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Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly

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Summary

1. Local plant community assembly is influenced by a series of filters that affect the recruitment and establishment of species. These filters include regional factors that limit seeds of any given species from reaching a local site as well as local interactions such as post-dispersal seed predation and disturbance, which dictate what species actually establish. How these filters interact to influence recruitment into local assemblages, and whether they act differentially on individual species based on traits such as seed size or their provenance (i.e. native vs. exotic), has not been well examined. Such studies, however, are crucial for understanding community assembly and for making predictions about what species might be favoured under specific ecological circumstances.

2. We added 20 native and 19 exotic species that varied in seed size to undisturbed or experimentally disturbed subplots in and out of larger rodent exclusion plots at ten grassland sites across the Blackfoot River drainage in western Montana, USA.

3. Individually, exclusion of rodent seed predators and disturbance substantially increased cumulative (summed across all species) seedling recruitment. Exclusion of rodent seed predators enhanced recruitment to a greater extent in disturbed rather than undisturbed plots and for native species compared with exotics, while disturbance enhanced recruitment to a greater extent for exotics compared with natives. Examination of individual species responses indicated that results were generalizable across species within each group and not driven by the response of a few species.

4. Seed size mediated these patterns. Notably, the positive effect of rodent exclusion on recruitment was greater for large- versus small-seeded species, while the impact of disturbance on recruitment was more pronounced for small-seeded exotics relative to other groups.

5. *Synthesis*. These results reveal that local 'filters' such as post-dispersal seed predation and disturbance can individually and collectively impose strong limitation on seedling recruitment into local assemblages. Seed size importantly predicts how strongly individual species are influenced by these local filters. Interestingly, *in situ* community filters have differential effects on native versus exotic species, suggesting that processes that limit native recruitment may not have the same inhibitory influence on exotics.

Key-words: community assembly, competition, disturbance, exotic species, invasion, plant population and community dynamics, post-dispersal seed predation, recruitment, seed limitation, seed size

Introduction

Interspecific variation in the magnitude of seedling recruitment into plant communities is largely responsible for creating unique local assemblages that vary in composition and in the relative abundance of component species (Platt 1975; Gross & Werner 1982; Tilman 1993; Weiher & Keddy 1999). Understanding community assembly and the determinants of local community structure therefore requires elucidating the factors that drive variation in the relative rates of recruitment among species (Grubb 1977; Eriksson & Ehrlén 1992; Grime 2006).

Community assembly is thought to be influenced by a series of 'filters' operating at different spatial scales. These filters whittle a potential pool of colonist species down to those that actually arrive and establish at any given site (Lawton 2000). Once propagules arrive at a given site, disturbance, which removes potential competition for microsites, has historically

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been considered the most important local filter affecting recruitment and establishment. For example, in experiments where disturbance is crossed with seed addition, removal of resident species often leads to greater recruitment of added species (Peart 1989; Turnbull, Crawley & Rees 2000; Zobel *et al.* 2000; Myers & Harms 2009). Yet while disturbance is clearly one determinant of local community composition, other less studied processes can also act as important filters that influence local patterns of seedling recruitment.

One such filter is post-dispersal seed predation by rodents. Dispersed seeds are often vulnerable to predation (Mittelbach & Gross 1984; Hulme 1993, 1998; Cummings & Alexander 2002), and high rates of seed predation from guilds such as rodents can suppress the recruitment, establishment and even population growth of individual species (Kauffman & Maron 2006; Maron & Kauffman 2006; Bricker, Pearson & Maron 2010; Zwolak *et al.* 2010; Pearson, Callaway & Maron 2011) with the potential to alter community composition (Brown & Heske 1990; Curtin *et al.* 1999; Howe & Brown 2000), although community-level studies are still surprisingly rare.

Disturbance and seed predation influence plant regeneration via different but potentially interacting mechanisms. Disturbance removes competition from resident vegetation for resources such as nutrients, light and water, as well as freeing suitable microsites for germination, which can influence the probability that seeds establish as seedlings (Harper 1977; Crawley 1992). In contrast, post-dispersal seed predation influences how many seeds are ultimately available to recruit. Since the processes of microsite and seed limitation are not mutually exclusive (Eriksson & Ehrlén 1992; Maron & Gardner 2000; Calviño-Cancela 2007; Clark *et al.* 2007; Aicher, Larios & Suding 2011), competition and seed predation can potentially interact to limit recruitment of individual species. Quantifying this interaction requires seed sowing experiments where seeds are added to sites with and without resident vegetation while also being protected or exposed to seed predators. To date, most seed sowing experiments have ignored seed predation as a factor that can influence recruitment (but see Howe & Brown 2000; Jutila & Grace 2002) and instead focused on examining whether adding novel species to local assemblages revealed evidence for dispersal limitation (Myers & Harms 2009). Results from such experiments may be misleading if a sizeable fraction of added seeds are eaten prior to germination.

