0.290; richness x fire: $F_{1,45}$=0.4, *P*=0.523; richness x exotic species x fire: $F_{1,138}$=1.3, *P*=0.273).

Exotic cover

Invader cover (Fig. 2) was significantly higher in burned than unburned plots ($F_{1,50}$=17.1, *P*<0.001). The full model showed that fire had similar effects on invader cover across the range of species richness (fire x richness: $F_{1,69}$=0, *P*=0.956) and independent of invader identity (fire x exotic species: $F_{2,94}$=3.86, *P*=0.340). Invader cover decreased with native species richness ($F_{1,58}$=12.4, *P*<0.001), and this pattern did not differ between burned and unburned plots (no fire x richness interaction). The relationship between richness and invader cover varied among exotic species ($F_{2,98}$=9.4, *P*<0.001). The negative relationship between invader cover and native species richness was steepest for knapweed (richness x exotic species interaction: $F_{2,98}$=3.49, *P*=0.034), which had the highest cover relative to other exotics at low richness, but similar cover to toadflax at medium and high richness (Fig. 2). Cinquefoil had the lowest cover overall, except at high richness where all the exotics had similar cover (Fig. 2).

Native cover

In the uninvaded subplots, there was a significant interaction between richness and fire ($F_{1,46}$= 8.2, *P*=0.006) where native cover was similar across richness levels under unburned conditions and was higher in plots that were burned (Fig. 3). Contrasts of the least squares means showed that native cover was significantly lower in burned than unburned plots at low richness (t_{46}=3.2, *P*=0.003) and there was a trend toward higher cover in burned than unburned plots at high richness, but this difference was not significant (t_{46}=-1.8, *P*=0.084). In the uninvaded subplots (Fig. 3), native cover increased with richness ($F_{1,46}$=12.0, *P*= 0.001) and was lower in burned than unburned plots ($F_{1,46}$=10.8, *P*=0.002).

Across all subplots (that is, including uninvaded and invaded subplots) native cover was lower in burned than unburned assemblages ($F_{1,44}$=3.9, *P*=0.056). There was greater native cover in assemblages with increasing richness (Fig. 4; $F_{1,42}$=21.1, *P*<0.001). To test for invader impact, we determined whether native cover was lower in invaded than uninvaded subplots. We found that native cover was lower in invaded subplots overall ($F_{2,138}$=10.8, *P*<0.001). Moreover, the strength of invader impact decreased significantly with richness (richness x invasion interaction; $F_{3,138}$=4.9, *P*=0.003; Fig. 4). The three-way interaction was marginally significant (richness x invasion x fire, $F_{3,138}$=2.1, *P*=0.101). In unburned plots native cover was only impacted by knapweed and toadflax at low richness, but high richness assemblages resisted impact (Fig. 4). In contrast, in burned plots native cover was always lower in invaded than uninvaded subplots, for all the exotic species and across all levels of richness (Fig. 4). The two-way interactions between fire x invasion ($F_{3,138}$=1.3, *P*=0.266) and fire x richness ($F_{1,41}$=0.8, *P*=0.364) were not significant.

Recruitment

Overall, invasion by knapweed decreased native seedling abundance (exotic species: $F_{3,170}$=2.77, *P*=0.043), especially in unburned relative to burned plots (fire x exotic species: $F_{3,170}$=3.28, *P*=0.022) and tended to weaken with increasing richness (fire x exotic x richness: $F_{3,174}$=2.22, *P*=0.087). Knapweed significantly reduced seedling counts in unburned plots at low species richness (t_{184}=-3.95, *P*<0.001). Otherwise, native seedling abundance did not differ significantly in burned and unburned plots ($F_{1,43}$=0.0, *P*=0.965) or with richness ($F_{1,43}$=0.02, *P*=0.891) regardless of exotic identity (Fig. 5).

Discussion

Although theory and empirical work suggest that native cover can separately depend on species richness, the impact of invaders, or disturbance, it remains unclear how communities will respond to a disturbance after invasion has already taken place. We found a buffering effect of richness in three ways: 1) native cover was lower in burned than unburned plots at low species richness, whereas there was little difference in native cover at higher richness levels; 2) invasive cover decreased at higher levels of richness; and 3) when the assemblages were invaded the exotic species had a significant impact on natives in low richness assemblages, but the exotics did not have this impact at higher levels of richness. In contrast, in invaded assemblages this buffering effect of richness was lost after a disturbance and the invaders had a significant negative impact on natives at all levels of richness.

