

Trade-offs between seed size and biotic interactions contribute to coexistence of co-occurring species that vary in fecundity

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Abstract

1. Despite theoretical advances, the ecological factors and functional traits that enable species varying in seed size and fecundity to coexist remain unclear. Given inherent fecundity advantages, why don't small-seeded species dominate communities?
2. In perennial grasslands, we evaluated whether small-seeded species are less tolerant of competition from the community dominant bunchgrass than large-seeded species, but also less vulnerable to seed predation by mice. We also explored whether trade-offs involving competitive tolerance include two other functional traits, height and leaf mass per area (LMA). We added seeds of 17 forb species to plots where bunchgrass competition and rodent seed predation were manipulated across sites varying in bunchgrass productivity and thus competitive intensity. Seeds were added at densities mimicking interspecific variation in fecundity among target species.
3. Standardizing for differences in fecundity (i.e. seed input, which enabled us to evaluate inherent interspecific differences in susceptibility to biotic interactions), bunchgrass competition more greatly reduced recruitment and establishment of small- versus large-seeded species, whereas rodent seed predation more greatly reduced the recruitment of large- versus small-seeded species. Plant height and LMA were unrelated to the competition effect size.
4. Small-seeded species abundance decreased across sites increasing in bunchgrass productivity, whereas this was not the case for large-seeded species. For adult plants but not seedlings, community-weighted functional trait means (CWM) for seed size, height and LMA increased in plots with versus without bunchgrass competition and the CWM for seed size and height also increased at sites with greater bunchgrass productivity (for adults only). In contrast, rodent seed predation had no significant effects on CWM seed size.
5. At the end of the experiment, adult abundance positively correlated with plant fecundity in plots lacking bunchgrass, indicating the inherent advantages accrued to high fecundity small-seeded species. However, with bunchgrass competition, abundances were equalized across species due to reduced competitive tolerance of high fecundity small-seeded species.

6. *Synthesis.* Our results suggest that coexistence among subordinate forb species varying in seed size and fecundity is in-part due to a trade-off involving competitive tolerance and fecundity, mediated by seed size and associated functional traits.

KEYWORDS

coexistence, community assembly, competition, functional traits, grassland forbs, post-dispersal seed predation, seed size, trade-offs

1 | INTRODUCTION

Understanding the mechanisms enabling co-occurring species to coexist has been of great interest to ecologists for decades (Chesson, 2000; Gause, 1932; Lotka, 1925; Tilman & Pacala, 1993). One class of important coexistence mechanisms involves life-history trade-offs (Kneitel & Chase, 2004). Species possess traits that enable them to perform well under one set of ecological circumstances but these same traits inhibit their performance under other ecological conditions. A classic example of a poorly resolved coexistence problem involving life-history trade-offs concerns how species that differ in fecundity, which trades off with propagule size, coexist (Rees, Condit, Crawley, Pacala, & Tilman, 2001). Highly fecund small-seeded plant species should have great advantages over less fecund larger-seeded species, because all things being equal, more seeds should generate more offspring in the next generation. Yet, the smallest-seeded species do not dominate in most communities. Furthermore, although some theory predicts an optimal seed size/fecundity value for any given locale (Levin & Muller-Landau, 2000), fecundity and seed size vary by many orders of magnitude among co-occurring species (Aarssen & Jordan, 2001; Harper, Lovell, & Moore, 1970; Jakobsson & Eriksson, 2000; Westoby, Jurado, & Leishmann, 1992). Thus, what mechanisms maintain seed size diversity, and hence species diversity, within plant communities (Muller-Landau, 2010; Rees et al., 2001)?

Recent theory posits that seed size diversity and coexistence are maintained through a fecundity-stress tolerance trade-off (Muller-Landau, 2010). If sites vary in stress across the landscape, large-seeded species are hypothesized to be able to recruit more abundantly in stressful sites than smaller-seeded species owing to their greater stress tolerance. However in less stressful sites, small-seeded species are hypothesized to recruit more abundantly than larger-seeded species by dint of their higher fecundity. Spatial and/or temporal variation in the stressfulness of sites, together with a fecundity-seed size-stress tolerance trade-off, enables species differing in fecundity and seed size to coexist (Muller-Landau, 2010). While these predictions are intriguing, to our knowledge this theory has not been fully tested.

Furthermore, one factor that is not explicitly considered in Muller-Landau's theory (2010), as well as older competition-colonization theory (Shmida & Ellner, 1984; Tilman, 1994; Tilman & Pacala, 1993), is the role of other functional traits. Theory has mainly examined the effects of trade-offs involving seed size or fecundity

per se (Chesson, 2000; Jakobsson & Eriksson, 2000; Lönnberg & Eriksson, 2013), ignoring other functional traits that may also influence demographic performance across spatially variable conditions (Adler et al., 2014; Kraft, Godoy, & Levine, 2015; Laughlin, 2014; Pérez-Ramos, Matías, Gómez-Aparicio, & Godoy, 2017). While seed size can influence a plant's germination cues (Pearson, Burslem, Mullins, & Dalling, 2002) and its subsequent ability to contend with local hazards (Leishman & Westoby, 1994; Leishman, Wright, Moles, & Westoby, 2000; Moles & Westoby, 2004), other functional traits may influence performance at later life stages. Specifically, traits such as plant height and leaf mass per area (LMA) may be involved in trade-offs because they influence an individual's ability to acquire resources versus its ability to tolerate abiotic conditions or competition (Díaz et al., 2016; Grime, 1977; Kunstler et al., 2016; Seifan, Seifan, Schiffers, Jeltsch, & Tielbörger, 2013; Westoby, Falster, Moles, Vesk, & Wright, 2002). Historically, at the global scale, the major functional traits of seed size, height and specific leaf area (and thus LMA) were thought to be mostly orthogonal to each other (Westoby, 1998), and thus operate somewhat independently. These different traits may influence plant performance at different points in a plant's life history, with these effects potentially shifting depending on the abiotic and/or biotic environment.