Not only can filters such as disturbance and seed predation influence recruitment into communities, but these factors can importantly interact with traits of colonizing species to influence ultimate outcomes. One trait that may critically determine the outcome of these filtering processes is seed size (Rees 1995; Turnbull, Rees & Crawley 1999). Large-seeded species can be highly vulnerable to rodent seed predation (Brown *et al.* 1986; Reader 1993; Hoffman, Redente & McEwen 1995; Celis-Deiz, Bustamante & Vasquez 2004; Ferreira, Bruna & Vasconcelos 2011; Pearson, Callaway & Maron 2011) whereas small-seeded species are thought to respond more favourably than large-seeded species to disturbance that removes competitors (Reader 1993; Turnbull, Rees & Crawley 1999). These observations suggest that small-seeded species should dominate in disturbed sites, particularly with high levels of post-dispersal seed predation, which may differentially suppress the larger-seeded colonists. Alternatively, large-seeded species should dominate in undisturbed sites, particularly where post-dispersal seed predation is less intense. We know of no experimental work beside that of Reader (1993) that has examined how disturbance and post-dispersal seed predation differentially influence species that vary in seed size to determine patterns of local recruitment into plant assemblages.

A final question concerns whether exotic species respond the same way as native species do to these local filters. In general, successful exotic species are excellent colonizers that are thought to benefit from disturbance (Hobbs 1991; Mack *et al.* 2000; Parker 2001; Kellogg & Bridgham 2004; Britton-Simmons & Abbott 2008), but many natives do as well (Turnbull, Crawley & Rees 2000; Zobel *et al.* 2000; Myers & Harms 2009). Whether disturbance has similar effects on colonization of natives versus exotics remains unclear. As for post-dispersal seed predation, studies that have compared natives to exotics in their susceptibility to seed predation have produced equivocal results. Shahid, Garneau & McCay (2009) found much higher post-dispersal seed loss for natives versus exotics in eastern North America, whereas Blaney & Kotanen (2001) found no difference in seed predation between natives and exotics in similar systems. Remarkably, few studies have compared emergence and establishment of multiple exotic and native species; the interactive effects of disturbance and rodent seed predation on recruitment of these groups have not been examined.

Here, we explore the individual and interacting influence of post-dispersal rodent seed predation, disturbance and seed size on the recruitment of exotic and native species into grassland sites. By sowing exotic and native seeds into separate disturbed and undisturbed subplots inside and outside of larger rodent exclusion plots, we examined: (i) the extent to which rodent seed predation and/or disturbance influenced seedling recruitment into local assemblages, (ii) whether the effects of rodent exclusion and/or disturbance on recruitment varied depending on the seed size of species and (iii) whether native and exotic species differed in their responses to seed predation and/or disturbance, particularly as a function of seed size.

Materials and methods

Our experiment was established at 10 sites scattered over a > 450 km^2 area of semi-arid *Festuca scabrella*- and *F. idahoensis*-dominated grasslands in the Blackfoot River drainage in western Montana (47° 01′ 13.11″ N, 113° 07′ 59.21″ W). Average precipitation is 32 cm year^{-1}. The most abundant small mammal seed consumer at our sites is the deer mouse (*Peromyscus maniculatus*). Montane voles (*Microtus montanus*) and Columbian ground squirrels (*Spermophilus columbianus*) are also present, but *M. montanus* occurs at very low densities (Maron, Pearson & Fletcher 2010) and *S. columbianus* is primarily herbivorous. Other small mammals only occur sporadically

and at very low numbers on our sites (Maron, Pearson & Fletcher 2010).

At each site, we established a rodent exclosure and paired rodent exclosure control plot that were 10–20 m apart. At five sites, these plots were 10 m × 10 m, and at the remaining five sites, they were 10 m × 15 m. We constructed rodent exclosures from 0.625 × 0.625 cm wire mesh fencing that we buried 40 cm into the ground. Fencing extended 60 cm aboveground and was topped with 20 cm of solid aluminium flashing to prevent rodents from climbing over the top. We maintained snap traps within exclosures to ensure they were secure. Although rodent exclosures did not exclude birds or invertebrates, experimental seed depots in exclosures went largely untouched, suggesting that animals other than rodents remove few seeds in our system (J.L. Maron & D.E. Pearson, unpubl. data).

In July 2009, we established six 0.5 m × 0.5 m subplots randomly located within each rodent exclosure and rodent exclosure control plot, but ≥1 m from the plot edge (Fig. 1). The corners of each subplot were permanently marked with rebar and a numbered metal tag. We randomly assigned half the subplots to a disturbance treatment and the other half to a no-disturbance control treatment. One disturbance and one no-disturbance subplot were randomly chosen to be controls for seed addition, and received no seeds. The remaining four subplots received seeds of either native or exotic species. Vegetation within subplots assigned to the disturbed treatment was killed in early July using the broad spectrum, low-persistence herbicide Roundup (Monsanto Corporation, Saint Louis, MO, USA). Several weeks after the herbicide application, we disturbed the top 10 cm of soil and removed dead vegetation from each subplot using a hoe. One disturbed and one undisturbed subplot within each rodent exclosure and rodent exclosure control plot received seed from either 20 native species or 19 exotic species. One native species (*Collinsia parviflora*) and one exotic species (*Veronica verna*) were ultimately eliminated from all analyses because there was substantial natural recruitment of these annual species swamping out the effects of added seeds for these species. All other species added are shown in Table 1. Species added as seed occur in grasslands within the Blackfoot River drainage