The lower native cover, in uninvaded assemblages, in burned plots is somewhat surprising given the natives' historic exposure to the local fire regime and was driven by changes in native cover in low richness assemblages (Fig. 3). The low richness assemblages in our study were similar to natural grasslands in Montana and only contained two bunchgrasses, *Festuca idahoensis* and *Koeleria macrantha*, which are susceptible to fire whereas many forbs present in higher richness communities do not change in cover (Antos *et al.* 1983). These grasses were also the dominant species in the high richness plots (S. M. Pinto *et al.*, *unpublished data*), so the trend toward decreased native cover after fire may be because the overall native response depended on these dominants (Hillebrand *et al*. 2008). A reduced model showed that grass cover did not vary with richness ($F_{1,41}$=0.40, *P*=0.532), but decreased with fire ($F_{1,38}$=38.8, *P*<0.001). In contrast, native forb cover increased with richness ($F_{1,42}$=15.7, *P*<0.001), but did not vary with fire ($F_{1,45}$=0.58, *P*=0.450). Our results two years after an experimental burn agree with previous observational studies in this system that found a decrease in native grasses one year after a wildfire (Antos *et al.* 1983) and survival was four times higher for exotics than natives after a fire (Pearson *et al*. 2012). The susceptibility of the dominant grasses suggests that they are good competitors in a static environment, but worse at dealing with disturbances like fire (Seabloom *et al*. 2003; MacDougall 2005). Like other studies, we also found an increase in native abundance with more native species in the community (Naeem *et al*. 1995; Tilman *et al*. 1996; Maron & Marler 2008a).

Theory suggests that higher native species richness will buffer changes due to invasion and disturbance (Naeem 2002; Hooper *et al.* 2005; Ives & Carpenter 2007), but it is unknown how invaded community-resilience will fair when faced with disturbance. Like many studies at local scales we found a decrease in invasive cover at higher richness (Tilman 1997; Stachowicz *et al*. 1999; Levine 2000; Naeem *et al*. 2000; Dukes 2002; Zavaleta & Hulvey 2004; Davies *et al*. 2005; Fargione & Tilman 2005). Our work also supports findings from other studies that invaders are more successful after disturbance (Elton 1958; D’Antonio & Vitousek 1992; Burke & Grime 1996; Hierro *et al*. 2006; D’Antonio *et al.* 1999), but none have examined whether the impact of invaders on natives changes after a disturbance. Our approach of examining these factors together suggests that fire overrides the buffering effect of richness on invader impact. In the absence of fire, invaders had weaker impacts on native cover as native richness increased; however, fire eliminated this diversity-based resilience to invader impact.

Differing results between studies of invader impact across a richness gradient may be explained by the change in impact after disturbance. Previous work on these assemblages also revealed less impact of invaders in high vs. low richness assemblages (Maron & Marler 2008), which contrasts work that found a weak relationship (Dukes 2002) or a greater impact at high richness (Zavaleta & Hulvey 2004). One reason for these differing results may be the relationship between impact and disturbance (DiTomaso *et al*. 2006). For example, Dukes (2002) found no relationship between richness and impact in older assemblages whereas in newer assemblages, which were similar to areas disturbed by gophers, there was a slight decrease in impact at higher richness levels. As in previous work with these assemblages, we found that without disturbance and seven years after invasion impact decreased at higher levels of species richness. That is, without a disturbance, native cover was significantly decreased by invaders in low richness assemblages whereas at high richness levels native cover was similar in invaded and uninvaded subplots. However, disturbed plots had higher invader abundance than undisturbed plots across richness levels and subsequently invaders had an impact on natives at all levels of richness.

Richness may not provide a buffer to invader impact after disturbance due to an increase in resource availability. After losing some biomass, compensatory growth is common in plants that experience disturbance (Belsky *et al*. 1993) and invader cover may increase more than native cover because more resources become available (Davis *et al*. 2000). The higher invasive cover in disturbed plots, regardless of native richness, is part of the reason why richness no longer buffered the impact of invaders on natives after disturbance. A late-summer fire may be particularly beneficial to exotics that already occur in the system, because with rapid growth and pheonologies that extends later in the year than the natives, the exotics can capture resources made available by the fire (Sheley *et al*. 1998).