If trait-performance trade-offs for individual species are strong, then they should be manifest at the community level. In other words, community-weighted means for traits that confer individual performance advantages under particular abiotic or biotic conditions should also change accordingly. Researchers have often examined shifts in community-weighted trait values across environmental gradients to infer the adaptive value of traits given particular abiotic or biotic conditions (Cornwell & Ackerly, 2009; HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Laughlin & Messier, 2015; Shipley, Vile, & Garnier, 2006). Yet, less commonly have researchers experimentally tested how particular biotic interactions drive community-weighted trait averages across abiotic gradients to influence coexistence (Adler, Fajardo, Kleinhesselink, & Kraft, 2013; HilleRisLambers et al., 2012; Siepielski & McPeck, 2010).

We hypothesize that competitive tolerance might trade-off with seed size and other functional traits and thus act analogously to stress tolerance in Muller-Landau's model. In perennial grasslands, the cover of dominant bunchgrasses can vary spatially, influencing the amount of relatively bare interstitial space among adult bunchgrasses, and hence levels of competitive intensity imposed on subordinate species that recruit in those interstitial spaces. We previously

reported initial results from a seed addition experiment in grasslands in western Montana where we found that the recruitment of species possessing functional traits including large-seededness, taller height, lower C/N ratio and lower water use efficiency were less negatively affected by bunchgrass competition than smaller-seeded species that were less tall, had higher C/N ratios and higher water use efficiency (Maron, Hajek, Hahn, & Pearson, 2018). However, within the context of the same experiment, we also demonstrated that post-dispersal seed predation by mice had greater suppressive effects on the recruitment of larger-seeded species compared to smaller seeded ones, thereby working in the opposite direction of bunchgrass competition (Maron et al., 2018; Maron, Hajek, Hahn, & Pearson, 2019). In temperate grasslands, old fields and other habitats, a growing body of work indicates that rodents focus on larger-seeded species, disproportionately suppressing their recruitment compared to smaller-seeded species (Dylewski, Ortega, Bogdziewicz, & Pearson, 2020; Brown & Heske, 1990; Larios, Pearson, & Maron, 2017; Maron, Pearson, Potter, & Ortega, 2012; Reader, 1993). These effects have not been considered in research examining the factors influencing the maintenance of seed size diversity within communities (Larios et al., 2017).

Here, we build on this previous work (Maron et al., 2018, 2019) by following the fate of species and communities that assembled within our experimental plots beyond recruitment. We examine patterns of cumulative recruitment (i.e. recruitment of species over years 1 and 2 of our experiment [year 1 results were previously reported; Maron et al., 2018]), as well as adult plant establishment 3 years after seed addition. Specifically, we address the following questions not considered previously (Maron et al., 2018, 2019). First, does competitive tolerance vary predictably based on seed size, height or LMA, and does seed size alone predict vulnerability to seed predation? Although multiple functional traits might affect seedling and adult plant performance and thus competitive tolerance, seed size alone should influence vulnerability to seed predation. Second, are species-level trade-offs between seed size (or height or LMA) and competitive tolerance manifest at the community level by shifting community-weighted mean (hereafter CWM) trait values in plots with or without bunchgrass competition? Similarly, does greater vulnerability of large-seeded species to seed predation shift CWM seed size higher in versus outside of rodent exclosures? CWMs for functional traits can suggest strategies that successfully influence recruitment, establishment and coexistence under different abiotic and biotic conditions (Violle et al., 2007). Third, how does natural spatial variation in bunchgrass abundance influence the abundance of species based on their seed size, height or LMA? At sites where bunchgrass cover is greater, there is less interstitial space and the strength of competition with bunchgrass is likely higher than at sites with less bunchgrass productivity. We hypothesize that this gradient in bunchgrass productivity should shift the relative advantages of being small- versus larger-seeded across space, with smaller-seeded species being more disadvantaged at high compared to low productivity sites. In contrast, larger-seeded species should be less disadvantaged at high productivity sites. Fourth, are spatial differences in the performance

of individual species across a productivity gradient manifest at the community level by shifting CWMs for traits? Finally, one important initial result of our prior work was that regardless of whether we manipulated interactions or not, species with higher annual fecundity (and hence that had more seeds initially added to plots) experienced greater recruitment than species with lower annual fecundity (Maron et al., 2018, 2019). Thus, does bunchgrass competition or seed predation equalize or exaggerate initial differences in relative abundances of target species that are related to fecundity?

2 | MATERIALS AND METHODS

2.1 | Sites

Our experiment was conducted in the Blackfoot Valley in western Montana (47°01'N, 113°07'W). The valley supports semi-arid perennial grasslands that are dominated by the native bunchgrass, rough fescue (*Festuca campestris*). Rough fescue monopolizes space and constrains recruitment of forb species that germinate in the interstitial spaces between these grasses (Maron et al., 2012, 2018), as has been found for other dominant grasses in perennial grasslands (Aguilera & Lauenroth, 1995; Pert, 1989). While forbs are collectively subordinate in terms of cover/biomass, they make up the majority plant diversity.

We performed our experiment at 10 sites spread across a >450 km² area. In 2018, plots at one of these sites were destroyed, so here we report results from nine sites. Sites were arrayed across a steep gradient of rough fescue productivity (as quantified by its above-ground biomass and litter; Maron et al., 2019). Most study sites were a minimum of 0.75 ha in size, although one site was 0.15 ha. The distance between sites ranged from 200 m to over 50 km.

