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BIOTIC CONTROLS OF PLANT COEXISTENCE

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Rodent seed predators and a dominant grass competitor affect coexistence of co-occurring forb species that vary in seed size

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Abstract

1. Propagule size and number often vary by several orders of magnitude among co-occurring plant species. Explaining the maintenance of this variation and understanding how propagule size contributes to coexistence remain a central challenge for community ecologists. The dominant paradigm is that a competition–colonization trade-off maintains interspecific variation in seed size, but empirical support is limited and other coexistence mechanisms, such as size-dependent seed predation, have not been examined.
2. We examined how seed size, fecundity, and other functional traits of 18 co-occurring perennial forbs trade-off with both vulnerability to rodent seed predation and competitive response to a community-dominant perennial bunchgrass. We added seeds of these species to 1 m^2 plots at 10 sites where we factorially manipulated rodent seed predation and competition from the community dominant, *Festuca campestris*. For a given plot, seeds of each species were added at densities that reflected the fecundity (i.e., per capita seed production) for each species. Moreover, we varied total seed density among plots by adding seeds at one of five relative densities (0, 0.25. 0.5, 1.0, and 1.5 times each species' fecundity) to examine how fecundity affected overall recruitment for each species.
3. There was a trade-off between seed size and fecundity, as expected, but larger seed size was also associated with greater plant height, lower C/N ratios, and lower water use efficiency, suggesting that seed size represented a "resource acquisitive" trait syndrome (as quantified by trait principal component scores).
4. In the field experiment, the suppressive effects of seed predation on seed recruitment rate increased with increasing seed size. In contrast, smaller seeded species with less resource-acquisitive traits were more negatively affected by competition from *F. campestris* than were species with more resource acquisitive traits.
5. *Synthesis*. While the competition–colonization trade-off has been the predominant mechanism thought to maintain coexistence among species that vary in fecundity and seed size, our work suggests that susceptibility to rodent seed predation and competitive response to community dominants represent alternative mechanisms that can differentially influence plant recruitment of species based on their seed size and associated traits.

KEYWORDS
coexistence, community assembly, *Festuca campestris*, functional traits, *Peromyscus maniculatus*, seed predation, seed size, trade-offs

1 | INTRODUCTION

Plant communities consist of co-occurring species that often vary in seed size by 2–6 orders of magnitude (Aarssen & Jordan, 2001; Harper, Lovell, & Moore, 1970; Jakobsson & Eriksson, 2000). Due to the ubiquitous life-history trade-off between propagule number and propagule size, orders of magnitude difference in seed size often translates to a great disparity in fecundity among co-occurring species. As predicted by coexistence theory (Chesson, 2000), if species have similar niches, high-fecundity species should have an inherent advantage since their average fitness (sensu Chesson, 2000) is substantially higher than that of larger seeded species. Thus, a long-standing challenge for ecologists has been determining what mechanisms maintain variation in seed size, and hence species diversity, given vast differences in fecundity among species.

The traditional theoretical solution to this conundrum is that there are strong trade-offs between fecundity, interspecific competitive ability, and dispersal that enable coexistence. High-fecundity small-seeded species are good colonizers but poor competitors, whereas low-fecundity large-seeded species are superior competitors but poor colonizers (Chesson, 2000; Shmida & Ellner, 1984; Tilman, 1994; Tilman & Pacala, 1993). Although this trade-off has dominated thinking about how coexistence occurs among species that vary in fecundity and seed size (Rees, Condit, Crawley, Pacala, & Tilman, 2001), these models make a number of assumptions that are unlikely met in nature (Adler & Mosquera, 2000; Kisdi & Geritz, 2003). For example, this theory assumes unrealistically large competitive asymmetries among species (Adler & Mosquera, 2000; Kisdi & Geritz, 2003) and strict linear competitive hierarchies. It also typically considers competition among propagules attempting to colonize an open site rather than cases where an arriving propagule experiences resistance to colonization because open sites are adjacent to a resident heterospecific adult (Yu & Wilson, 2001). Moreover, empirical support for a competition–colonization trade-off related to seed size remains limited (Rees, 1995; Turnbull, Manley, & Rees, 2005; Turnbull, Rees, & Crawley, 1999; Viola et al., 2010).

In perennial grasslands, dominant long-lived grasses monopolize space, and these plants and their litter constrain recruitment of forb species that germinate in the interstitial spaces between these grasses (Aguilera & Lauenroth, 1995; Pert, 1989). Unlike in annual systems, forb diversity in some perennial grasslands is unlikely to be constrained by direct competition between different species of perennial forbs during the recruitment phase. Instead, forb recruitment is more likely influenced by differences among species in their ability to recruit near large adult bunchgrasses (and their litter). Some studies indicate that larger seeded species may have advantages in these circumstances since they are often less sensitive to local hazards such as shade, litter, and competitors than smaller seeded species (Leishman, Wright, Moles, & Westoby, 2000; Moles & Westoby, 2004; Reader, 1993). Whether this is due to seed size per se or other unmeasured functional traits is unclear. Regardless, greater sensitivity of small-seeded species to dominant competitors might be counterbalanced by the advantage of greater fecundity, which increases the probability that some seeds encounter benign sites. Thus, rather than a trade-off between competitive ability and colonization (or fecundity), a trade-off between competitive response (as measured by sensitivity to competition from the community dominant) and fecundity may be sufficient to promote coexistence.