Invader cover was higher in burned assemblages, supporting the hypothesis that invaders thrive after disturbance. In other studies, *C. stoebe* decreased after annual-prescribed spring fires (Emery & Gross 2005) or a mid-summer wildfire (Besaw *et al*. 2011), whereas studies of *P. recta* (Lesica & Martin 2003) and *L. dalmatica* (Jacobs & Sheley 2003) found that a temporary increase in reproduction stimulated by fire did not cause a longer term increase in invader density. In a forested system, the response of toadflax to fire differed between sites that had different pre-treatment invader abundances (Jacobs & Sheley 2003). This suggests that differing results between studies may be due invader abundance and the underlying native diversity, which we manipulated in our study. Furthermore, the timing and intensity of the fires can also influence invader abundance (Emery & Gross 2005) and we applied a low intensity fire at a time of year when fires normally pass through the local grasslands. Here, the invasive species may have fared better since their growing season goes later into the fall than the natives (Pearson *et al*. 2012; Wolkovich & Cleland 2011), thus they did not burn as easily as the natives that had senesced and may therefore have been able to take advantage of the resources made available by the fire. Since these are long lived individuals, it is more likely that the higher invader cover two years after the disturbance is due to the adults getting bigger rather than an increase in germination. Our study shows that two years after a late-summer fire the cover of three exotic perennials remained higher than in unburned plots.

Despite invader cover and impact being higher in burned than unburned plots, two patterns demonstrate impact does not necessarily scale with invader cover after fire. First, despite large differences in cover the three exotics differed all had an impact on native cover. That is, after the fire cinquefoil had a significant impact on natives, suggesting that even at low abundance invaders can impact native cover. This supports previous work, which found that cinquefoil has a high per capita impact on natives (Maron & Marler 2008a). Second, regardless of differences in cover across richness levels the invaders always had an impact on natives after fire. Similarly Dukes (2002) found a low cover of invaders at high richness could still have a strong impact on native biomass. A previous study using these assemblages demonstrated that, without disturbance, invader impact scales with exotic biomass (Maron & Marler 2008a); in the current study we did not quantify the strength of impact but found that after a disturbance invaders at low abundances impact native cover. Again, this implies that invaders pre-emptively use resources made available by the fire leading to an increase in invader cover and impact.

We found the degree of decline in invader cover with richness was different for each exotic species. Seven years after experimental invasion, we found a strong hierarchy to invader cover at low richness and little difference in cover at high richness. Cinquefoil was the least abundant at low native richness and remained at a similar cover as richness increased (Fig. 2). Knapweed was the strongest invader in low richness plots, but native richness caused a large decrease in knapweed cover and at high richness its cover was similar to the other exotics. Toadflax had a greater cover than cinquefoil across richness levels, but was comparable to knapweed at higher richness levels. In contrast, previous work with these assemblages found that knapweed was always the most abundant invader (Maron & Marler 2008a). Three factors may have led to an increase in toadflax abundance relative to knapweed over the last four years. First, toadflax germinates in the spring and may therefore take better advantage of wet springs than knapweed that germinates in the fall. Second, knapweed has a deep taproot (Watson & Renney 1974) whereas toadflax spreads by horizontal roots (Vujnovic & Wein 1997), which can help adults increase in size. Third, a root weevil (*Cyphocleonus achates*) has increased in abundance in our plots in the last two growing seasons (*personal observation, S. Pinto*) and kills knapweed adults. However, knapweed recruitment increases after adults die (Ortega *et al.* 2012).

In our study, changes in native and invader cover are unlikely to be caused by changes in recruitment. In local grasslands, many of the invasive and native species are long-lived perennials, so we are unlikely to see a change in cover two years after the fire due to germination. However, it could be argued that the effect of fire on recruitment could cause a change in invasive and native cover over a longer time period. One predicted mechanism for changes in cover after a disturbance is that fire would decrease the abundance of the competitively superior species, free up some bare ground, and therefore cause an increase in germination. However, we did not find any strong effects of fire on native recruitment (Fig. 5). We saw a trend toward decreased invader recruitment after fire (S. Pinto *et al.,* unpublished data), but there was a lot of variation in seedling abundance within treatments. Therefore, it seems doubtful that changes in recruitment after fire will have big effects on native or invasive cover in the short or long term.