2.2 | Target species and seed addition experiment

We selected 18 species of common perennial forbs that varied in seed size and had a strong fecundity-seed size trade-off (Maron et al., 2018). One of these species (*Clematis hirsutissima*) never germinated in any plot, leaving 17 focal species that we could evaluate. Focal species varied by almost three orders of magnitude in seed weight and over two orders of magnitude in annual fecundity (Table 1). In addition, we previously measured plant height and LMA (see Maron et al., 2018 for how plants were sampled for trait measurements) on naturally occurring focal plants in the field. We chose to focus on plant height and LMA in addition to seed size because these traits represent different axes of Westoby et al.'s (2002) trait dimensions that we thought could be important in affecting competitive tolerance to bunchgrass. For example, seed size can influence a plant's ability to deal with litter or shade early in its life history (Leishman & Westoby, 1994; Leishman et al., 2000; Moles & Westoby, 2004). Height can affect a plant's ability to compete for light, and LMA is correlated with photosynthetic capacity and the ability to

TABLE 1 Focal species (from smallest seeded to largest seeded), their mean annual fecundity, mean seed weight, leaf mass per area (LMA) and height

Species	Mean fecundity	Mean seed weight (mg)	Mean LMA	Mean height (cm)
<i>Antennaria microphylla</i>	1,244	0.044	0.010	34.5
<i>Penstemon procerus</i>	926	0.046	0.008	15.1
<i>Erigeron pumilus</i>	6,629	0.069	0.009	30.6
<i>Achillea millefolium</i>	1,277	0.088	0.004	25.6
<i>Potentilla glandulosa</i>	12,587	0.096	0.010	31.7
<i>Artemisia ludoviciana</i>	4,918	0.14	0.006	14.9
<i>Heterotheca villosa</i>	5,177	0.58	0.007	25.0
<i>Arnica sororia</i>	59	0.75	0.007	34.2
<i>Geum triflorum</i>	127	0.77	0.007	29.4
<i>Zigadenus venenosus</i>	290	1.37	0.007	35.0
<i>Eriogonum umbellatum</i>	494	2.16	0.007	13.2
<i>Lomatium triternatum</i>	37	3.65	0.009	37.6
<i>Gaillardia aristata</i>	230	3.92	0.011	28.1
<i>Balsamorhiza sagittata</i>	150	8.33	0.008	40.2
<i>Geranium viscosissimum</i>	36	8.68	0.008	33.1
<i>Lupinus sericeus</i>	78	20.92	0.007	44.3
<i>Lithospermum ruderales</i>	138	31.08	0.008	23.4

acquire resources (Westoby et al., 2002). As is often the case at larger spatial scales (Westoby, 1998), none of these traits were strongly correlated with each other for our 17 species (log10 seed size ~ height: $r = 0.35$, $p = 0.16$; seed size ~ LMA: $r = 0.19$, $p = 0.46$; height ~ LMA: $r = 0.23$, $p = 0.37$).

At each site, in summer 2016, we established four 1 m² experimental plots. Two plots were randomly located inside of a 10 m × 10 m (or in two cases 10 m × 15 m) rodent enclosure (0.5 m between plots) and two plots that were spread across randomly selected locations outside of rodent enclosures. One of two plots inside and one of two plots outside each rodent enclosure were randomly chosen to receive a bunchgrass reduction treatment. The other plots served as unmanipulated controls. To implement the bunchgrass reduction treatment, in early July 2016, we carefully applied the herbicide Roundup® (Monsanto Corp., active ingredient: Glyphosate) only on rough fescue plants (avoiding or protecting other species) in each plot and subsequently removed the dead plant material a few weeks later (by cutting vegetation at ground level without disturbing the soil).

To assess the effectiveness of our bunchgrass reduction treatment, within each quadrat we visually assessed the percent cover of graminoids and we measured litter depth with a meter stick at 12 randomly stratified locations across each quadrat. If experimental seed addition plots contained any resident adult focal species, we made sure to remove all flowers from these individuals to ensure that recruitment would reflect the influence of experimental seed addition as opposed to in situ production of seeds.

Rodent enclosures were made of welded wire fencing dug 50 cm into the ground, extending 80–100 cm above-ground and topped with sheet metal to prevent mice from climbing over them (see Maron et al., 2012 for details). They effectively excluded deer mice *Peromyscus maniculatus*, the primary seed consumer in the Blackfoot

Valley, along with montane voles *Microtus montanus* and Columbian ground squirrels *Spermophilus columbianus*. *Microtus montanus* occurs at very low densities (Maron, Pearson, & Fletcher, 2010) and *S. columbianus* is mostly herbivorous. Seed predation by birds is minimal and ants in the grassland where we worked are primarily carnivorous (J.L. Maron & D.E. Pearson, unpubl. data).

We collected seeds of focal species for our seed addition experiment in summer 2016. For five species (*Artemisia ludoviciana*, *Balsamorhiza sagittata*, *Gaillardia aristata*, *Lithospermum ruderales* and *Lupinus sericeus*), we used mostly wild collected seed but we had to purchase some additional seed to obtain sufficient stocks for our experiment, which we mixed in with wild collected seed. Collected seeds were brought back to the lab, cleaned and then counted or weighed into groups that represented the average estimated fecundity of each species (see Maron et al., 2018, 2019 for details of how fecundity was estimated for each focal species). Briefly, for species that produced multiple flowering stalks that were connected via ramets underground (i.e. species with clonal growth: *Achillea millefolium*, *Antennaria microphylla*, *Erigeron pumilus*, *Eriogonum umbellatum* and *Heterotheca villosa*), we estimated fecundity as the average number of flowering stalks that species produced per patch of flowering stalks and then multiplied this value by the average number of seeds per stalk. For non-clonal species, we simply estimated the average number of seeds produced by individuals of average size. In two separate years, fecundity was negatively correlated with seed size (Maron et al., 2018; J.L. Maron & D.E. Pearson, unpubl. data). Seed mass alone explains the majority of interspecific variation in annual fecundity based on an analysis of log fecundity as a function of log10 seed mass (partial $R^2 = 0.539$) height (partial $R^2 = 0.001$) and LMA (partial $R^2 = 0.005$).

We added seeds of all focal species to the same experimental 1 m² plots at densities equal to the estimated fecundity value for

each species. Thus, seed density varied by species to reflect their differences in fecundity, but every plot received the same total number of seeds (summed across all species). We recognize that this approach does not weigh fecundity by the natural abundance of each species. Rather than normalizing fecundity based on field estimates of abundance, which may or may not be at equilibrium, we instead opted to control for variation in abundance (by adding seeds at a density representing the average fecundity of one individual). Thus, our design captures how recruitment and subsequent adult abundance are influenced by variation among species in annual fecundity alone, which enables an evaluation of the role of different coexistence mechanisms in equalizing ultimate abundance differences.