The potential advantage that large-seeded species have in terms of competitive response, however, may be offset by greater vulnerability of these species to seed predation by generalist rodents. In many temperate communities, large-seeded species suffer greater seed loss than small-seeded species (Larios, Pearson, & Maron, 2017). As a result, their recruitment is disproportionately suppressed by small mammal consumers (Brown & Heske, 1990; Hulme, 1998; Larios et al., 2017; Maron, Pearson, Potter, & Ortega, 2012; Reader, 1993). We are unaware of any studies that have explicitly investigated the relationship between coexistence and trade-offs between fecundity, seed size, sensitivity to competition, and vulnerability to seed predators or determined whether there may be other functional traits that covary with seed size that might also play a key role in their enhanced ability to cope with hazards such as litter and competitors. (but see Jakobsson & Eriksson, 2000; Lönnberg & Eriksson, 2013).

Here, we test the hypothesis that seed size variation and coexistence among forb species within perennial grassland communities is shaped by trade-offs among fecundity, susceptibility to rodent seed predation, and sensitivity to competition from the dominant bunchgrass. We hypothesize that dominant bunchgrasses act analogously to "local stressors" (sensu Muller-Landau, 2010), differentially inhibiting recruitment and establishment of forb species. We predict that the advantage of being large-seeded likely resides less with competitive superiority over heterospecific forb seedlings and more with reduced sensitivity to competition from dominant adult competitors (Tilman, 1988). However, we also predict that these species will be more vulnerable to postdispersal rodent seed predation than co-occurring smaller seeded species (Maron et al., 2012; Reader, 1993).

To test these predictions, we experimentally quantify how postdispersal seed predation by rodents and competition from the community dominant bunchgrass, *Festuca campestris*, influences the recruitment and subsequent abundance of 18 co-occurring perennial grassland forbs that vary in seed size (Table 1). We examine how these interactions influence recruitment across a range of seed densities that reflected inherent differences in fecundity among species and differences

TABLE 1 Co-occurring target species, mean seed weight, and fecundity (i.e., mean number of seeds produced per individual plant). See Section 2 for how fecundity was assessed

Target species	Abbreviation	Seed WT (mg)	Fecundity
Antennaria microphylla (Asteraceae)	ANMI	0.044	1,244
Penstemon procerus (Plantaginaceae)	PEPR	0.046	926
Erigeron pumilus (Asteraceae)	ERPU	0.069	6,629
Achillea millefolium (Asteraceae)	ACMI	0.088	1,277
Potentilla glandulosa (Rosaceae)	POGL	0.096	12,587
Artemisia ludoviciana (Asteraceae)	ARLU	0.14	4,918
Heterotheca villosa (Asteraceae)	HEVI	0.58	5,177
Arnica sororia (Asteraceae)	ARSO	0.75	59
Geum triflorum (Rosaceae)	GETR	0.77	127
Zigadenus venenosus (Liliaceae)	ZIVE	1.37	290
Eriogonum umbellatum (Polygonaceae)	ERUM	2.16	494
Lomatium triternatum (Apiaceae)	LOTR	3.65	37
Gaillardia aristata (Asteraceae)	GAAR	3.92	230
Clematis hirsutissima (Ranunculaceae)	CLHI	6.40	32
Balsamorhiza sagittata (Asteraceae)	BASA	8.33	150
Geranium viscosissimum (Geraniaceae)	GEVI	8.68	36
Lupinus sericeus (Fabaceae)	LUSE	20.92	78
Lithospermum ruderale (Boraginaceae)	LIRU	31.08	138

in seed densities within species. Additionally, by quantifying functional traits of these target plants, we explore whether seed size represents a wider syndrome of covarying traits that predicts performance across different biotic conditions.

2 | MATERIALS AND METHODS

Our research took place in the Blackfoot Valley in western Montana (47°01′13.11″N, 113°07′59.21″W), a >450 km^2 area within semiarid perennial grasslands dominated by rough fescue, *F. campestris*, in association with a rich diversity of native perennial forbs. The primary small mammal seed consumer in these grasslands 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 mostly herbivorous. Seed predation by birds appears to be minimal and there are no seed-harvesting ants in this system (J. L. Maron & D. E. Pearson, unpubl. data).

2.1 | Target species, fecundity, and traits

We selected 18 focal species of common co-occurring forbs based on their variation in seed size (Table 1). Although not all focal species occurred at all of our study sites, they all occurred at a subset of these sites (Table S1). To determine how fecundity varied as a function of seed size, we estimated total seed production for each target species. Fecundity was measured on adult plants that had no visible evidence of herbivory. For three target species (*Balsamorhiza sagittata*, *Lithospermum ruderale*, and *Lupinus sericeus*), we utilized fecundity estimates (in the absence of herbivory) from our previous work (Amsberry & Maron, 2006; Bricker & Maron, 2012; Bricker, Pearson, & Maron, 2010), and for *Artemisia ludoviciana*, we obtained fecundity estimates from the literature, which were also made in *F. campestris* grasslands in western Montana (Harvey, 1981). For the rest of our target species, we quantified average per capita seed production in June and July 2016. To do this, we randomly selected a minimum of five individuals of average size per site from a minimum of at least four sites (n > 20 individuals per species, average distance between high and low productivity sites = 35.5 km). We estimated fecundity of each individual by counting the number of seeds in one undamaged head or fruiting body and multiplying that number by the total number of heads or fruits produced by that individual. Focal plants sampled for fecundity were generally not close enough to heterospecifics for light competition to be severely limiting to fecundity (although there certainly could have been competition below-ground). Thus, our estimates of fecundity for

herbivore-free individuals are a rough approximation to what is average maximum fecundity for each species.