Our results show that fire did not fundamentally alter the diversity-invader abundance relationship. Rather, exotic perennial forbs all increased after fire across richness levels. However, we found that fire did increase the impact that invaders had on natives. Our study supports the common finding that invasives thrive after disturbance (e.g. Hobbs & Huenneke 1992; Hierro *et al.* 2006). Even natural disturbances, such as a late-summer fire in grassland assemblages, can favor invasives and cause a decrease in native cover and potentially create an alternative stable state where communities are dominated by exotic forbs (Scheffer & Carpenter 2003).

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Figure 1. Each plot was 3 x 3 m and divided into four subplots, which were 1.3 x 1.3 m, divided by a 40 cm buffer. In the original study (Maron & Marler 2007, 2008a) there were 146 plots arranged in three blocks separated by 6 m. Plots were separated by 3m within a block. In the current study we used a subset of 52 plots. Species richness and disturbance were randomly assigned plot-level treatments. The invasion treatment with seeds of either *C. stoebe, P. recta,* or *L. dalmatica* was randomly applied at the subplot-level with one subplot left uninvaded as a control.

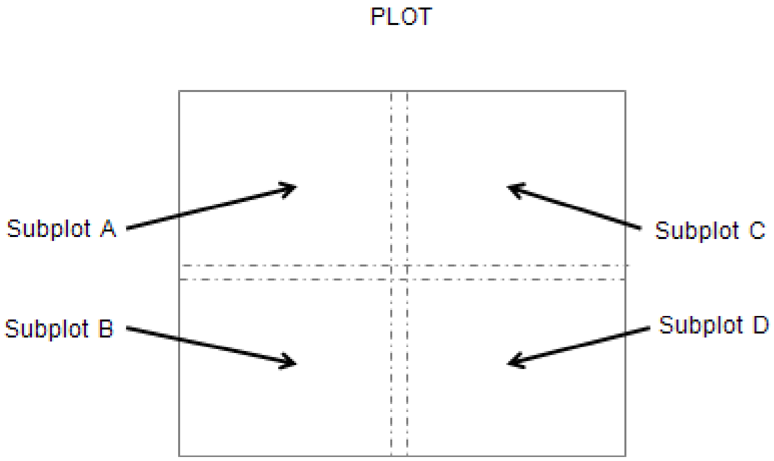


Figure 2. The effect of native species richness and fire on the percent cover of three invasive species: *C. stoebe, L. dalmatica*, and *P. recta*. Seven years after invasion, invader cover was lower at higher richness levels. Two years after the fire, invader cover was higher in burned than unburned plots.

