

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

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Summary

1. Competition has historically been viewed as the predominant process affecting plant community structure. In particular, it is often assumed that the dominant resident species is the superior competitor and therefore has large impacts on plant community diversity. This assumption, however, is seldom tested. As well, there are a variety of other processes such as dispersal limitation and seed predation that can influence community structure, although the relative importance of these processes in relation to competition from resident species is still unclear.

2. We examined how interspecific competition, dispersal limitation and post-dispersal seed predation by mice individually and interactively influenced the richness and diversity of local plant assemblages in grasslands of western Montana.

3. We added seeds of 20 mostly locally uncommon native species to subplots in and out of larger rodent exclosure plots. Using a ‘species-blind’ approach, we manipulated competition from resident plants in these subplots by removing the same amount of cover of one dominant species or several common species.

4. The species richness and diversity of local assemblages was higher in subplots with seed addition than without. Across all levels of the other treatments, average richness for subplots without competitor removal was lower than for competitor removal treatments. However, the removal of one locally dominant species had similar effects to removal of several common species. In contrast, preventing seed predation by mice did not have significant effects on richness. There were no significant interactions between the treatments.

5. *Synthesis.* Our results reveal a hierarchy of filters that determine local community structure. Many regionally rare species were dispersal limited and established after the seed addition, regardless of release from competition or the presence of seed predators. Subsequently, we found competitive equivalence between dominant and common species.

Key-words: determinants of plant community diversity and structure, dispersal limitation, dominance, relative abundance, seedling establishment, species richness

Introduction

The process of community assembly is conceptualized as a series of regional and local filters that species must sequentially pass through before establishing (Ricklefs 1987; Keddy 1992). Yet traditionally, interactions at the local level, particularly competition, have been viewed as the primary driver determining local plant diversity (Tilman 1982; Chase & Leibold 2003). The importance of other processes, such as dispersal limitation or consumers, relative to competition was unclear because each process was historically studied in isolation (Abulfatih & Bazzaz 1979; Heske, Brown & Guo 1993;

Foster & Tilman 2003). However, recent advances in meta-community theory and empirical work show that the interplay between regional and local processes can determine local community structure (Leibold *et al.* 2004; Cottenie 2005; Myers & Harms 2009b).

With respect to competition, a widely held assumption is that dominant resident species provide strong competitive resistance to colonization by prospective community members. That is, competitive ability is often correlated with species’ relative abundance in plant communities (Weiner 1990; Pennings & Callaway 1992; Schwinning & Fox 1995; Facelli & Temby 2002). This idea is further supported by previous studies that found competition from the most abundant species changed community composition (Johnson & Mann

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1988) or decreased richness (Abulfatih & Bazzaz 1979; Wardle *et al.* 1999). On the other hand, less abundant species may be strong competitors because in sum they may occupy more niche space than a single dominant species (Tilman 1982; Chase & Leibold 2003). Results from previous studies have found that both dominant species (Emery & Gross 2006; Gilbert, Turkington & Srivastava 2009) as well as many rarer ones (Lyons & Schwartz 2001; Zavaleta & Hulvey 2004) can competitively exclude individuals of potential colonist species from establishing. Studies of invasibility have similarly shown that several species can inhibit invasibility via niche-based complementarity, but that competitively dominant single species can have similar effects (Loreau & Hector 2001; Wardle 2003; Fargione & Tilman 2005). Many natural communities are characterized by a habitat-forming dominant species, so it is also possible that resident species can enhance local diversity by facilitating the establishment of recruits (Bruno, Stachowicz & Bertness 2003). In many field removal studies, however, it is not understood whether response to competitive release is actually due to differences in the abundance of removed species or due to the specific identity of the species being removed. Examining how seedling establishment in the field is affected by removal of a range of species of different abundances would help overcome limitations of experimental designs that manipulate a few species in greenhouses or under non-equilibrium conditions (Goldberg & Werner 1983; Goldberg 1996).