We measured a variety of plant functional traits in addition to seed size for each of our 18 focal species. Our goal was to determine whether seed size was correlated with other traits that might suggest that seed size is part of a broader "trait syndrome" reflecting either a "resource acquisitive" or "resource conservative" strategy. To accomplish this, at six of our 10 sites, we haphazardly selected 10 reproductively mature individuals of each focal species for trait measurements. All individuals had little to no sign of herbivory or other physical damage. We chose individuals that were representative of the population in terms of size and height. These individuals were different from those for which we estimated fecundity because we measured functional traits earlier in the season than fecundity. We measured plant height (i.e., the highest point of photosynthetically active leaf tissue; for species with basal rosettes, we measured the height of the tallest basal leaves) and collected one leaf from each individual to be scanned for analysis of specific leaf area (SLA). Leaves were wrapped in wet paper towel, placed in a plastic bag and transported to the laboratory inside a cooler. Collected leaves were scanned within 24 hr of collection, then dried at 70°C for 24–48 hr and weighed. Leaf area was calculated using ImageJ software (version 1.48). Leaf weight and area data were used to calculate SLA (cm^2/g). SLA is an important trait in plant growth and resource acquisition (Lambers & Poorter, 1992; Westoby, Falster, Moles, Vesk, & Wright, 2002). Additionally, we collected leaf tissue from five individuals of each focal species at each site. These leaves were air-dried and sent to the Colorado Plateau Analytical Laboratory for determination of $\delta^{13}C$ and %N and %C. $\delta^{13}C$ values provide an integrated measure of water use efficiency, the gain in carbon per unit of water loss (Dawson, Mambellli, Plamboeck, Templer, & Tu, 2002).

2.2 | Seed addition experiment

At each of our 10 sites, we initiated a fully factorial experiment where we manipulated the presence or absence of small mammal postdispersal seed predators and competition from the dominant bunchgrass, rough fescue. Sites were ≥1 ha, and the distance between sites ranged from several 100 m to over 50 km. At each site, we established twenty 1 m^2 plots, with corners marked with rebar and a unique numbered metal tag. If adult focal species occurred in experimental plots, we prevented their seed production by cutting off flowering stalks. Ten plots were spaced evenly (0.5 m between plots) inside 10 × 10 m (or in some cases 10 × 15 m) rodent exclosures (see Maron et al., 2012 for a detailed description of rodent exclosures). Ten plots were spread across randomly selected locations within each 1 ha site outside of rodent exclosures. Rodent exclosures had snap traps set inside to protect against entry by errant mice, which was rare.

In half of the 1 m^2 plots, we manipulated the competitive environment by killing and removing all rough fescue plants and their litter within each plot. Rough fescue is the dominant species in these grasslands; thus removing these plants and their litter clears space that is potentially available for seed germination and plant recruitment. We carefully sprayed only rough fescue plants (avoiding other species) in each plot with the herbicide Roundup® (Monsanto Corp., active ingredient: Glyphosate) and subsequently removed the litter a few weeks later (by cutting vegetation at ground level without disturbing the soil). In mid-August 2016, we added seed mixes to experimental plots. Seeds of all species except *A. ludoviciana* were collected from plants in the Blackfoot Valley. For *B. sagittata*, *Geum triflorum*, *Geranium viscosissimum*, and *L. sericeus*, we used mostly wild-collected seed but had to purchase some seed, which was mixed in with wild-collected seed, to obtain sufficient stocks for our experiment. *Artemisia ludoviciana* seeds were added in October because seeds of this species do not mature until then. Each plot received either no seeds or seeds of all 18 focal species at densities of 0.25, 0.5, 1.0, and 1.5 times each species' fecundity (i.e., the average fecundity of a single individual). Seed density and competition treatments were randomly assigned to plots. For *Erigeron pumilus*, we did not have enough seeds to add to the 1.5× plots. In total, we established 10 sites × 20 plots/site = 200 plots.

Starting in spring 2017, we censused all plots at all sites, carefully identifying and counting all seedlings. Our first census occurred during early April, when seedlings were first emerging. Recruitment continued for the next month or two (depending on species), with our final census performed in early to mid-June. To quantify whether our competition removal treatment was effective, at our final census, we also recorded the percent cover of live rough fescue and all graminoids in each plot. We also used a metric ruler to record litter depth at 12 randomly stratified locations across each plot.

2.3 | Analyses

In order to determine whether seed size covaried with the other functional traits we measured, we performed a principle components analysis (PCA) using the prcomp function in R (R Core Team, 2017). The analysis used the correlation matrix of the traits.