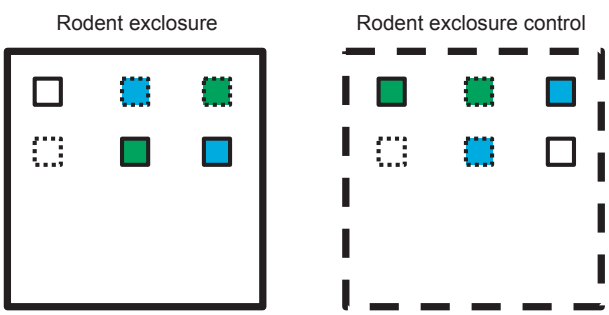

Fig. 1. Cartoon showing experimental design. Each large square depicts a rodent exclosure (———) or rodent exclosure control (– – – –). Rodent exclosures and associated control plots were either 10 m × 10 m or 10 m × 15 m, depending on site. Inside rodent exclosure or control plots, we established a series of subplots (0.5 m × 0.5 m; depicted by smaller boxes) that were either disturbed (– – – –) or undisturbed (———). To these subplots, we added seeds of either 20 species of natives (green colour) or 19 species of exotics (blue colour). Small uncoloured boxes represent control subplots to which we did not add seeds. This basic design, initiated in 2009, was replicated in 2010 (replicated subplots not shown) with the exception that control subplots (no seeds added) were not re-established in 2010. See Methods for details.

but were relatively uncommon at our experimental sites (J.L. Maron and D.E. Pearson, unpubl. data). The exceptions to this were the native species *Lupinus sericeus* and *Lithospermum ruderale*, which occurred in moderate abundance at some sites, but were chosen because they are among the few large-seeded native species. Using relatively uncommon species enabled us to determine whether their low local abundance was due to competition, seed predation or a combination of these factors once dispersal limitation was experimentally overcome. Seeds used in our experiments were collected in summer 2009 from plants that grew in the Blackfoot River drainage. Only filled, undamaged seeds were used. Seeds were added in late August 2009, except for one native species (*Delphinium bicolor*) and four exotic species (*Chenopodium album*, *Hypericum perforatum*, *Melilotus officinalis* and *Verbascum thapsus*), which were added in early October since seeds of these species were not ready for collection before August. To account for the fact that small-seeded species typically produce many seeds and large-seeded species produce relatively fewer seeds, we varied the quantity of seeds added to each subplot accordingly. With a few exceptions (due to initial inaccuracies with estimating seed weights of particular species), we added 50 seeds per subplot for species with seeds > 0.006 g, 100 seeds per subplot for species with seeds ≤0.006 g and > 0.001 g, and 175 seeds per subplot for species with seeds ≤0.001 g. For those species for which we added 100 seeds or more, seed number was estimated by counting out the relevant number of seeds and determining the average weight per batch (n = 10), and thereafter weighing seed to attain the target seed number per batch.

In the summer of 2010, we repeated this experiment by establishing five more 0.5 × 0.5 m subplots within each rodent exclosure or rodent control plot. Three of these five subplots were randomly chosen to be disturbed (as in 2009) and then randomly selected to receive (i) native seed, (ii) exotic seed or (iii) no seeds. The two remaining undisturbed subplots received either native or exotic seeds. Undisturbed no seed-addition plots established in 2009 served as undisturbed no seed-addition controls in 2010. In early September 2010, we added the same species of exotic and native seeds (collected in summer 2010), at the same amounts, to subplots as we did in 2009 (Table 1). These subplots were censused for seedlings in June/July in the year following seed addition. In subplots to which we added exotic seed, we clipped all flowers/seed heads from plants on which these occurred (a few individuals in the 2009 seed-addition subplots began to flower in 2011) to prevent new seed input. All plants in these plots will be killed when the experiment ends to ensure exotics do not establish.