In August 2016, we added mixes of seed of all focal species (except *Artemisia ludoviciana* which was added on October) to the +competition and -competition seed addition plot inside and outside of each rodent enclosure at each site. We added no seeds to two additional plots inside and outside of rodent enclosures so as to control for recruitment from a pre-existing seedbank or from seeds dispersing into experimental plots from resident plants outside of those plots. These no-seeds-added plots had minimal recruitment into them throughout the experiment, indicating the lack of a long-term seed bank, something we have observed in other experiments (Maron et al., 2012). However, in our seed addition plots, we did observe recruitment of some species in the second year after seed addition (indicating limited seed dormancy), but in the third year after seed addition recruitment of new seedlings of any target species was minimal.

In 2017–2019, we used a 1 m² quadrat gridded into 100 10 cm × 10 cm cells to carefully identify and count all individuals of all focal species in each plot at all sites. We censused experimental plots in June, which is the peak of the growing season. Plants typically senesce in early to mid-July. Some plots contained a few resident adults of the same species as we added as seed. We recorded the location of these individuals within each sampled quadrat at the beginning of the experiment and destroyed their flowers every year so they could not disperse seeds into the plots. Species that occurred in plots due to our seed addition could be differentiated from existing resident adults based on their location but also commonly based on their size (even 3 years after seed addition). Added species were typically smaller than residents; in our system, plants grow very slowly and take many years to reach their full size. We also removed flowers or early developing seeds from resident adult plants that grew outside but adjacent to our experimental plots to ensure that natural seed rain from these individuals did not confound our results. In every census, seedlings (i.e. newly recruited plants in any given year) could be easily identified because they either had cotyledons or were much smaller than adult plants, which we define as those individuals >1 year of age.

2.3 | Analyses

To examine the efficacy of bunchgrass reduction (as well as rodent exclusion) on mean percent graminoid cover (square root transformed) and mean litter depth in each plot, we used a linear mixed

model with competition, seed predation and their interactions as fixed factors. Site was included as a random effect.

2.4 | Quantifying effect sizes for bunchgrass competition and seed predation

To determine whether there were trade-offs between functional traits and competitive tolerance or vulnerability to seed predation, we first averaged the cumulative number of seedlings that established across years (2017–2018) and the number of adults established (2019) for each of our 17 target species in plots with each treatment combination (+/-competition or rodents). Most seedling recruitment occurred in 2017, in the spring/summer after our seed addition, but some species had additional recruitment in year 2 (2018). There were very few seedlings that recruited into plots in 2019. We then calculated effect sizes for bunchgrass competition and seed predation as the log response ratio (LRR): $\ln(\text{number of cumulative seedlings or adult plants in } + \text{ plots} / \text{number of cumulative seedlings or adult plants in } - \text{ plots})$. The LRR standardized for difference in fecundity across species so that effect sizes are comparable across species regardless of fecundity. Next, we constructed separate linear regression models, one with each LRR (competition or seed predation effect sizes) as the response variables and each of the functional traits as the predictor variable. For the competition LRR effect size, we focused on seed weight (\log_{10} -transformed here and for all additional analyses), height and LMA. For the rodent LRR effect size, we only examined seed weight, since height and LMA have no relevance to the vulnerability of seeds to predation. We included an 'age' term in the model which enabled us to examine whether effect sizes for recruitment (i.e. cumulative seedlings across years) or final adult plant establishment (i.e. adults in year 3) differed. The interaction between functional trait and 'age' allows evaluation of whether the relationship between an effect size and functional trait changed between seedling recruits and established adults. This was of interest because we hypothesized that the effect of any given functional trait might change depending upon whether we examined the abundance of seedlings or adults. Species was included as a random effect to account for the multiple measurements per species. Thus, for each LRR response variable, the predictors were trait, age and the trait-by-age interaction term, with species as a random effect.

2.5 | Effects of bunchgrass competition and seed predation on CWM functional traits

We explored how the traits of our assembled communities were influenced by the interactions we experimentally manipulated by calculating the CWM values for each of the three traits. Community-weighted trait means were calculated using the `FD` package in `R` (Laliberté & Legendre, 2010) and were based on the abundances of cumulative seedlings (in years 1 and 2) and adults in year 3 of the experiment. We then examined how competition

and seed predation influenced the CWM trait scores for seedlings and adults. To do this, we used separate linear mixed models for each CWM trait with bunchgrass removal, rodent exclusion, 'age', and all interactions as fixed effect predictor variables. Site was a random factor, and rodents and competition were nested, respectively, to account for the split-plot and repeated measures nature of our design.

2.6 | Individual species responses and CWMs across the natural productivity gradient

We examined how abundances of cumulative seedlings and adult plants (2019) for each target species responded to the natural productivity gradient and how these responses depended on their functional traits. To accomplish this, we constructed a generalized linear mixed model with number of adult plants as the response variable. Species, site productivity, 'age' (cumulative seedlings or adults in 2019), and all interactions were included as fixed effects. Site and species nested within site were included as random effects. We used a Poisson error distribution and included an observational-level random effect to account for overdispersion (Harrison, 2014). For each species, we extracted the relationship (i.e. slope) between abundance and site productivity for each species \times year combination in the unmanipulated control plots. We then regressed these slopes against each functional trait of interest: seed weight, LMA and height. Models were run separately for each functional trait. We included 'age' and the interaction between functional trait and year. The interaction term allowed us to determine whether the relationship between the establishment slope and functional trait changed between seedling recruits and established adults. We also included species as a random effect to account for the multiple measurements per species.

Additionally, to determine how variation across sites in productivity influenced the CWMs in control plots where we did not manipulate competition or seed predation, we used linear mixed models with site productivity (g dry biomass m^{-2}), year and their interaction as fixed effects. Site productivity was centred and scaled ($\mu = 0$, $\sigma = 1$) so that intercepts were evaluated at mean, rather than zero, productivity (Gelman & Hill, 2007). Site was included as a random effect to account for the multiple measurements made within each site across years.