To determine how our competition removal treatment affected *F. campestris* cover and average litter depth, we used ANOVA with site and site × competition treatment as random effects, implemented using the lmer function in the lme4 package in R (Bates, Maechler, & Bolker, 2013). The random terms account for differences in *Festuca* cover among sites that could influence the competitive effect of *Festuca*. For analysing seedling recruitment data, our goal was to determine whether the effect of rodent seed predation and/or competition from *F. campestris* varied systematically among species based on either their seed size alone or their multivariate trait values. To do this, we first modelled the functional form of each species' recruitment function in each +/- rodent and +/- competition scenario using the general approach described by Poulsen, Osenberg, Clark, Levey, and Bolker (2007). Recruitment functions describe how seedling recruitment varies as a function of seed input. We created saturating Beverton–Holt models, implemented in the nlme package in R (Pinheiro, Bates, DebRoy, Hiesterkamp, &

Willigen, 2017), of the following general form to describe each species' recruitment function:

$$R = \frac{aS}{1+bS} \quad (1)$$

where R is the number of seedling recruits, S is the seed input, or number of seeds added to a plot, a is a density-independent parameter that describes the proportion of seeds recruiting in the absence of any density dependence, and b is a density-dependent parameter that is proportional to seed input and density-dependent survival.

None of the focal species showed any evidence of saturating recruitment with increasing seed input (see Figure S1 for examples of recruitment curves for a subset of focal species), so Equation (1) collapsed into the following simple linear model:

$$R = aS \quad (2)$$

As our experiment was a split-plot factorial design, we extended Equation (2) to incorporate multiple treatments and the nested structure of the design using the following equation for each species:

$$R_{ijkl} = 0 + a_{ij}S + r_k + w_{jk} + e_{ijkl} \quad (3)$$

The slope (a) of each recruitment function describes the proportion of seeds that recruit into seedlings estimated for each level of the competition (i) and rodent (j) treatments. Random effects parameters were included to account for variation among sites (r_k) and for the split-plot nature of the competition treatment and seed density plots nested within rodent plots (w_{jk}). e_{ijkl} describes the residual error. Since there was no or very low recruitment from the seed bank for each species, we set the intercepts to zero. When we allow the models to estimate intercepts, they were very small (although sometimes intercepts were slightly negative which lacks biological realism), never significantly different than zero, and did not substantially change the estimated slopes. We also considered generalized linear mixed models with a Poisson distribution. However, the linear models fit well (residuals were evenly spread around the mean) and produced quantitatively very similar estimates as the Poisson models. Therefore, we proceeded with the linear models because the slopes conveniently estimate the proportion of seeds that recruit as seedlings (see Equations 2 and 3). Thus, the only fixed effects' coefficients estimated by the model were the four slopes (a_{ij}) for the relationship between seed input (S) for a given species and number of recruits of that species (R) for the four rodent and competition treatment combinations. *Clematis hirsutissima* did not germinate in any plot at any site, so this species was excluded from these analyses. Models were implemented using the lmer function in the lme4 package in R (Bates et al., 2013). We calculated R^2m values and R^2c for each model, which describe the variance explained by the models' fixed effects and fixed plus random effects, respectively (Nakagawa & Schielzeth, 2013), using the r.squaredGLMM function in the MuMIn package in R (Barton, 2013).

For examining the effects of postdispersal seed predation by mice, we calculated the maximum recruitment in each plot for each species (regardless of census) and performed analyses on these values. As postdispersal seed predation influences the number of seeds available to recruit, our interest was to explore how seed predation affected maximum recruitment. However, for calculating the effects of rough fescue competition on recruitment, we used data from the final census since competition could influence both sites available for recruitment and also subsequent survival of seedlings that recruit. For calculating combined effect of rodent seed predation and competition, we used data from the final census in June because this is the most conservative estimate of combined effects, but the results from earlier censuses were qualitatively similar.

To calculate the effect sizes of seed predation and competition, we subtracted the slope (a) of that species' recruitment function when mouse seed predation or competition was present (i.e., not manipulated) from the slope of each species' recruitment function when they were experimentally protected from rodents (but in the presence of rough fescue) and competition from *F. campestris* (in the presence of rodents). The combined effect of seed predation and competition was calculated from the recruitment slope when both interactions were absent minus the control treatment where both interactions were present. These calculations assume that differences in recruitment in and out of rodent exclosures are due to seed consumption, although we acknowledge the possibility that some seeds could be removed by rodents and subsequently cached. The difference in slope describes the effect size of each biotic interaction on proportional seedling recruitment across the range of seed densities added for each species. To evaluate how the effect size of rodent seed predation, competition, and the combined effect differed among species with different seed weights (or trait values), we regressed each effect size over the mean seed weight of each species and the plant trait principal component score (Plant trait PC). Seed size (mg) was $\log_{10}$ transformed to improve normality. In these analyses, species was the unit of replication (n = 17 species). To determine how differences in fecundity across species (as represented by differences in the number of seeds of each species added to plots in the 1.0 seed density treatment) influenced the average number of seedlings that established in plots, and how this differed between control plots and plots where competition from *F. campestris* and seed predation by rodents was eliminated, we used ANCOVA (in Systat ver. 10.0). In this model, fecundity ($\log_{10}$ transformed) was the covariate, experimental treatment was a fixed factor and mean seedlings established per plot ($\log_{10}$ transformed) was the response variable.