Post-dispersal seed predation by rodents is another local process that 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, Warton & Westoby 2003), which can in turn change species' abundances (Brown & Heske 1990; Edwards & Crawley 1999; Bricker, Pearson & Maron 2010; Pearson, Callaway & Maron 2011; Maron *et al.* 2012). Of the few studies that have concurrently examined seed predation and competition, two found that seed predation on the strongest competitor can decrease its abundance (Samson, Philippi & Davidson 1992; Howe & Brown 2001). Yet whether the establishment of potential colonist species is influenced by competition from resident species and seed predation or whether these processes interact remains unclear (Turnbull, Crawley & Rees 2000). For example, in areas with sparse vegetation, and therefore low competition, seeds may be more visible and therefore more readily consumed by seed predators than in areas with intact resident vegetation.

Finally, the diversity and relative abundance of species in local communities may be less influenced by local processes and more affected by regional scale influences (Ricklefs 1987; Hubbell 2001), such as seed dispersal. Dispersal limitation occurs at a regional scale, where it controls local species richness via immigration of species from the regional source pool (Hubbell 2001). Empirical evidence from many communities demonstrates that dispersal limitation constrains local species richness (Tilman 1997; Turnbull, Crawley & Rees 2000; Brown & Fridley 2003; Foster & Tilman 2003; Wilsey &

Polley 2003). However, a regional process may not be the sole determinant of community structure and dispersal limitation may interact with the local biotic processes of seed predation and competition (Leibold *et al.* 2004). For example, many local communities are structured via species-sorting (Cottenie 2005) based on: (i) the regional influence of dispersal abilities that determine seed arrival to a local site, (ii) whether niche requirements are met at the local site and (iii) local biotic limitations, such as competitive exclusion and seed predation. Specifically, dispersal limitation may influence seed predation and competition; certainly there can be no local interactions between species if their seeds never arrive at a site (Schupp & Fuentes 1995; Harms *et al.* 2000; Clark *et al.* 2007). Of the few studies that have examined these processes concurrently, one found that the importance of dispersal limitation for community assembly depended on the competitive effect of the dominant species (Myers & Harms 2009a). Furthermore, dispersal limitation may be more important in determining diversity in areas of low productivity and therefore low competition (Foster 2001; Houseman & Gross 2006).

Although regional and local processes that affect local plant diversity have each individually been shown to be important, the relative importance of dispersal limitation, competition and seed predation in affecting the structure of local communities is poorly known (Maron *et al.* 2014). Previous work in western Montana grasslands revealed that rodent seed predation can influence the establishment and abundance of large-seeded species (Bricker, Pearson & Maron 2010; Pearson, Callaway & Maron 2011; Bricker & Maron 2012; Maron *et al.* 2012; Pearson, Potter & Maron 2012) and can interact with disturbance to influence recruitment into local sites (Maron *et al.* 2012). The influence of competition or its interaction with other processes on community structure, however, remains unclear. A single locally dominant species (the most abundant species in a plot) may be the strongest competitor or several locally common species (e.g. the species ranked second through sixth in abundance) may create a more competitive environment because together they occupy more niche space. Alternatively dominant and common species may be competitively equivalent, because of similarities in resource requirements for autotrophs (Goldberg & Werner 1983). However, these local processes could be swamped out by regional dispersal processes, such as in a 'mass-effects meta-community' (Leibold *et al.* 2004), or interactions between regional and local processes may determine community structure. Here, we experimentally test how dispersal limitation, competition from dominant vs. common species and post-dispersal seed predation by mice individually and interactively influence local plant community richness and diversity in these grasslands.

Materials and methods

STUDY SYSTEM

Our study was conducted at eight sites that spanned ~50 km across the grasslands in the Blackfoot Valley in western Montana. These

grasslands are dominated by rough fescue (*Festuca campestris*), but several other graminoids can be locally dominant. Most of the rare species in the region tend to be annual or perennial forbs (Appendix S1, Supporting Information). 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, Pearson & Fletcher 2010).