2.7 | Effects of bunchgrass competition and seed predation on equalizing adult abundance

Finally, to determine whether the mean fecundity of each focal species predicted its final abundance and how this varied in plots with competition and rodent seed predation manipulated, we constructed a generalized linear mixed model with the number of adult plants that established in each plot as the response variable. Log_{10} -transformed fecundity of each species, competition, rodent seed predation and all interaction terms were included as a fixed

factors. In this analysis, the rodent and competition treatments were nested within site as random effects. We used a Poisson error distribution with an observation-level random effect to account for overdispersion.

3 | RESULTS

Treating rough fescue with herbicide had its intended effect. Three years after the removal treatment graminoid cover was reduced nearly 5-fold from 64.3% ($\pm 4.8\%$ SE) in the control plots to 11.7% ($\pm 2.1\%$ SE) in the fescue removal plots ($F_{1,27} = 178.9$, $p < 0.0001$). In contrast, rodent exclusion had no effect on graminoid cover ($F_{1,27} = 0.7$, $p = 0.40$) and there was no fescue removal \times rodent exclusion interaction on graminoid cover ($F_{1,27} = 1.5$, $p = 0.23$). Litter depth was also significantly reduced nearly 3-fold from 38.5 mm (± 6.5 mm SE) in the control plots to 14.7 mm (± 6.5 mm SE) in the fescue removal plots ($F_{1,27} = 16.4$, $p < 0.001$) but not by rodent exclusion ($F_{1,27} = 0.26$, $p = 0.61$) and there was no fescue removal \times rodent exclusion interaction ($F_{1,27} = 0.2$, $p = 0.66$).

3.1 | Effect sizes for bunchgrass competition and seed predation

Bunchgrass competition as quantified by the log response ratio more negatively affected small versus large-seeded species ($F_{1,15} = 15.7$, $p < 0.001$), was weak for seedlings but over twice as strong for adults ('age' term: $F_{1,15} = 22.0$, $p < 0.0003$), and the slope of the seed size versus competition effect size became steeper for adults versus seedlings (seed size \times 'age' interaction; $F_{1,15} = 9.9$, $p < 0.008$; Figure 1a). Neither LMA ($F_{1,15} = 1.1$, $p = 0.30$) nor height ($F_{1,15} = 0.4$, $p = 0.52$) influenced competition effect size. Seed predation by mice more negatively affected large versus small-seeded species ($F_{1,15} = 6.1$, $p < 0.027$; Figure 1b), but this effect size did not change based on plant 'age' (cumulative seedlings vs. adults; $F_{1,15} = 0.3$, $p = 0.58$), and the age \times seed size interaction was also non-significant ($F_{1,15} = 1.6$, $p = 0.22$).

3.2 | Effects of bunchgrass competition and seed predation on CWM functional traits

The CWM for seed size significantly increased in plots with versus without bunchgrass competition ($F_{1,18.4} = 12.9$, $p < 0.003$), and was larger for adults versus seedlings ('age' term: $F_{1,34.1} = 60.7$, $p < 0.001$). As well, the effect of competition had stronger effects on CWM seed size for adults versus seedlings (competition \times 'age' interaction; $F_{1,35.2} = 5.1$, $p < 0.031$; Figure 2a,b). For seedlings, CWM seed size was slightly but non-significantly greater in the +competition plots compared to the -competition plots (contrast = 0.14, 95% CI = -0.04 to 0.31, $t = 1.6$, $p = 0.12$, Figure 2a), whereas for established adults the CWM for seed size was significantly greater in the + versus -competition plots (contrast = 0.37,

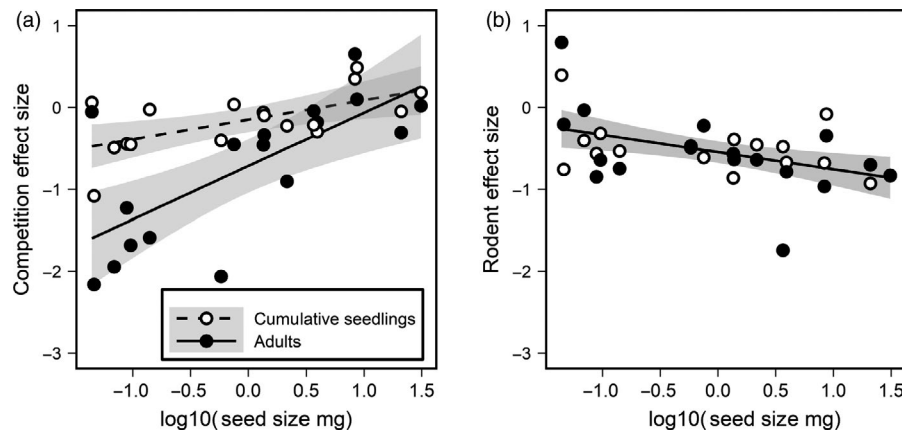


FIGURE 1 Mean effect size of (a) bunchgrass competition and (b) rodent seed predation on the proportion of seeds that establish as seedlings (open circles) and adults (filled circles) for target species as a function of seed weight (\log_{10} transformed). In (a) lines are fit through seedling (dashed line) and adult (solid line) data, whereas in (b) the line is fit through all the data. Effect size calculated as the log response ratio (see Section 2 for details)