3 | RESULTS

3.1 | Seed size, fecundity, and functional traits

Our 18 target species varied by over three orders of magnitude in their seed size (Table 1). Across all species, there was a significant seed size–fecundity trade-off, with smaller seeded species producing more seeds than larger seeded species (R^2 = 0.58, $F_{1,16}$ = 21.97, slope = −0.68 ± 0.15 *SE*, p < 0.0001; Figure 1). The first axis of the

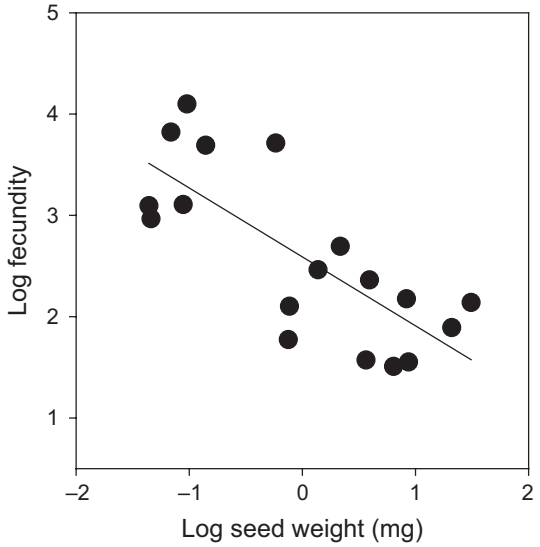

FIGURE 1 Trade-off among species between seed weight and fecundity. Each circle represents mean seed size and fecundity for a unique species

PCA explained almost 53.7% of the variation among species in functional traits whereas the second PC axis explained an additional 14.8% of the trait variation (Figure 2). Traits related to resource use (increasing plant height, lower C/N ratio, and less negative $\delta^{13}C$ [an integrative measure suggesting less water use efficiency compared to more negative values]) were associated with the first PCA axis with larger seeded species tending to be taller, with lower leaf C/N ratio and lower water use efficiency compared to smaller seeded species (Figure 2). SLA and to a lesser extent, leaf % N contributed to the second PC axis (Figure 2).

3.2 | Experimental results—comparisons of recruitment slopes across all seed densities

Experimental removal of *F. campestris* and its litter significantly reduced graminoid cover, from 69.5% ± 2.6% *SE* in controls to 12.3% ± 2.6% *SE* in removal plots ($F_{1,18}$ = 212.3, p < 0.0001, Figure S2). Similarly, litter depth was reduced from 38.3 ± 4.9 mm *SE* in controls to 17.4 ± 4.9 mm *SE* in removal plots ($F_{1,9}$ = 14.5, p < 0.004).

Since recruitment curves of species were all linear (Figure S1), we were able to assess how the competition and rodent exclusion treatment influenced the slopes of each species' recruitment function. These recruitment functions were described reasonably well by our linear mixed model (Equation 3 for the 17 species, with R^2m ranging from 0.12 to 0.69 (M = 0.28) for June survey data and from 0.15 to 0.71 (M = 0.34) using the maximum number of recruits (Tables S2 and S3). Differences in the estimated slopes of each species' recruitment curve quantifies the extent to which competition from *F. campestris* or rodent seed predation reduced the proportion of seeds that successfully recruited into plots.

Across all species, the suppressive effect of seed predation on proportional recruitment decreased with increasing seed size, meaning that larger seeded species where more negatively affected by seed predation than smaller seeded species (Figure 3a; $F_{1,15}$ = 8.9, R^2 = 0.37, slope = −0.059 ± 0.020 *SE*, p = 0.009). These effects also varied (marginally) significantly based on the PC1 scores of plant traits (Figure 3d; $F_{1,15}$ = 3.1, R^2 = 0.17, slope = −0.012 ± 0.007 *SE*, p = 0.098). In contrast, the suppressive impacts of *F. campestris* competition on proportional recruitment did not vary significantly among species based on seed weight (Figure 3b; $F_{1,15}$ = 1.1, R^2 = 0.07, slope = 0.012 ± 0.011 *SE*, p = 0.31), but it varied

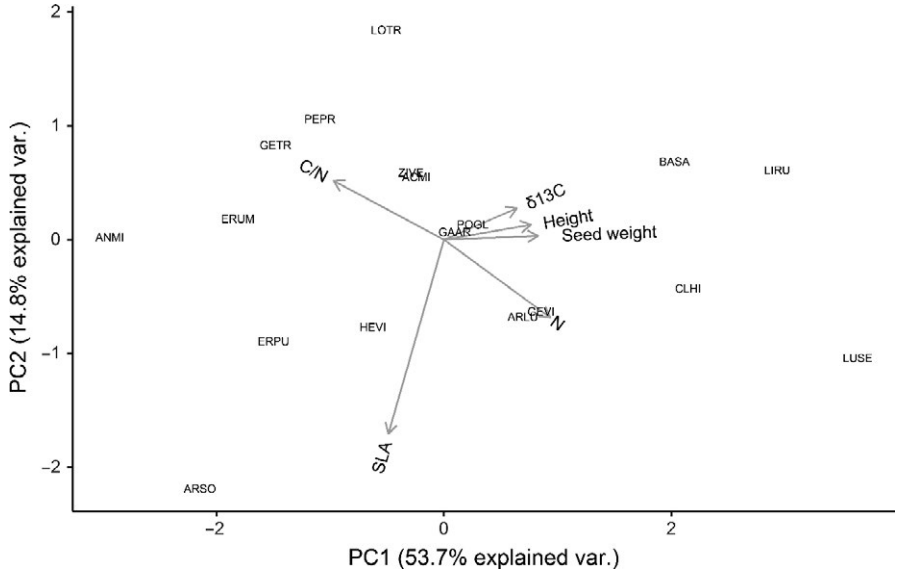

FIGURE 2 Principle components analysis of the functional traits: seed size (weight), plant height, leaf nitrogen, C/N, SMA, and $\delta^{13}C$ (as a measure of water use efficiency) for each of our 18 target species. The key to species abbreviations is shown in Table 1. The length of each arrow relates to the strength of each particular trait and the direction of the arrow indicates the relationship of the trait values relative to either the first or second PC axis