ANALYSES

We conducted three separate analyses of our field data using SAS (version 9.2). In all analyses, seed-addition control plots (i.e. plots with no seeds added) were excluded because there was zero to very little seedling recruitment in subplots of any treatment combination (lsmeans = 0.41–1.23 seedlings per subplot depending on treatment combination). In the first two analyses, we used the GLIMMIX module to examine the total number of seedlings that recruited into each subplot across species, that is, pooled seedling counts. First, we performed a four-way ANOVA to test the individual and interactive effects of rodent exclusion, disturbance, seed origin (native vs. exotic) and year on the total number of seedlings that recruited into each subplot. Site was included as a random factor, but because it is only a blocking variable test statistics for it are not reported. Denominator degrees of freedom were calculated to account for the split-plot design (i.e. rodent exclosure plots 'split' to accommodate subplots assigned to the disturbance and seed origin treatments). We also included the

Table 1. Identity and characteristics of native and exotic species added to seed-addition subplots, in order of their individual seed weight

Species	Origin	Life history	Seed weight (g)	Seed size bin	Rodent exclusion	Disturbance	Rodent exclusion × disturbance
Lithophragma glabrum	Native	Perennial	0.00005	Small	–	–	–
Potentilla arguta	Native	Perennial	0.00009	Small			
Verbascum thapsus	Exotic	Biennial	0.00009	Small		**	
Erigeron pumilus	Native	Perennial	0.00010	Small		**	
Saxifraga oregano	Native	Perennial	0.00012	Small	–	–	–
Linaria vulgaris	Exotic	Perennial	0.00013	Small		**	
Sisymbrium altissimum	Exotic	Annual/biennial	0.00013	Small		**	
Hypericum perforatum	Exotic	Perennial	0.00014	Small		**	
Linaria dalmatica	Exotic	Perennial	0.00017	Small	–	–	–
Potentilla recta	Exotic	Perennial	0.00020	Small		**	
Zigadenus venenosus	Native	Perennial	0.00023	Small			
Dodecatheon conjugens	Native	Perennial	0.00024	Small	–	–	–
Poa pratensis	Exotic	Perennial	0.00024	Small	–	–	–
Delphinium bicolor	Native	Perennial	0.00045	Small	–	–	–
Taraxacum officinale	Exotic	Perennial	0.00048	Small			
Lactuca serriola	Exotic	Annual/biennial	0.00057	Small		*	*
Heterotheca villosa	Native	Perennial	0.00063	Small	**		
Collomia linearis	Native	Annual	0.00091	Large	**	**	*
Geum triflorum	Native	Perennial	0.00124	Large			
Anemone multifida	Native	Perennial	0.00133	Large	–	–	–
Rumex crispus	Exotic	Perennial	0.00152	Large		**	
Carduus nutans	Exotic	Biennial	0.00153	Large	**	*	
Fritillaria pudica	Native	Perennial	0.00158	Large			*
Stipa richardsonii	Native	Perennial	0.00160	Large			
Centaurea stoebe	Exotic	Perennial	0.00195	Large			
Chenopodium album	Exotic	Annual	0.00214	Large	**		
Melilotus officinalis	Exotic	Annual/biennial	0.00216	Large			**
Gaillardia aristata	Native	Perennial	0.00246	Large		**	
Cirsium vulgare	Exotic	Biennial	0.00257	Large		**	
Astragalus drummondii	Native	Perennial	0.00340	Large	–	–	–
Lithospermum arvense	Exotic	Annual	0.00366	Large		**	
Tragopogon dubius	Exotic	Biennial	0.00767	Large	**	**	**
Lomatium macrocarpum	Native	Perennial	0.00806	Large	**		
Balsamorhiza sagittata	Native	Perennial	0.00908	Large	**	**	
Lithospermum ruderale	Native	Perennial	0.02037	Large	**	**	
Cynoglossum officinale	Exotic	Biennial	0.02269	Large			
Lupinus sericeus	Native	Perennial	0.02360	Large			

Stars indicate a significant (**$P < 0.05$) or marginally significant (*$0.05 \leq P < 0.10$) increase in abundance in response to rodent exclusion, disturbance or the multiplicative combination of rodent exclusion and disturbance (rodent exclusion × disturbance interaction) as tested with MANOVA (see Appendix S1 for treatment means). Seed size bin is based on seed weight. Species with dashes in columns were not included in the model because of no or very limited recruitment across all treatments, sites and years. See Methods for details.

rodent exclusion plot × year interaction as a random factor to account for any autocorrelation among subplots established within the same rodent treatment plot and year. Because there were no significant interactions between year and any other treatment factors ($P > 0.05$), we removed these terms from the model reported here. Second, to examine how seed size mediated treatment effects, we grouped the added species into a small-seeded 'bin' if seed weight was < 0.0091 g (the median seed weight and a natural break in the seed distribution of seed weights among species) and put heavier-seeded species into a separate large-seeded 'bin'. We used these two discrete seed weight categories rather than treating seed weight as a continuous covariate (and using ANCOVA) for several reasons. First, many species had zero recruitment in a majority of subplots of a given treatment combination, and this skewed raw data made covariate analysis problematic. Second, seed weight among species was not normally distributed. By binning species of a given seed weight, we could sum across multiple species that recruited into a given subplot, creating a response variable that was more tractable for analysis. We ran an identical ANOVA as just described but included seed size bin as another fixed factor in the model and the subplot as a random factor to account for any autocorrelation in response among seed size bins added to the same subplot. For this analysis, we were particularly interested in examining the seed size bin by treatment interactions since significant interactions would indicate that treatment effects differed among species groups based on seed size. We do not report the main effects of year, origin, rodent exclusion or disturbance from this model, as these results were not substantially different from those from the first analysis. To account for positive skew in the seedling recruitment data, we ran both pooled-species analyses with an underlying negative binomial distribution. For both analyses, we report least squared means (±1 SEM) in the Results.