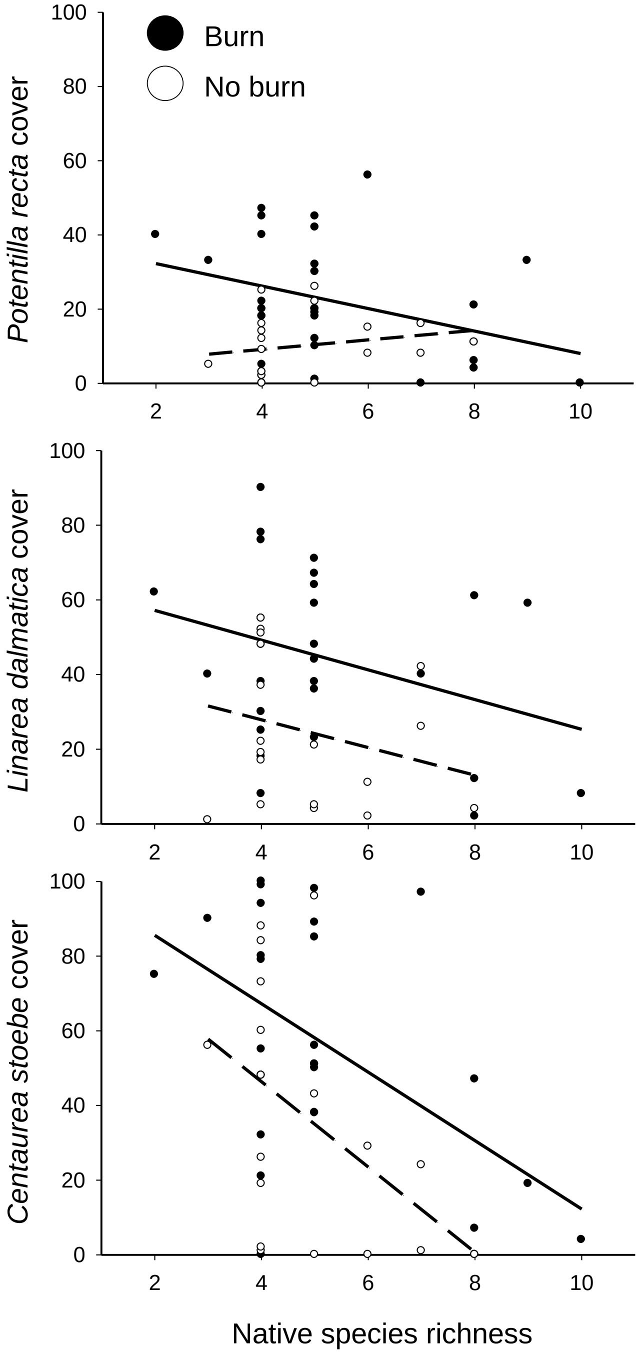


Figure 3. Least squares means of native cover in uninvaded subplots at low, medium, and high levels of species richness within unburned and burned plots. The ANOVA was conducted with species richness as a continuous covariate (see Methods), but to compare the LS means and to present the information clearly we examined three specific levels of richness. The star indicates a significant difference between burned and unburned plots at that level of richness. Error bars represent the standard error.