EXPERIMENTAL DESIGN

We performed a factorial experiment that crossed three treatments: with/without a seed addition to test for dispersal limitation, in/out of mice exclosures (to test for effects of seed predation) and competitor removals of dominant, common or no species. There were a total of 96 subplots (2 seed addition $\times$ 2 mice exclosure $\times$ 3 competition $\times$ 8 sites; Fig. 1). This involved adding seeds of 20 native species to 0.5×0.5 m subplots where we had removed the dominant species only, several common species or no species. Treatment was randomly assigned to subplots, which were randomly located in or out of larger 10×10 m rodent exclusion plots (Fig. 1). Although the species we added are present in the system, most of them were rarely present at local sites (J. L. Maron & D. E. Pearson, unpubl. 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 that had higher local abundance: *Lupinus 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 >0.001 g and 175 seeds per subplot for species with small seeds ≤ 0.001 g. We chose these seed numbers to account for variation in seed production among species due to trade-offs between seed size vs. seed number (Turnbull *et al.* 2004). 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 had the highest natural establishment of the 20 added species (S. M. Pinto *et al.*, unpubl. data).

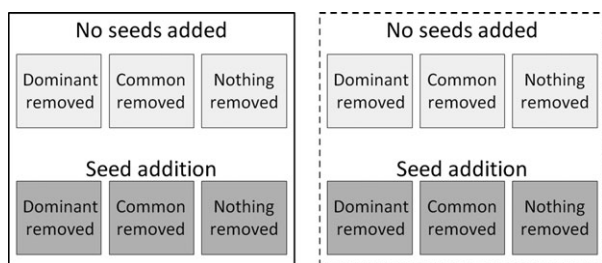


Fig. 1. Experimental design. The large squares represent the mice exclusion plots (10×10 m) and exclusion controls (10×10 m) that were 10–20 m away. The small squares represent subplots that were 50×50 cm on a side and nested within the larger mice exclusion plots. Within these larger plots, we performed a factorial cross of seed additions (20 species) and competitor removals (three levels), to test for dispersal limitation and competitive effects respectively. Treatments were randomly assigned to subplots in and out of mice exclosure plots. The design was replicated at eight sites in the Blackfoot Valley, Montana (see Methods for details).

To test for effects of seed predation, exclosures were constructed using a 60-cm-high welded wire fence (mesh size = 0.625×0.625 cm) topped with aluminium flashing to prevent mice from climbing over and buried 40–50 cm underground to prevent mice entry from underground. 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. Exclosure-control plots, of identical size, were located 10–20 m away from each rodent exclosure.

Species removals were designed to test for differences in competitive effects between dominant (the locally most abundant species in a subplot) and common (the species ranked second through sixth in abundance in a subplot) 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 (Appendix S2 lists the 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 our dependent variables, richness and diversity, do not quantify species identity. To estimate cover of the species targeted for removal, we used a 50×50 cm quadrat with string marking 25 equal sized squares, with each square representing 4% of the plot area. For the dominant treatment, we removed 40% of the area in the subplot that was composed of the locally dominant species (as quantified by our subplot-specific rank abundance curve). For the common species treatment, we started with the species ranked at 2 and consecutively removed 3–6 species until 40% cover was removed. Hence, locally abundant and common species were defined by relative abundance measured within a specific subplot and species identity within these categories varied across subplots. We removed the same amount of cover so that each removal 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). To perform the removals, we diluted an herbicide (round-up, 5% concentration) and painted it on the targeted species. We painted the targeted species glyphosate in late June 2010 and returned in late July 2010 to clip the dead vegetation. The biomass was dried in ovens at 70°C and weighed.

To test how our treatments influenced ultimate species richness and diversity 2 years after treatment application, in June 2012, we used a 0.5×0.5 m quadrat divided into 25 squares and counted the number of squares in which each species that was rooted in the subplot occurred. This measure of diversity included resident species that were established before the treatments and those that were part of the seed addition. Furthermore, diversity was measured based on the species that occurred in an individual subplot regardless of which species (removed or not, added or not) occurred in any other treatments.

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 and separately compared the number of squares (out of a total of 25) in which the targeted dominant or common species occurred over the 3 years of our experiment.

To test whether the treatments had lasting effects on community structure, in 2012, we examined changes in local species richness and

diversity, including resident and added species. We measured diversity using the inverse Simpson's index, which is the reciprocal of the dominance measure (where 1 would indicate complete dominance), and thus, the Simpson's index measures how many species would be represented in the community if they all had equal abundances.