In the seed size analysis, we omitted species that recruited into < 3 subplots across all sites and years (Table 1). Because differing numbers of exotic versus native species were included in each pooled-species analyses, the number of seeds added for each group (i.e. summed across relevant species) also differed. For species included in the first

analysis, more total seeds were added to native ($\bar{x}$ = 2465 ± 0.9) than exotic seed-addition plots ($\bar{x}$ = 2375 ± 0.9; $F_{1,119}$ = 9639, P < 0.0001), while for species included in the second analysis, more exotic than native seeds were added ($F_{1,119}$ = 264281, P < 0.0001), particularly of small-seeded ($\bar{x}$ = 1150 ± 0.6 and $\bar{x}$ = 625 ± 0.6 exotic and native seeds, respectively) versus large-seeded species ($\bar{x}$ = 865 ± 0.6 and $\bar{x}$ = 875 ± 0.6 exotic and native seeds, respectively; origin × seed size bin, ANOVA, $F_{1,158}$ = 244891, P < 0.0001). To assure that differences in recruitment between exotics and natives and seed size bins obtained in pooled-species analyses were not driven by differences in seed number, we ran identical models to those described above but with per capita recruitment (i.e. total seedlings per subplot divided by the total number of seeds added) as the response variable rather than total recruitment. The overall results from these revised models were comparable to those obtained in the original analysis. Thus, we only report results from the original analyses of total recruitment.

In the third analysis, we evaluated the response of individual species to rodent exclusion and disturbance while accounting for interdependencies of multiple species in the same subplot using the MANOVA module in SAS. Since this module cannot incorporate random factors, we could not explicitly account for the split-plot design (i.e. nesting of subplots within rodent exclusion treatments and sites). However, we were able to partially account for the design, specifically autocorrelation among subplots assigned to the same treatment per site, by averaging the number of seedlings counted per species, treatment and site across years. Similarly because the MANOVA module cannot model non-normal distributions, we log-transformed (ln + 1) recruitment data to reduce positive skewness. As with the seed size analysis, those species with scant recruitment were excluded from the MANOVA.

Results

EFFECTS OF RODENT SEED PREDATION AND DISTURBANCE ON SEEDLING RECRUITMENT

Overall, there was greater recruitment in 2011 than 2010 ($F_{1,19}$ = 23.77, P < 0.001), but all year by treatment interactions were non-significant (P > 0.05). There was also significantly higher seedling recruitment into subplots within rodent exclosures ($\bar{x}$ = 39.7 ± SEM 5.4) compared with those outside of rodent exclosures ($\bar{x}$ = 26.9 ± 3.7; $F_{1,9}$ = 9.27, P < 0.015), where we observed extensive evidence of mouse seed predation (e.g. feeding piles and mouse faeces) following seed addition, and higher recruitment into disturbed ($\bar{x}$ = 44.5 ± 5.7) versus undisturbed subplots ($\bar{x}$ = 24.0 ± 3.1; $F_{1,113}$ = 47.48, P < 0.001). Moreover, there was a significant rodent exclusion × disturbance interaction ($F_{1,113}$ = 6.22, P < 0.015): rodent exclusion had stronger effects on recruitment into disturbed subplots than undisturbed subplots (Fig. 2).

DIFFERENCES BETWEEN NATIVES AND EXOTICS IN SEEDLING RECRUITMENT

Exotics had significantly greater recruitment into seed-addition subplots ($\bar{x}$ = 39.9 ± 5.10) than did natives ($\bar{x}$ = 26.8 ± 3.45; $F_{1,113}$ = 19.8, P < 0.001, Fig. 2) across rodent and disturbance treatments. Of particular interest was how exotic versus native species differed in their response to rodent exclusion or disturbance. Rodent exclusion enhanced recruitment more markedly for natives than for exotics (rodent exclusion × origin interaction; $F_{1,113}$ = 10.71, P < 0.001, Fig. 2). Conversely, disturbance enhanced recruitment more markedly for exotics compared with natives (disturbance × origin interaction, $F_{1,113}$ = 5.56, P < 0.021; Fig. 2). The greater rodent effect evident in disturbed compared with undisturbed subplots did not differ significantly between exotic and native species (rodent exclusion × disturbance × origin interaction, $F_{1,113}$ = 0.23, P = 0,63, Fig. 2).