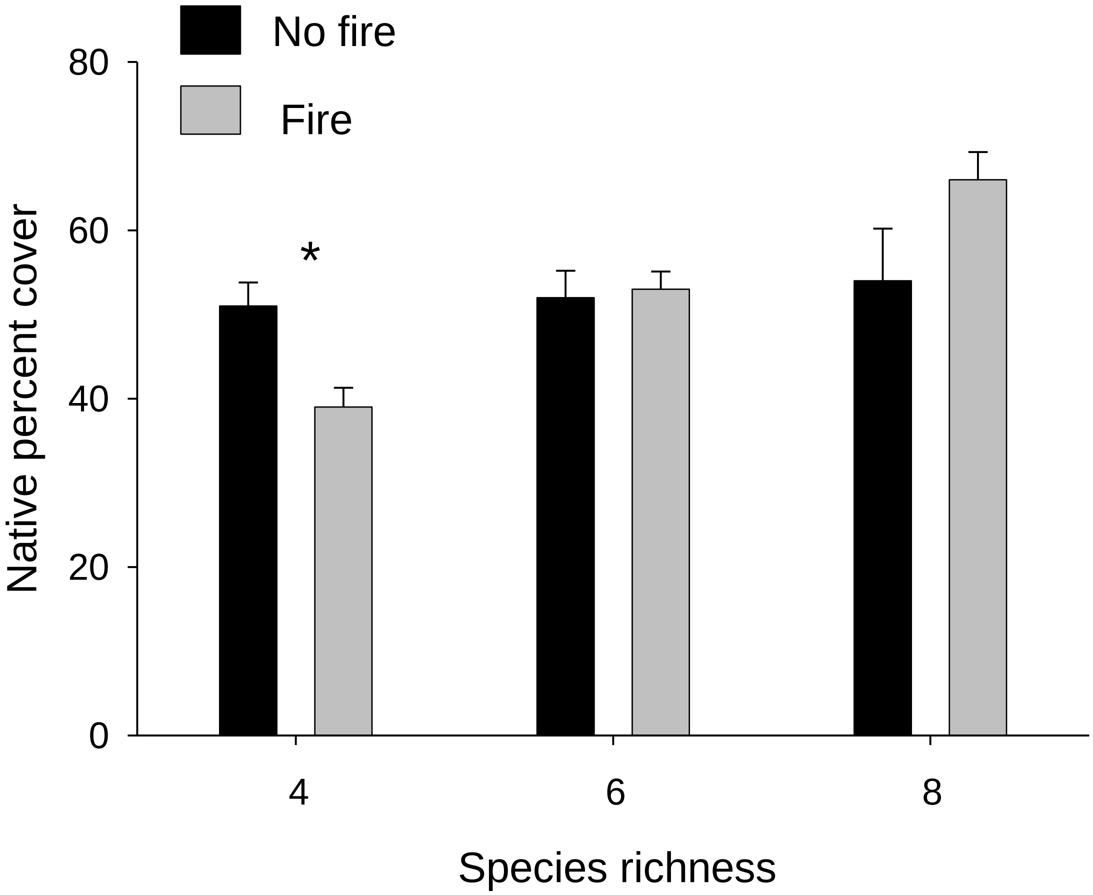


Figure 4. Effect of invasion and burning on native percent cover seven years after invasion and two years after fire. A significant impact of invaders on native cover, within a richness level, is indicated by a star that shows whether an invaded subplot had significantly less cover than the native subplot (*p<0.05). The ANOVA was conducted with species richness as a continuous covariate (see Methods), but to compare the LS means and to present the information clearly we examined three specific levels of richness. Error bars represent the standard error.