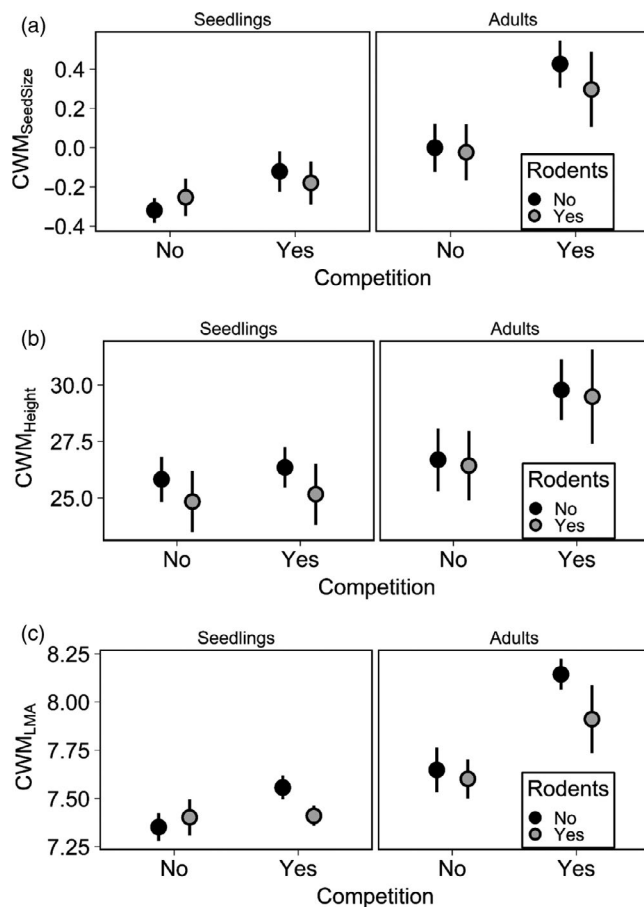


FIGURE 2 Effects of bunchgrass removal (competition no/yes) and rodent exclusion (rodents no/yes) on mean (\pm SE) community-weighted (a) seed size, (b) height and (c) leaf mass per area

95% CI = 0.19–0.55, $t = 4.1$, $p < 0.0003$, Figure 2b). Rodent seed predation and all other interactions did not significantly affect CWM seed weight (Tables S1–S3; Figure 2a,b). The results for CWM height and LMA mirrored the results for seed size, where

the effect of competition increased CWM height and LMA and both effects strengthened through time but there was no rodent effect (Figure 2c–f; Tables S1–S3).

3.3 | Individual species responses and CWMs across the natural productivity gradient

Species differed in how strongly their abundance changed across the productivity gradient (i.e. slopes estimated by the species by productivity interaction: $\chi^2 = 41.2$, $p < 0.0006$). As well, species differed in how their numbers changed based on plant 'age' (i.e. cumulative seedlings vs. adults; species by 'age' interaction: $\chi^2 = 137.7$, $p < 0.0001$). Smaller-seeded species decreased more strongly across the productivity gradient than did large-seeded species (Figure 3). This relationship did not change with plant 'age' (i.e. cumulative seedlings vs. adults, $F_{1,15} = 1.5$, $p = 0.23$) and the seed size by 'age' interaction was non-significant ($F_{1,15} = 0.2$, $p = 0.69$). Shorter species also decreased more strongly across the gradient than did taller species ($F_{1,15} = 5.3$, $p < 0.037$; Figure 3). This relationship did not change based on plant 'age' (cumulative seedlings vs. 2019 adults; $F_{1,15} = 0.6$, $p = 0.44$) and the seed size by 'age' interaction was non-significant ($F_{1,15} = 1.4$, $p = 0.25$). Species' LMA was not related to their change in abundance across the productivity gradient ($F_{1,15} = 0.03$, $p = 0.84$). 'Age' ($F_{1,15} = 0.05$, $p = 0.82$) and the 'age' \times year interaction ($F_{1,15} = 0.2$, $p = 0.64$) were also non-significant.

Community-weighted mean seed size increased with increasing site productivity ($F_{1,8.1} = 6.0$, $p < 0.041$), plant 'age' ($F_{1,7.3} = 34.0$, $p < 0.0006$), with this effect strengthening from seedlings to adults (productivity \times 'age' interaction; $F_{1,7.3} = 7.9$, $p < 0.026$; Figure 4a). The CWM seed size for recruits increased slightly, but not significantly, across the productivity gradient, whereas the CWM seed size for established adults increased more strongly across the productivity gradient (Figure 4a). CWM height and LMA were not affected by site productivity (height: $F_{1,8.1} = 0.5$, $p = 0.48$; LMA:

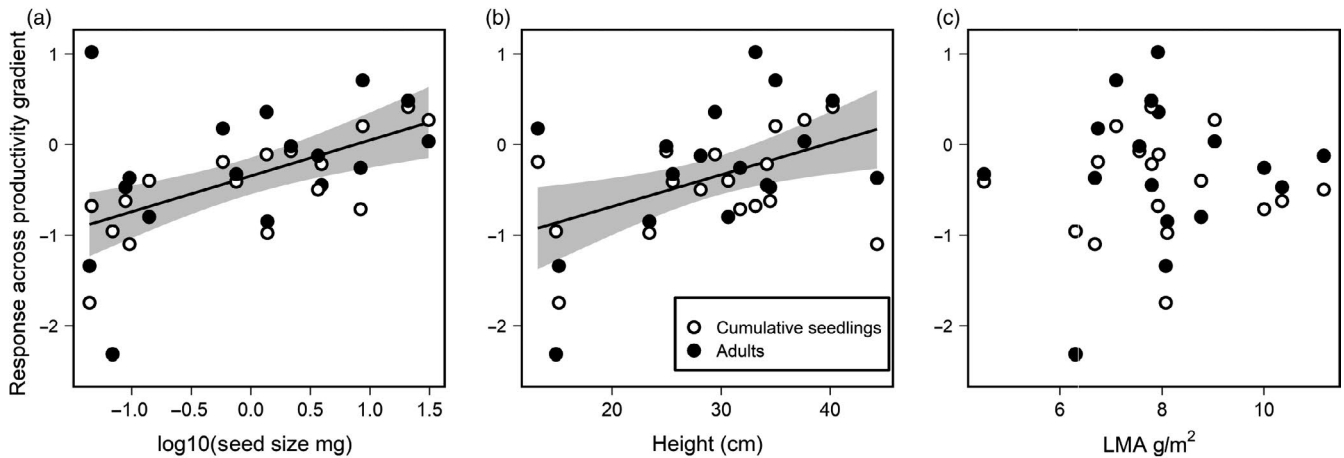


FIGURE 3 Slopes of relationship between abundance of seedlings (open circles) or adults (filled circles) and site productivity plotted as a function of their mean (a) seed weight, (b) height and (c) leaf mass per area. Each open or filled dot is a unique species. Data are from control plots where species were exposed to all interactions. Lines are fit through both seedling and adult data