EFFECTS OF SEED SIZE ON PATTERNS OF SEEDLING RECRUITMENT

The magnitude of rodent exclusion and disturbance effects also depended on whether species were small or large seeded. Large-seeded species benefitted significantly more from rodent exclusion than did small-seeded species (seed bin × rodent exclusion interaction, $F_{1,151}$ = 10.64, P < 0.001; Fig. 3), with this pattern not differing between exotics and natives (seed bin × rodent exclusion × origin interaction, $F_{1,151}$ = 0.10, P = 0.76) or between disturbance treatments (seed bin × rodent exclusion × disturbance interaction, $F_{1,151}$ = 0.06, P = 0.81; seed bin × rodent exclusion × disturbance interaction × origin interaction, $F_{1,151}$ = 1.3, P = 0.26). Although the positive effect of disturbance on recruitment did not depend on seed size overall (seed bin × disturbance interaction, $F_{1,151}$ = 1.32, P = 0.25), the greater disturbance effect seen for exotics over natives differed significantly by seed size (seed bin × disturbance × origin interaction, $F_{1,151}$ = 10.19, P < 0.002). Specifically, across rodent exclusion treatments, disturbance

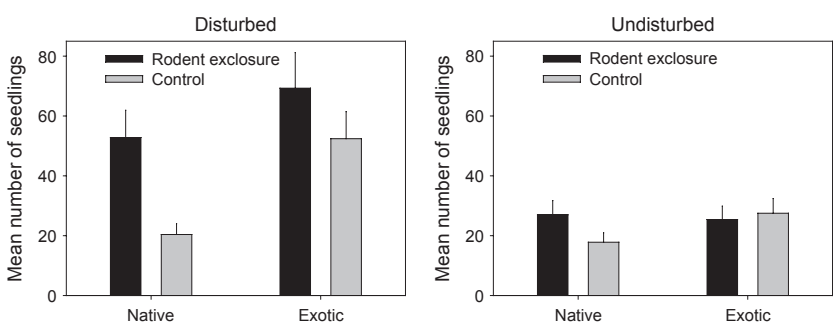

Fig. 2. Least square mean (+SEM) number of seedlings that recruited into disturbed (left) and undisturbed (right) subplots embedded in rodent exclosure and rodent exclosure control plots in the Blackfoot River drainage, Montana, USA. LS means are from generalized linear mixed model analysis (see Results for details).

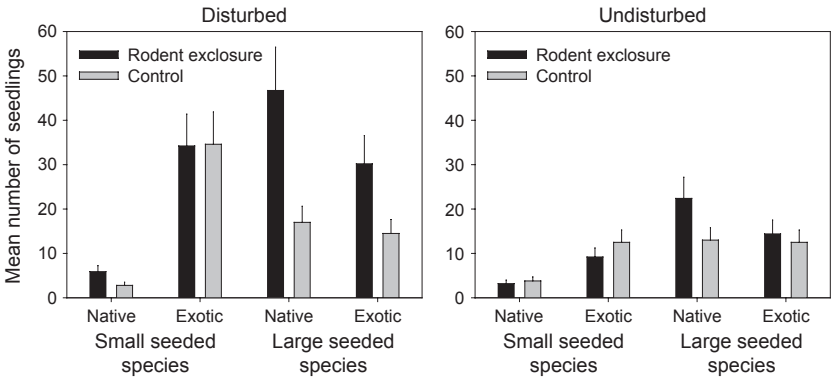

Fig. 3. Least square mean (+SEM) number of seedlings of small-seeded (seed weights < 0.00091 g) and large-seeded (seed weights ≥ 0.00091 g) native and exotic species that recruited into disturbed (left) and undisturbed (right) subplots embedded in rodent exclosure and rodent exclosure control plots. LS means are from generalized linear mixed model analysis (see Results for details).

had a particularly strong effect on small-seeded exotics versus a moderate effect on large-seeded exotics and natives and minimal effect on small-seeded natives (Fig. 3). The relatively weak response of small-seeded natives may have been partially driven by the fact that four of seven species in this group (versus two of nine small-seeded exotics) had no or nearly no recruitment across sites and treatments (Table 1). Across all treatments, recruitment was significantly greater for large- than small-seeded species (seed bin effect, $F_{1,151} = 96.33$, $P < 0.001$), but this pattern was driven by native species ($\bar{x} = 3.7 \pm 0.58$ vs. $\bar{x} = 21.9 \pm 3.18$ small- and large-seeded seedlings per subplot, respectively) rather than exotics ($\bar{x} = 19.2 \pm 2.81$ vs. 16.8 ± 2.45 small- and large-seeded seedlings per subplot, respectively; seed bin × origin interaction, $F_{1,151} = 130.98$, $P < 0.001$), as further conditioned by the disturbance treatment (i.e. seed bin × disturbance × origin interaction, Fig. 3).