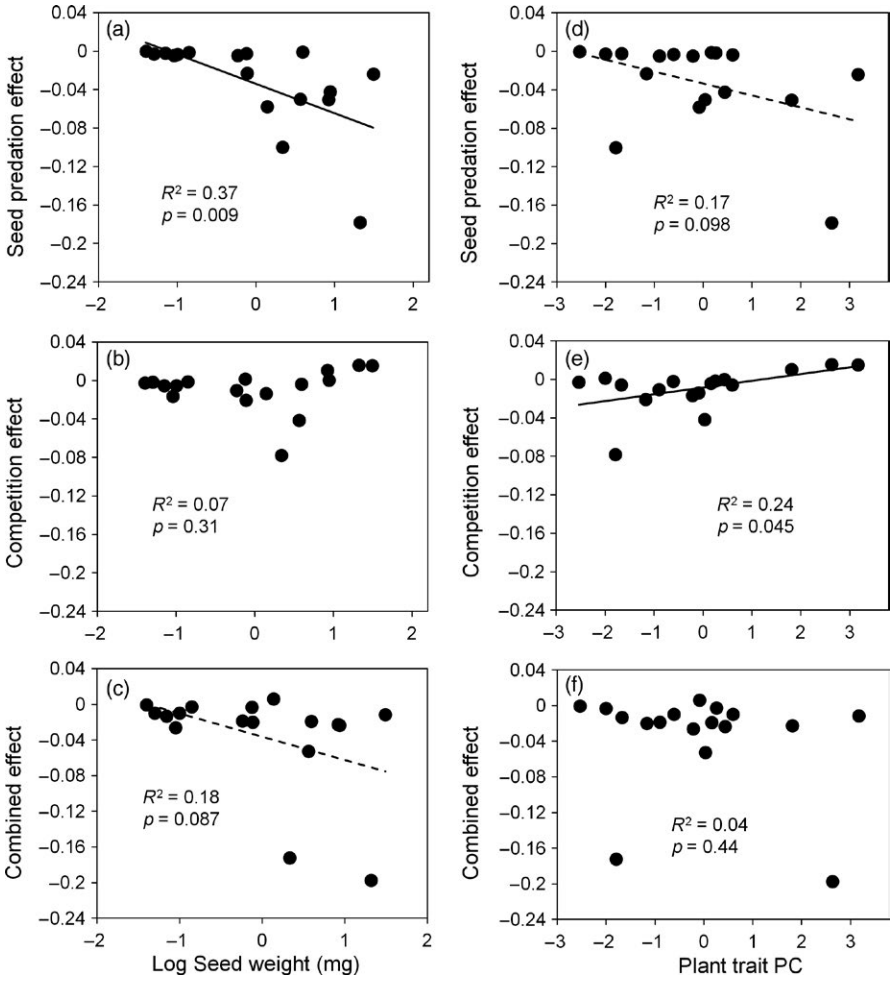

FIGURE 3 Relationships between $\log_{10}$ transformed seed size (mg) of each focal species and (a) the effect size of seed predation, (b) the effect size for competition, and (c) the combined effect size of both seed predation and competition. (d–f) Same effect sizes as in corresponding panels on left, but these are plotted against each species' trait principal component score (axis 1; see Figure 2). Effect sizes were calculated as the difference between recruitment slopes in the control plots (seed predators and competition present) and exclusion plots (seed predators, competition, or both excluded). Slopes represent the proportion of seeds added that recruited as seedlings calculated for each treatment. Each point represents a unique species

significantly with plant trait PC axis 1 scores (Figure 3e; $F_{1,15}$ = 4.8, R^2 = 0.24, slope = 0.007 ± 0.003 *SE*, p = 0.045). Species that were larger seeded and had more resource acquisitive traits experienced lower proportional suppression of recruitment by *F. campestris* than did species with more resource-conservative traits. Due to the fact that seed predation had greater proportional suppressive impacts on recruitment than did *F. campestris* competition, the combined effects of seed predation, and competition on the proportion of seeds that recruited tended to negatively influence large-seeded species more than small-seeded species (Figure 3c; $F_{1,15}$ = 3.3, R^2 = 0.18, slope = −0.051 ± 0.028 *SE*, p = 0.087) and was not related to the plant trait PC (Figure 3f; $F_{1,15}$ = 0.6, R^2 = 0.04, slope = −0.007 ± 0.009 *SE*, p = 0.44).

Among target species, average recruitment into plots was strongly related to their fecundity. That is, in plots where seeds were added at a density that reflected inherent fecundity differences between large- and small-seeded species, higher fecundity species experienced greater seedling establishment on average (Figure 4; ANCOVA, $F_{1,31}$ = 51.3, slope = 0.64 ± 0.08 *SE*, p < 0.0001). The intercept of this relationship was lower in plots with competition and seed predation (change in intercept = −0.32 ± 0.14 *SE*) compared to plots without these interactions (Figure 4; ANCOVA, $F_{1,31}$ = 4.9, p = 0.03).