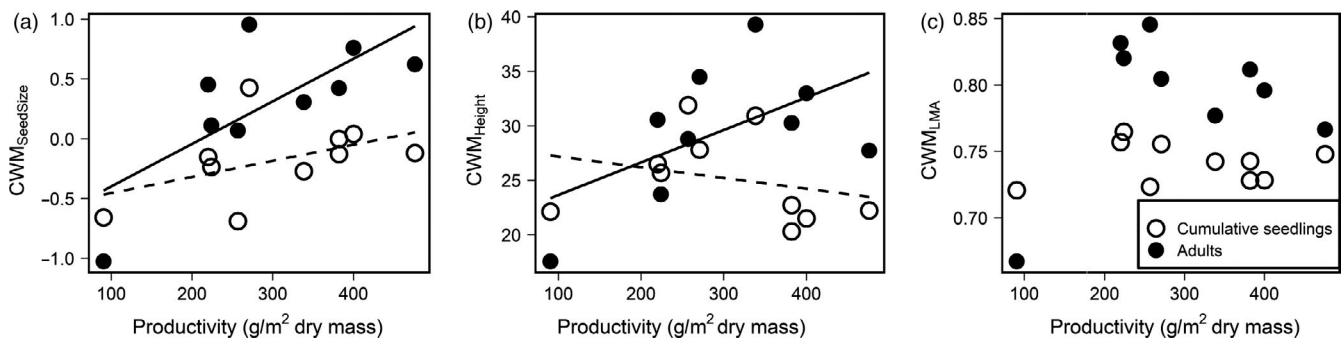


FIGURE 4 Community-weighted mean (a) seed size, (b) height and (c) leaf mass per area values for seedlings (dashed line, open circles) or adults (solid line, filled circles) across nine sites varying in productivity. Data are from control plots where species were exposed to all interactions

$F_{1,8.1} = 0.7, p = 0.44$; Figure 4b,c), but did increase from seedlings to adults (height: $F_{1,7.5} = 10.0, p < 0.015$; LMA: $F_{1,8.0} = 10.3, p < 0.01$; Figure 4b,c). The 'age' by productivity interaction was significant for height ($F_{1,7.3} = 7.9, p < 0.026$; Figure 4b) but not LMA ($F_{1,7.8} = 0.9, p = 0.38$; Figure 4c). The CWM height for seedling communities was slightly, but not significantly, negative across the productivity gradient ($\beta = -0.0099$, 95% CI: -0.041 to 0.021), whereas the adult CWM was slightly, but not significantly, positive across the productivity gradient ($\beta = 0.029$, 95% CI: -0.003 to 0.061 ; Figure 4b).

3.4 | Effects of bunchgrass competition and seed predation on equalizing adult abundance

Across treatments, adult abundance was marginally significantly positively correlated with \log_{10} -fecundity ($\chi^2 = 3.4, p = 0.065$), and suppressed by bunchgrass competition ($\chi^2 = 30.3, p < 0.0001$). Most importantly, however, there was a highly significant fecundity \times competition interaction ($\chi^2 = 30.3, p < 0.0001$). In the plots without bunchgrass competition, there was a strong positive relationship between fecundity and adult abundance, illustrating the inherent

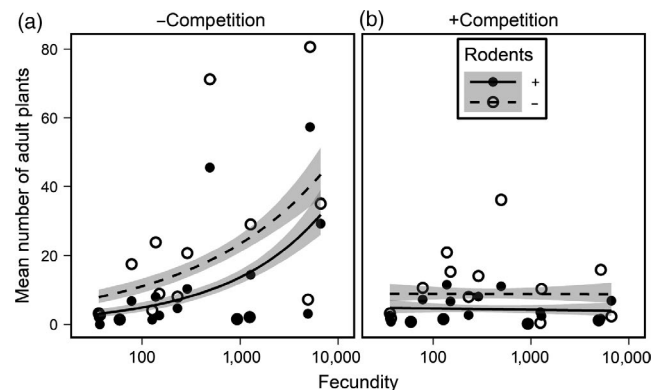


FIGURE 5 Mean final abundance of adults of each target species as a function of their fecundity (\log_{10} transformed) in plots (a) without bunchgrass competition and in plots (b) with bunchgrass competition. Open circles, plots in rodent enclosures, closed circles, plots open to rodents

advantages of high fecundity species ($\beta = 0.72$, 95% CI: 0.45 – 0.99 ; Figure 5a). However, in plots with bunchgrass competition, there was a slight negative relationship between fecundity and log abundance of adults ($\beta = -0.41$, 95% CI: -0.70 to -0.12 ; Figure 5b). Rodent seed

predation suppressed adult abundance ($\chi^2 = 8.4$, $p < 0.005$), with approximately 2.5 fewer individuals in control plots (mean = 1.9, 95% CI: 0.8–2.6) compared to the rodent exclusion plots (mean = 3.2, 95% CI: 1.8–5.7). The rodent effect did not vary significantly with fecundity ($\chi^2 = 0.6$, $p = 0.44$) and the competition \times rodent ($\chi^2 = 0.7$, $p = 0.41$) and the fecundity \times rodent \times competition interaction was non-significant ($\chi^2 = 0.2$, $p = 0.63$).