INDIVIDUAL SPECIES RESPONSES TO RODENT SEED PREDATION AND DISTURBANCE

Overall, both rodent exclusion ($F_{29,8} = 3.38$, $P = 0.038$) and disturbance ($F_{29,8} = 9.95$, $P = 0.001$) enhanced recruitment of individual species, although the interaction between these factors was not significant ($F_{29,8} = 1.60$, $P = 0.25$). A total of eight individual species, including three of 16 exotics analysed and five of 13 natives, benefited significantly from rodent exclusion (Table 1). Notably, seven of eight species with significant effects of rodent exclusion were classified as large rather than small seeded, supporting results from the pooled-species seed size analysis. The one exception, the native *Heterotheca villosa*, had the heaviest seeds of those classified in the small-seed bin. Disturbance promoted significant increases in recruitment of 14 species, including nine of 16 exotics and five of 13 natives (Table 1). In addition, disturbance had marginally significant effects on the recruitment of two exotics species. Species with the greatest response to disturbance tended to be small-seeded exotics (see Appendix S1 in Supporting Information), paralleling results from the pooled-species seed size analysis. Only two individual species, both exotics, showed a significantly greater effect of rodent exclusion under disturbed relative to undisturbed conditions (rodent × disturbance interaction); one additional exotic species and two natives showed a marginally significant effect. However, treatment means for a majority of exotic and native species trended in this direction (see Appendix S1 in Supporting Information), in support of results from pooled-species analyses.

Discussion

Our experiment examined the strength of two local processes that can individually limit recruitment of species into local assemblages once dispersal limitation is overcome. In isolation, both disturbance and exclusion of rodent seed predators enhanced recruitment of native and exotic species into local assemblages. Notably, these processes interacted in a multiplicative fashion – ameliorating both competition (via disturbance) and seed predation enhanced average seedling recruitment by 174% over what occurred in the presence of these constraining factors. Beyond this, we found that seed size had an important influence on how these filters operate. Small-seeded species, particularly exotics, recruited best in low competition, disturbed environments and were generally insensitive to rodent seed predation. In contrast, larger-seeded species experienced better colonization in environments free from rodent seed predation. Overall, rodent seed predation had greater effects on species of native versus exotic origin. Hence our results suggest that seed size presents a trade-off in relative recruitment success along disturbance-predation gradients that could affect community composition. Additionally, the effects of disturbance, rodent seed predation and seed size appear to operate differently for native and exotic species.

Many seed-addition experiments have shown that the removal of competitors (via disturbance) can enhance recruitment of added species (Sagar & Harper 1961; Putwain & Harper 1970; Gross & Werner 1982; Turkington, Klein & Chanway 1993; Jutila & Grace 2002; Mouquet *et al.* 2004) because resident vegetation often monopolizes microsites needed by colonizing species for germination. Alternatively, experiments have revealed that exclusion of rodent seed predators can boost the recruitment of single (Maron & Kauffman 2006; Nunez, Simberloff & Relva 2008) or a few focal species (Pearson & Callaway 2008; Bricker, Pearson Maron 2010; Zwolak *et al.* 2010; Pearson, Callaway & Maron 2011),

indicating that seed number can also be limiting. However, examinations of how rodent seed predation influences patterns of plant recruitment in a community context remain relatively rare (Brown & Heske 1990; Curtin *et al.* 1999; Howe & Brown 2000). Rarer still are studies that examine the importance of granivory relative to disturbance and other processes that can influence recruitment into local sites.

For native species overall (pooled across species of different seed sizes), the independent effects of disturbance and seed predation on recruitment were generally moderate and comparable in magnitude. However, the combined effects of these two processes were quite strong. Moreover, the strength of these factors varied substantially based on seed size, with large- versus small-seeded species benefitting much more from removal of both competition and seed predation (Fig. 3). Small-seeded species recruited at lower rates than large-seeded species under all conditions, and recruitment of this group was only enhanced, albeit minimally, when both filters were removed. Collectively, these results establish how fine-scale filters like competition and rodent seed predation can independently and interactively combine with important plant traits like seed size to influence recruitment in native plant communities.

Our results illustrate how seed-addition experiments aimed at quantifying the strength of dispersal and microsite limitation in plant populations (Clark *et al.* 2007) can be misleading if seed predators are ignored. Had we only conducted our experiment outside of rodent exclosures, as is usually the case in studies of this type, the modest recruitment of large-seeded natives might have been seen as evidence that suitable microsites for germination were lacking. However, the fact that recruitment substantially increased for seeds protected from rodents indicates that limited recruitment in plots open to rodents was driven by seed limitation imposed by rodent predation. This is likely to be a common problem when cryptic consumers of seeds are not accounted for in seed-addition experiments.