4 | DISCUSSION

Trade-offs are a central tenet of coexistence theory (Chesson, 2000; HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Siepielski & McPeek, 2010). Yet despite the importance of seed size trade-offs to coexistence in the theoretical literature (Muller-Landau, 2010; Rees et al., 2001; Shmida & Ellner, 1984; Tilman & Pacala, 1993), empirical tests are surprisingly rare and little attention has been paid to the potential role that generalist seed predators may play in these trade-offs (Larios et al., 2017). Moreover, most empirical tests of the implications of trade-offs between seed size and number for coexistence have been performed in annual systems where controls on recruitment are likely different than in perennial grasslands (Leishman, 2001; Rees, 1995; Turnbull et al., 2005, 1999). Working in perennial-dominated grasslands, we conducted a seed addition experiment using 18 co-occurring species that vary in seed size to examine the effects of seed predation and competition from the community dominant on plant recruitment. This experimental approach differs from most prior studies that have used variation in traits exhibited within existing communities to infer coexistence mechanisms (Siepielski & McPeek, 2010). We found strong seed size–fecundity trade-offs, as expected. However, seed size was correlated with resource-acquisitive traits indicative of a trait syndrome which was a

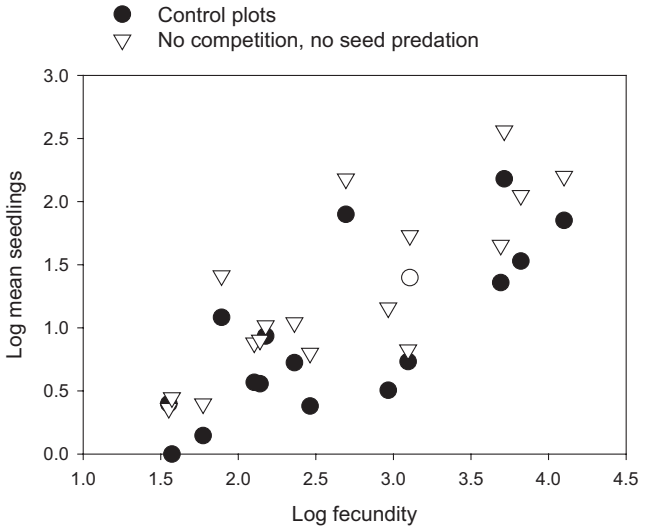

FIGURE 4 Positive relationship between log fecundity and log mean seedling recruitment in plots with all interactions present (filled circles) and seed predation and competition absent (open triangles). Each point is a unique species. $R^2 = 0.59$, $p < 0.001$ for all interactions, $R^2 = 0.21$, $R^2 = 0.66$, $p < 0.001$ for no interactions

better predictor of competitive responsiveness than seed size alone. Our experiments revealed that smaller seeded species (with less resource-acquisitive functional traits) were more negatively affected by competition than were larger seeded species (Figure 3e), whereas larger seeded species (with more resource acquisitive functional traits) were proportionately more strongly affected by postdispersal seed predation (Figure 3a). Overall, these findings suggest important roles of competitive responsiveness (i.e., sensitivity to competition) and seed predation as fitness equalizing mechanisms that can influence plant coexistence.

The greater proportional suppression of recruitment of large than smaller seeded species by a generalist seed predator (i.e., deer mice) is similar to what has been shown in other studies in temperate systems (Brown & Heske, 1990; Connolly, Pearson, & Mack, 2014; Hoffmann, Redente, & McEwen, 1995; Howe & Brown, 2000; Hulme, 1998; Reader, 1993), and from previous work, we performed in the same system (Maron et al., 2012). Moreover, in long-term and large-scale experiments, this biased seed predation has been shown to shift plant community composition in favour of small-seeded species compared to plots where rodents have been long excluded (Allington, Koons, Morgan Ernest, Schutzenhofer, & Valone, 2013; Brown & Heske, 1990; Brown, Davidson, Munger, & Inouye, 1986). Despite these and other results, generalist seed predators are not currently thought to be important in influencing coexistence (Larios et al., 2017). Instead, *specialist* enemies have figured more prominently in coexistence theory (Connell, 1978; Janzen, 1970; Sedio & Ostling, 2013). Similarly, seed predation has also been mostly ignored in trait-based, community assembly research (Larios et al., 2017). In our system, the reduced level of postdispersal predation on small-seeded species by mice appears to be an important equalizing mechanism (sensu Chesson, 2000) that acts to offset advantages of large-seeded species.

Recently, Muller-Landau (2010) proposed a new theory to explain the maintenance of seed size variation. In her model, if large-seeded species are more stress tolerant than small-seeded species, any variation in the degree of environmental stress across the landscape enables recruitment and persistence of both stress tolerant (but low fecundity) larger seeded species with less stress tolerant (but higher fecundity) smaller seeded species. Although "stress" in Muller-Landau's (2010) model is considered to come from abiotic sources, one biotic source of stress could be competition from community dominants. Muller-Landau (2010) proposed that a potential advantage that large-seeded species may possess is the ability to recruit into more stressful sites than those of smaller seeded species. We extended this idea, examining whether there were differences among target forb species in their responses to competition from the dominant species in our system, rough fescue. By testing 18 target species, our goal was to determine whether seed size and associated functional traits likely influence competitive tolerance of all fob species that occur in this system to *F. capestris*. We found that variation in competitive response among species (in terms of how this proportionally influenced recruitment) was correlated not with seed size per se, but with combined correlated trait values as measured by a PC axis 1 score. Species possessing trait values suggestive of a more resource acquisitive strategy (i.e., lower leaf C/N ratios, larger seed size, and lower water use efficiency) were less negatively affected by competition (in terms of how this affected their recruitment) compared to species with traits that are more associated with a resource-conservative strategy. It makes sense that seed size alone influences vulnerability to seed predators since seed size reflects the amount of resource that is available to a seed predator. In contrast, competitive response appears to be controlled by a suite of traits that enable species to garner resources under competitive circumstances, as opposed to seed size alone. In other words, seed size is part of a syndrome of functional traits that reflect the ability of plants to garner resources not just early on but also later in life. This finding that seed size may be linked to a broader resource-acquisition trait syndrome suggests that seed-size trade-offs may extend beyond their effects on recruitment into later life-history stages. These differences in traits among our target species reflect potential niche differences. Whether reduced sensitivity to dominant competitors possessed by species with reduced fecundity can counterbalance the fitness advantages of small-seeded high-fecundity species possess remains unclear and can only be assessed with longer term demographic assessments of target species.