For local community richness and the Simpson's index in 2012, we conducted separate split-plot three-way ANOVAs, where rodent exclusion was applied at the whole plot level ($n = 8$) and removal treatments and seed addition were applied to subplots ($n = 96$) in and out of exclosures. Since some of these species established naturally in the control subplots, the analysis compared richness in seed addition vs. no-seeds added control subplots. Site was included as a random factor. All analyses were performed using SAS (version 9.3, SAS Institute Inc., Cary, North Carolina, USA).

Results

Removal treatments successfully reduced the abundance of both the targeted local dominant species ($F_{2,81} = 121.08$, $P < 0.001$) and the targeted common species ($F_{2,93} = 35.36$, $P < 0.001$) 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 S2).

Two years post-seed addition, there was a sustained increase in overall local species richness ($P < 0.001$; Table 1, Fig. 3). Of the 20 species we added, 16 established in at least one plot in 2011 (Table 2). Across all levels of the other

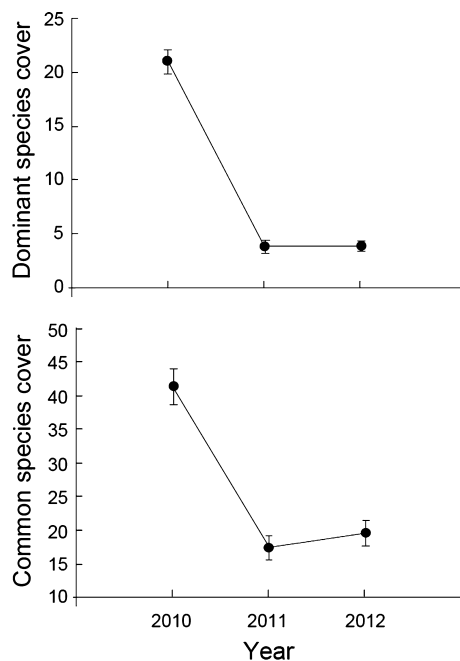


Fig. 2. Local abundance of the targeted species in the dominant (top panel) and common (bottom panel) species removal treatments, before the treatment in 2010 and after the treatment in 2011/2012, estimated by the number of squares for each species in a subplot (for a potential total 25 squares for each species, per subplot). 'Dominant species cover' is the least-square mean of the number of squares for the local dominant in the subplot. 'Common species cover' is the least-square mean of the summed number of squares of the species removed in that subplot.

Table 1. Summary of generalized linear mixed models for the individual and interacting effects of treatments on local species richness and diversity (inverse Simpson's index)

	Richness	Diversity
Seed addition	$F_{1,70} = 23.5$, $P < 0.001$	$F_{1,70} = 14.1$, $P < 0.001$
Mice exclosure	$F_{1,7} = 0.7$, $P > 0.4$	$F_{1,7} < 0.1$, $P > 0.9$
Removals	$F_{2,70} = 10.2$, $P = 0.001$	$F_{2,70} = 15.1$, $P < 0.001$
Seeds $\times$ Mice	$F_{1,70} = 0.5$, $P > 0.5$	$F_{1,70} = 0.3$, $P > 0.5$
Seeds $\times$ Removals	$F_{2,70} = 1.7$, $P > 0.2$	$F_{2,70} = 1.6$, $P > 0.2$
Mice $\times$ Removals	$F_{2,70} = 0.5$, $P > 0.6$	$F_{2,70} = 0.1$, $P > 0.8$
3-way	$F_{2,70} = 0.5$, $P > 0.6$	$F_{2,70} = 1.2$, $P > 0.3$

treatments, mean ($\pm$ SEM) baseline species richness was 12.6 ± 0.8 species in the no-seeds added subplots and 16.4 ± 1.0 species in the seed addition subplots. The impact of seed predators on local richness did not vary between seed addition and control subplots (Table 1, mice exclosure $\times$ seed addition), nor was the main effect of mice exclosure significant ($P > 0.4$). Overall richness was higher in competitor removal subplots than in the no-removal subplots ($P = 0.001$; Table 1). Across all levels of the other treatments, average richness ($\pm$ SEM) for subplots without competitor removal was 12.0 ± 0.9 species, whereas the species richness in competitor removal subplots averaged 15.5 ± 1.1 for the dominant removal and 16.0 ± 1.1 when common species were removed. Contrasts revealed 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: $t_{70} = 3.77$, $P < 0.001$). The common and dominant removal treatments, however, 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 (Table 1).