By quantifying the impacts of *in situ* filters on native community assembly, we could contrast these results with those obtained when only exotics were added to plots. This enabled us to address a central question in invasion biology – do exotic species respond the same way as natives to local filters that influence plant community assembly and relative abundance? We found that exotics differed from natives in their responses to removal of both competition and rodent seed predation. Removal of competition via disturbance had a greater positive effect on recruitment of exotic species than of natives overall, with small-seeded exotic species responding more favourably to disturbance than either large-seeded or small-seeded natives. Why did exotics exhibit a stronger response to disturbance than natives, especially considering the subset of small-seeded species? Differences in life-history strategies between our native and exotic species pools offer a possible clue. Most exotics, and particularly those with the largest responses to disturbance, were annual/biennials (see Appendix S1, Table 1), whereas all but one of the native species we added to subplots were perennials (discounting the one we eliminated from analyses), despite the small seed sizes of many of these species. Within any given seed size, annual/biennial species are likely to be better colonists compared with perennials (Rees 1995). Hence, one possible explanation for the stronger response to disturbance we observed for exotics over natives is that most exotics that have successfully established in recipient communities have already gone through a 'colonization filter'. As a result, a random draw of established exotic species is more likely to contain a greater proportion of ruderal species, which are likely to be superior colonizers (particularly under disturbed conditions) than might a random draw of natives. However, native plants in our system may also be particularly poorly represented by species with ruderal strategies. Although there are several common native annuals known to respond favourably to disturbance that we did not add to our plots (e.g. Ortega & Pearson 2005), the overwhelming majority of native grassland species in our region are perennials (Lackschewitz 1991).

Exotics also differed from natives in that they were generally less sensitive to the filter imposed by rodent seed predation, particularly in relation to how they responded to disturbance. Despite the fact that rodents provided strong biotic resistance to a few individual exotics (see Appendix S1, Table 1; Pearson, Potter & Maron in press), the overall effect of this filter at the community level was weaker suppression of exotics than natives. As seen with natives, rodent predation primarily impacted large- versus small-seeded exotics, but the magnitude of this effect was reduced for exotic relative to native species overall (Fig. 3). In previous studies of apparent competition between natives and exotics that involve rodents, exotic plants have been shown to provide a refuge for rodents, which can then exert strong consumer pressure on nearby native plants (Orrock, Witter & Reichman 2008; Dangremond, Pardini & Knight 2010). Since exotics occur at relatively low densities in our system, we speculate that if apparent competition is occurring, it is operating entirely through an enhanced preference of mice for native versus exotic seeds, particularly among large-seeded species. In many respects, our results mirrored those from one of the few previous studies to examine how seed size interacts with rodent seed predation and disturbance (Reader 1993; Reader 1997). Although Reader (1993) ignored origins of the species involved (83% of his species were exotic), he found that small-seeded species in Canadian old fields were favoured under disturbed conditions whereas large-seeded species were favoured when granivorous rodents were excluded. By controlling for origins, we show that (i) the increased response of small-seeded species to disturbance in our system was primarily driven by exotics whereas (ii) the increased response of large-seeded species to protection from rodent granivory was driven more by natives. Thus, while disturbance and rodent seed predation influence both native and exotic species recruitment, the specific response of each of these groups differed. Collectively, these results shed important light on how seed size might fundamentally influence community assembly across environments that vary in disturbance and seed predation pressure, and how the evolutionary history of community

context may influence how different species respond to such filters.

Ultimately, community structure is determined both by how regional and local filters influence seed arrival and subsequent seedling recruitment, and also by longer-term patterns in seedling and juvenile plant survival. Although we do not yet know how ultimate community structure or diversity will be affected by the early recruitment patterns we report here, we did re-census our 2009 seed-addition plots in 2011 to determine if patterns changed from year one to year two after seed addition. We found that the general patterns reported here were not substantially changed after an additional year. In the grasslands in which we work, most plants are quite long-lived, and at least for a few forbs where extensive demographic data are available, mortality is highest at the seedling stage (Bricker 2009). Once individuals survive their first summer, mortality declines substantially (Bricker 2009). As such, it is likely that the short-term impacts of our treatments on seedling recruitment are likely to ultimately influence longer-term patterns of community structure and diversity.

Our experiment sheds light on notions about how mixed annual/perennial grasslands might be organized. Historically, small-seeded plants (often annuals) have been thought to persist in gaps created within the matrix of dominant perennial vegetation (Levins & Culver 1971). In this framework, larger-seeded perennials are often considered superior competitors (Harper, Lovell & Moore 1970; Gross & Werner 1982; Crawley & May 1987) whereas the smaller-seeded annuals are considered fugitive species. These ideas have been supported by sowing and other experiments that suggest that large-seeded species have an establishment advantage over small-seeded species (Gross & Werner 1982; Gross 1984; Eriksson & Eriksson 1997; Turnbull, Rees & Crawley 1999). We similarly found greater recruitment of large- versus small-seeded species across all treatments, and greater recruitment of small-seeded versus large-seeded exotic species in disturbed subplots. Yet, typically seed predation has been ignored in classic ideas about the organization of grassland communities (Grace 1999; Tilman 2004). Our experiment suggests that seed limitation, imposed by granivores, may be common across certain large-seeded species that do not need disturbance to establish in grasslands**.** Applying local community filters to exotics and natives simultaneously indicated that the exotics recruited better overall and were generally less suppressed by rodent seed predation and more released by disturbance than were the natives. Future studies that examine how exotic plants evade native filters to overrun native communities and attain dominance could shed light on these outcomes.

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Supporting Information

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

Appendix S1. Table showing mean number of seedlings of each species that recruited into seed-addition subplots by treatment.

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