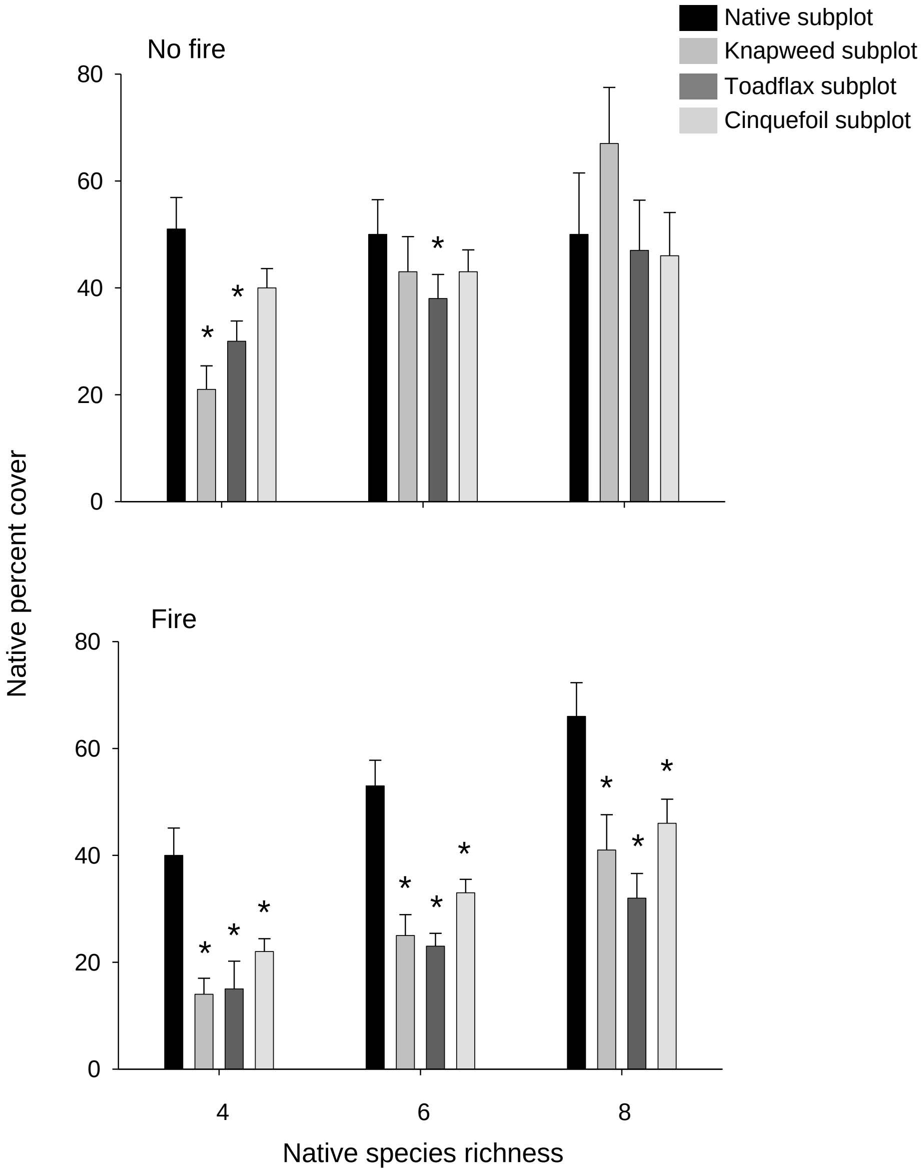
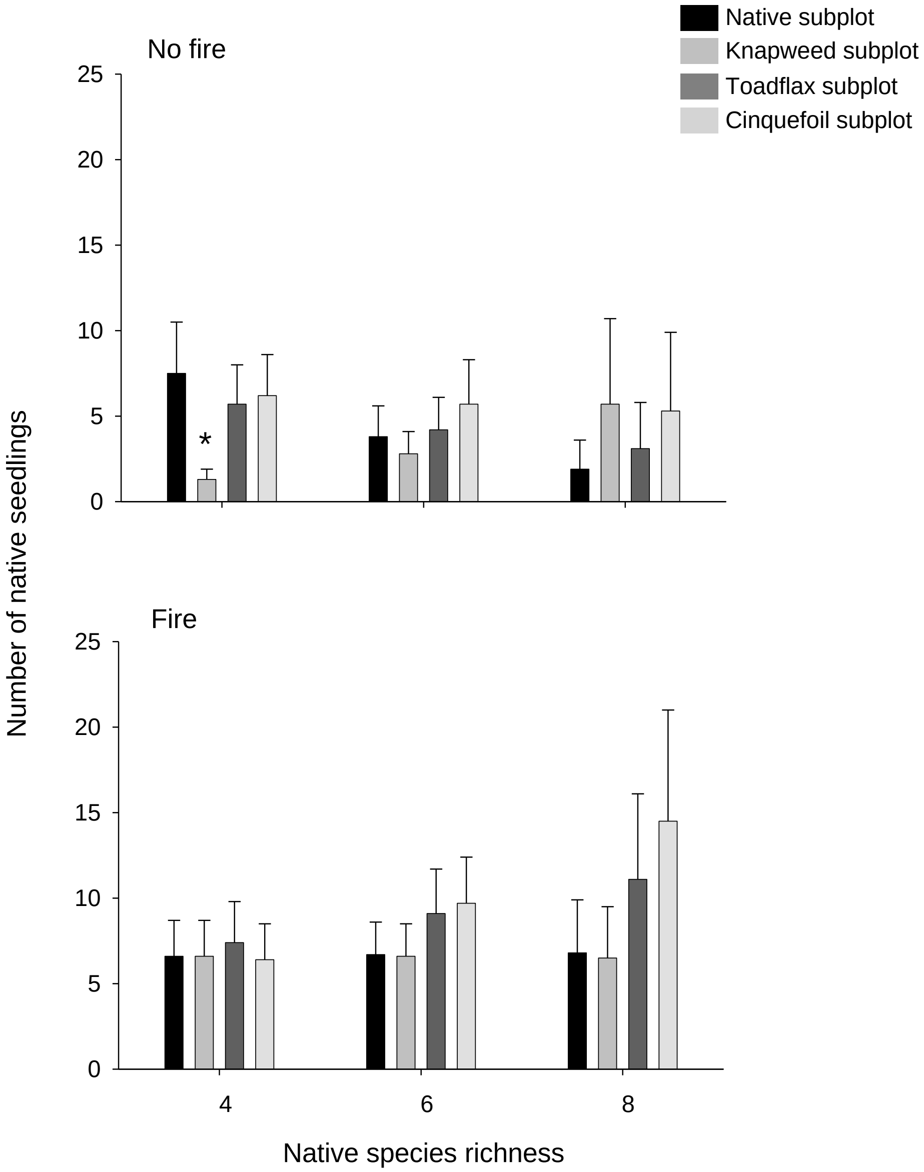


Figure 5. Effect of invasion and burning on native seedling abundance seven years after invasion and two years after fire. A significant impact of invaders on native cover, within a richness level, is indicated by a star that shows whether an invaded subplot had significantly fewer native seedlings than the native subplot (*p<0.05). The ANOVA was conducted with species richness as a continuous covariate (see Methods), but to compare the LS means and to present the information clearly we examined three specific levels of richness. Error bars represent the standard error.



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