Local community diversity (Fig. 4), including resident and added species, increased with the seed addition ($P < 0.001$; Table 1) from a mean Simpson's index ($\pm$ SEM) of 7.6 ± 0.6 in the no-seeds added subplots to 9.3 ± 0.6 in the seed addition subplots, across all levels of the other treatments. Diversity also increased with the removals ($P < 0.001$; Table 1) from a mean Simpson's index ($\pm$ SEM) of 6.8 ± 0.7 in the no-removal subplots to 9.6 ± 0.7 with the dominant removed and 9.0 ± 0.7 with the common species removed. Similarly to patterns with overall community richness, contrasts revealed that although removals increased diversity relative to the control (common vs. control: $t_{70} = 4.1$, $P < 0.001$, dominant vs. control: $t_{70} = 5.2$, $P < 0.001$), there was no difference in diversity between common or dominant removal treatments ($t_{70} = -1.2$, $P = 0.24$; Fig. 4). Neither mice exclusion nor any of the interactions had a significant effect on diversity (Table 1).

Discussion

Dispersal limitation, competition and seed predation can be important in structuring plant communities, but the relative

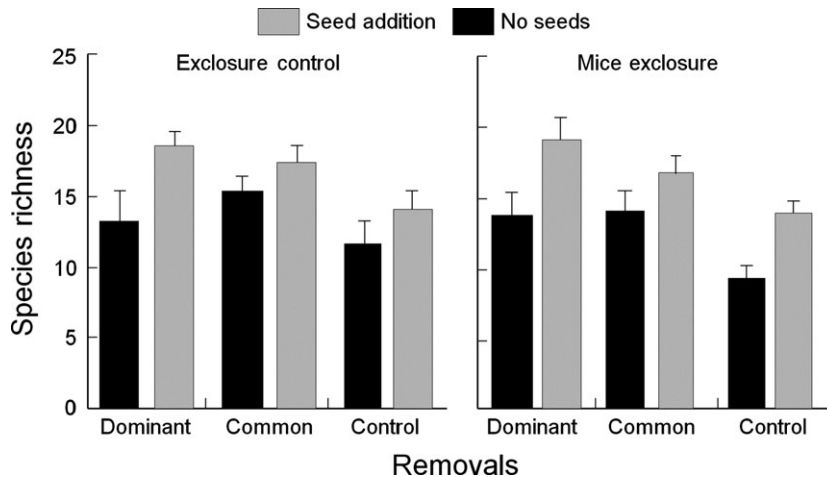


Fig. 3. Least-square means ($\pm$ SEM) of local species richness, including resident and added species, of subplots that received seed addition and removal treatments, in (right panel) and out (left panel) of larger mice exclosures. LS means are from the generalized linear mixed model analysis.

importance and interactive effects of these processes are unclear. Surprisingly, we found no significant interactions between these processes, perhaps due to the overriding importance of the seed addition treatment. Our data support a conceptual picture for community assembly of processes acting as sequential filters (Ricklefs 1987; Keddy 1992) and the meta-community concept of the importance of both regional and local processes (Leibold *et al.* 2004). Although competition was historically emphasized as a central process determining plant community structure, we found a hierarchy to these filters where broad-scale dispersal limitation had a larger effect on local community richness (Fig. 3) and diversity (Fig. 4) than local filters of competitive release or mice exclusion. Our

Table 2. 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 out of the 20 added species occurred in at least 1 subplot, shown in the 'established in 2011' column