Although the local filters of competition and seed predation differentially affected the proportion of seeds that recruited across our target species, in absolute terms, average levels of recruitment among our target species was strongly correlated with plant fecundity (Figure 4). Neither competition with *F. campestris* nor seed predation by deer mice reversed the recruitment advantage that high-fecundity species experienced (Figure 4). These powerful differences among species in recruitment, tied directly to fecundity,

suggest that fitness differences can be quite strong in our system. It is worth noting, however, that the conditions for germination were uncharacteristically favourable during the time when our experiment took place. Based on a weather station in the Blackfoot Valley (Ovando, MT), in 2017 spring precipitation (April–June) was 41% greater than the 30-year average for this period. The estimates of germination percentage for 8 of our focal species (those that were shared across experiments) were, on average, three times higher than previous germination estimates for these species based on seed addition experiments in this same system (Maron et al., 2012; J. L. Maron & D. E. Pearson, unpubl. data). Moreover, in 2017, rainfall occurred regularly enough throughout the period when seeds were germinating that we never saw large bouts of mortality due to hot and dry periods that commonly kill seedlings in this system. These observations suggest that variation among years in conditions that promote seedling recruitment and establishment may favour highly fecund species in "good years" whereas in more typical years, the availability of safe sites might be more limiting to small-seeded species. If true, this variability could lead to coexistence through a temporal storage effect (sensu Warner & Chesson, 1985).

The above interpretation is bolstered by the fact that smaller seeded species are not numerically dominant over larger seeded species in natural populations across our sites (J. L. Maron, K. L. Hajek, & D. E. Pearson, unpubl. data). This suggests that there are other stabilizing mechanisms that prevent the dominance of highly fecund small-seeded species. We speculate that, in more typical recruitment years, not only are overall levels of recruitment lower but also these species may experience greater density-dependent mortality following recruitment. In other systems, larger seeded species better tolerate negative density dependence than do small-seeded species (Lebrija-Trejos, Reich, Hernández, & Wright, 2016). One surprising result of our study was that the recruitment curves of all of our focal species, regardless of seed size, were linear (Tables S2 and S3, Figure S1). In other words, even at high seed inputs, we did not find evidence for saturation of microsites or density-dependent seedling mortality (J. L. Maron, K. L. Hajek, & D. E. Pearson, unpubl. data). One explanation for this may be that we did not add seeds to plots at high enough densities to saturate microsites. However, we added seeds of each target species to plots inside rodent exclosures at three times the fecundity of each species (up to 37,000 seeds of the most fecund species per m^2). Although not reported here, even in these plots we did not see evidence for saturating recruitment curves. Thus, we think that unusually favourable environmental conditions increased the overall suitability of sites for recruitment and subsequent seedling survival.

Explaining the dramatic variation in propagule size vs. number that occurs in natural plant communities in the context of trade-offs and coexistence theory has presented a long-standing challenge. We evaluated two relatively novel coexistence mechanisms within a perennial plant community and asked how the strength of these mechanisms differed across species that produce contrasting propagule size and numbers. Rather than taking a traditional approach and evaluating how well focal species competed against each other, we instead examined how competitive tolerance (i.e., sensitivity) to the community dominant varied among species based on their seed size and associated functional traits. We also explored the role of postdispersal seed predation by rodents in influencing variation in recruitment among species. Our results suggest that reduced sensitivity to competition from the local community dominant expressed by species with greater resource acquisitive traits (that tended to be the larger-seeded species) may be offset by an increased susceptibility to seed predation of larger seed species relative to smaller seeded species in this system. We also found evidence that seed size may represent a syndrome of traits that link lower fecundity species to greater competitive tolerance. This may be an unrecognized component that is necessary to fully understand seed-size fecundity trade-offs. As our results represent a single year of data obtained during a particularly good recruitment year, we suspect that temporal variation may also greatly influence these interactions. Nonetheless, our findings suggest that these biotic factors may influence coexistence processes within this perennial plant community.

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AUTHORS' CONTRIBUTIONS

J.L.M. and D.E.P. conceived the ideas and designed the methodology; J.L.M., D.E.P., and K.L.H. collected the data; J.L.M., K.L.H., and P.G.H. analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data used in this study are archived at the Dryad Digital Repository: https://doi.org/10.5061/dryad.p2h11s7 (Maron, Hajek, Hahn, & Pearson, 2018).

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