Species	Seed size category	Seed size (g)	Established in 2011
<i>Anemone multifida</i>	Small	0.00133	Y
<i>Astragalus drummondii</i>	Medium	0.00340	Y
<i>Balsamorhiza sagittata</i>	Medium	0.00908	Y
<i>Collinsia parviflora</i>	Small	0.00060	Y
<i>Collomia linearis</i>	Small	0.00091	Y
<i>Delphinium bicolor</i>	Small	0.00045	N
<i>Dodecatheon conjugens</i>	Small	0.00024	Y
<i>Erigeron pumilus</i>	Small	0.00010	Y
<i>Fritillaria pudica</i>	Small	0.00158	Y
<i>Gaillardia aristata</i>	Medium	0.00246	Y
<i>Geum triflorum</i>	Medium	0.00124	Y
<i>Heterotheca villosa</i>	Small	0.00063	Y
<i>Lithophragma glabrum</i>	Small	0.00005	N
<i>Lithospermum ruderae</i>	Large	0.02037	Y
<i>Lomatium macrocarpum</i>	Medium	0.00806	Y
<i>Lupinus sericeus</i>	Large	0.02360	Y
<i>Potentilla arguta</i>	Small	0.00009	Y
<i>Saxifraga oregana</i>	Small	0.00012	N
<i>Achnatherum richardsonii</i>	Medium	0.00160	N
<i>Zigadenus venenosus</i>	Medium	0.00023	Y

results also lend further support to the many studies in grassland systems that found evidence for dispersal limitation (Ehrlén & Eriksson 2000; Nathan & Muller-Landau 2000; Brown & Fridley 2003; Fargione, Brown & Tilman 2003; Munzbergova & Herben 2005; Maron *et al.* 2014).

Early work on competition led to the assumption that the most abundant species must be the strongest competitor (McNaughton & Wolf 1970; Grime 1973). However, we found the common and dominant removal treatments caused a similar competitive release. This similarity is somewhat surprising since the dominant species had a much higher biomass than the common species combined, and high biomass is often a good indicator of competitive strength in plants (White & Harper 1970; Schwinning & Weiner 1998). In scenarios of size uneven competition, such as between seedlings and established individuals, the large neighbouring taxa may have equivalent competitive effects on the smaller juveniles (Goldberg 1996). Competition from the common species may have been comparable, 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 functional categories had a similar effect to removing one dominant graminoid, this suggests that there is strong competition for shared resources between plant species in this system. For the germinating seedlings, the bare ground created by removing large established individuals may be more important than the type of species being removed. We detected no species-specific pattern in seedling responses to removals, supporting the idea that the removals themselves were more important than the type (dominant vs. common) of species being removed. Thus, the competitive equivalence of the dominant and common groups of species may be due to (i) similarity in resource requirements, (ii) low encounter probabilities for specific pairs of species, (iii) size asymmetries between dominant/common adults and the establishing seedlings (Goldberg & Werner 1983).

Other studies have found contrasting results for the effect of competitor removals on diversity. In some studies, the dominant species determined native seedling establishment,

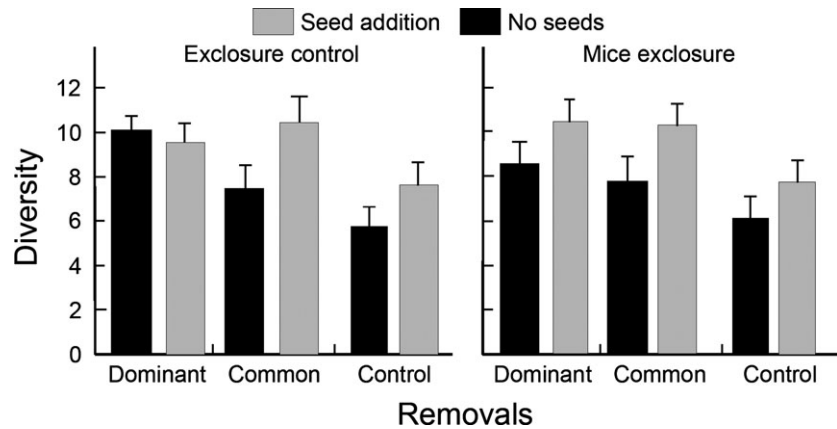


Fig. 4. Least-square means ($\pm$ SEM) of diversity, measured by the inverse Simpson's index, for subplots with seed addition and removal treatments, in (right panel) and out (left panel) of larger mice exclosures. LS means are from generalized linear mixed model analysis.

but this effect depended on the functional identity of the dominant (Emery & Gross 2006; Gilbert, Turkington & Srivastava 2009; Myers & Harms 2009a). In contrast, other studies have found that the rare species in a community reduce establishment by exotics (Lyons & Schwartz 2001; Zavaleta & Hulvey 2004). In our study, removal of competitors was species-blind, and so the competitive release was more likely due to the local cover of the species rather than their specific identity (but see Emery & Gross 2007). This was especially true for the common species where our removal treatment involved 34 different species (Appendix S2). 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.

Although our current method of removing species does not allow us to examine competitive release from specific species, results revealed that abundant species (both locally dominant and common species) created a competitive environment that limited local richness. Two years after treatment application, there was a sustained increase in overall community richness, which could be caused by seedling establishment of added species after removals (seedling species richness of the 20 added species in 2011, seed addition $\times$ removal: $F_{2,70} = 3.4$, $P = 0.040$). Additionally, previous work that manipulated disturbance and seed addition in this system found that removing all the vegetation from subplots led to an increase in seedling abundance of added species (Maron *et al.* 2012, 2014). Thus, both the partial or complete removal of resident vegetation provided a competitive release for establishing species.

We did not find that seed predation influenced broad measures of plant community structure. Previous work in this system revealed that mice limited establishment and abundance of specific species, particularly large-seeded species (Pearson, Callaway & Maron 2011; Maron *et al.* 2012) like *L. sericeus* and *Lithospermum ruderalis* (Bricker, Pearson & Maron 2010) and *Tragopogon dubius* (Pearson, Potter & Maron 2012). Maron *et al.* (2012) also found higher seedling abundance of the added species, especially after a disturbance, in plots with seed addition and seed-predator exclusion. However, in the current study, we did not find that seed predation affected

local richness or diversity. The similarity in richness and diversity in plots 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 (Brown & Heske 1990; Heske, Brown & Guo 1993; Howe & Brown 2001). 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 individuals of a species recruiting in low numbers. If so, then seed predation may limit population level abundance and yet not affect the number of species present.

Although previous studies have demonstrated that dispersal limitation is widespread, it is not always clear whether abiotic or biotic factors are responsible for the lack of recruitment of some added species (Turnbull, Crawley & Rees 2000). In our experiment, we did not find a significant interaction between the seed addition and the removals, indicating that establishment was more limited by seed availability than competition from the species we removed. Because we concurrently excluded seed predators, we also know that species richness was not limited by seed predators eating the added seeds (but for limitations of population abundance see Pearson, Callaway & Maron 2011; Pearson *et al.* 2013; Maron *et al.* 2012; Connolly, Pearson & Mack 2014). Our results agree with those from other studies that did not find interactions between competition and dispersal limitation (e.g. Kalamees & Zobel 2002) and contrast with studies that found significant interactions (e.g. Foster 2001; Wilsey & Polley 2003; Myers & Harms 2009a). The lack of interactions in our study may be because our dependent variables, richness and diversity, serve as broad metrics of community structure. Although large-seeded species may be influenced by removal of seed predators or competition (Bricker, Pearson & Maron 2010; Pearson, Callaway & Maron 2011; Pearson *et al.* 2013; Maron *et al.* 2012; Connolly, Pearson & Mack 2014), our results suggest that the differences in establishment for a subset of species do not affect short-term species richness and

diversity. Similarly if only a few new species establish via the seed addition, it is unlikely that an interaction with the other processes would be evident for measures of broad community structure, at least in the short term.

Overall, we found evidence for strong dispersal limitation in this system. The seed addition significantly influenced richness and diversity. Our results also suggest that competition can be important in grassland systems and can limit community diversity, although its importance to plant community structure may be less than previously thought. In our study, competitive release may have been strong from the dominant species due to high biomass of the bunchgrasses and 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 not limited to specific species for two main reasons: (i) we removed species based on local abundance, rather than looking at specific species pairs and (ii) 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). A limitation of our study, however, is that the results are contingent on many of the added species being rare. It is possible, for example, that dispersal limitation would be less important if we added common species. It seems unlikely that our results reflect transient dynamics since the majority of the added species that established are slow-growing and long-lived perennials. We found little evidence for the effect of seed predators, or any interactions between these processes, on plant species richness and diversity in contrast to other work showing strong effects of seed limitation on population level abundance. 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, Crawley & Rees 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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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Rank abundance curve of plant species in the Blackfoot Valley before treatments were applied in 2010.

Appendix S2. Species removed, based on local abundance, for the dominant and common species competition treatments (in alphabetical order).