4 | DISCUSSION

Trade-offs are fundamental to understanding coexistence (Chesson, 2000; HilleRisLambers et al., 2012; Kneitel & Chase, 2004). Species that perform well under one set of ecological circumstances, and the traits that facilitate their enhanced function, perform more poorly in other circumstances. However, spatially replicated manipulative experiments are increasingly needed to quantify how species' traits link to their relative performance across a range of abiotic and biotic conditions (Adler et al., 2013; HilleRisLambers et al., 2012; Pérez-Ramos et al., 2017; Siepielski & McPeck, 2010). We employed such an approach to gain insight into how subordinate forb species that vary in fecundity and seed size coexist in a perennial grassland. We found a novel trade-off that likely contributes to coexistence among species differing in seed size and fecundity. Small-seeded species were less tolerant of bunchgrass competition than were large-seeded species, both at the recruitment stage but even more so as adults. This was reflected at the community level, as the CWM for seed size was higher in plots with versus without bunchgrass competition. The same was true for height and LMA, suggesting that these traits also influence adaptive outcomes of competition with the community dominant bunchgrass. Consistent with these experimental results, the abundance of small-seeded species also dropped across an increasing natural gradient of bunchgrass productivity (and thus likely competitive intensity), whereas this was not the case for large-seeded species. CWMs for seed size and height (but not LMA) also positively increased from lower to higher productivity sites, but these patterns were most apparent in the established adult communities. Finally, bunchgrass competition equalized differences in the relative abundance of target species, eliminating the higher abundances that were achieved by high fecundity small-seeded species in plots without competition. Although post-dispersal seed predation more negatively influenced the proportion of seeds that established as adults for larger-seeded low fecundity compared to smaller-seeded species, these effects did not influence CWM seed size, and the effects of seed predation on the relative final abundances of small- versus large-seeded species were relatively small. We discuss the implications of these patterns in more detail below.

4.1 | Effect sizes for bunchgrass competition and seed predation

Using log response ratios which control for differences among species in fecundity (i.e. seed input), we assessed how variation in seed

size (or other traits) per se influenced competitive tolerance or vulnerability to seed predation. We found that seed size predicted both competitive tolerance and vulnerability to seed predation. As our experiment progressed, bunchgrass competition imposed increasing mortality on small-seeded species through time, with most plants dying sometime after senescence in July (and green-up the following spring). In contrast, the effect size of seed predation did not change through time. Although this was not the case with seed predation, the legacy of seed predation on recruitment could still be seen in terms of its effect on the log response ratios of individual species at the end of the experiment.

In the first year of our experiment, we previously found that a combination of functional traits represented by a PCA score better predicted the effect size of bunchgrass competition on initial seedling recruitment than did seed size alone (Maron et al., 2018). Here, we hypothesized that two traits in particular, height and LMA, might correlate with competition effect size since these traits independently can influence resource capture (Díaz et al., 2016; Kunstler et al., 2016; Seifan et al., 2013; Westoby et al., 2002). Surprisingly, however, seed size alone better predicted the effect size of competition on cumulative recruitment over the first two years of the experiment (rather than in year 1 only) and final adult abundance than did height or LMA. While it is tempting to think that the stronger effects of seed size reflect how this trait integrates the effects of other measured functional traits on performance, correlations between seed size, height and LMA were relatively weak. An alternative explanation is that this result simply illustrates that in our system, traits that influence the regeneration niche (such as seed size in our case) can have long-lasting effects and take precedence over traits that influence the adult niche, as has been found for forest trees (Poorter, 2007). For long-lived perennials such as those we studied, often the most stringent filtering occurs at the recruitment stage.

4.2 | Effects of bunchgrass competition and seed predation on CWM functional traits

Pioneering trait-based work has revealed important trait-environment correlations consistent with a signature of strong competitive interactions among species (Cornwell & Ackerly, 2009; Grime, 2006; Maire et al., 2012). Yet, these observational studies have also been criticized because patterns do not always accurately reflect process (de Bello, 2012; Germain, Mayfield, & Gilbert, 2018; Mayfield & Levine, 2010). Using an experimental approach, we found that CWMs for seed size, plant height and LMA shifted significantly higher in plots with versus without bunchgrass competition only for established adult plant communities, not seedlings (Figure 2). Thus, at the community level, bunchgrass competition negatively affected the performance of smaller-seeded, shorter species with lower LMA values. Importantly, height and fecundity were uncorrelated ($r = -0.25$, $p = 0.33$) so these results represent the advantage of being taller, which is uncorrelated to any fecundity advantage.

Functionally, greater plant height should be advantageous in plots with bunchgrass because greater height can enable plants to better compete for light. Greater LMA typically implies slower rates of photosynthesis and slower relative growth rates (Díaz et al., 2016; Kunstler et al., 2016; Westoby et al., 2002), performance outcomes that do not seem like they would enhance competitive tolerance. However, in forests, species with lower LMA are favoured in high light gap environments (Poorter et al., 2008; Uriarte et al., 2010; Walters & Reich, 1999), which may be similar to our plots lacking bunchgrasses. It may be that limited nutrients and light in plots with bunchgrass decreases growth more than photosynthesis, favouring species with high LMA.

We found no significant effect of seed predation on CWM seed size. The reason for this is likely that small-seeded species were much more abundant in plots than low fecundity large-seeded species, with this difference in relative abundance likely swamping out smaller differences in the abundance of large-seeded species in and out of rodent exclosures. The rodent effect sizes also tended to be smaller than competition, at least for established adults (Figure 1).

4.3 | Individual species responses and CWMs across the natural productivity gradient

We evaluated whether spatial variation in bunchgrass productivity (likely driven by small-scale variation in both rainfall and the nutrient status of soils; Maron et al., 2019), and hence competitive intensity, potentially dictates differences in performance of large- versus small-seeded species. Although spatio-temporal variation has long been central to coexistence theory (Chesson, 1994; Tilman & Pacala, 1993), empirical tests have been fairly rare until recently, and most empirical work has examined temporal rather than spatial effects (i.e. Adler, HilleRisLambers, Kyriakidis, Guan, & Levine, 2006; Angert, Huxman, Chesson, & Venable, 2009; Usinowicz et al., 2017). We hypothesized that a trade-off involving competitive tolerance might be analogous to the trade-off involving 'stress-tolerance' in Muller-Landau's (2010) model, where natural spatial variation in productivity (as a result of small-scale variation in rainfall and nutrient availability) could promote coexistence by shifting the relative advantages/disadvantages of being large or small-seeded. Such correlations between functional traits and patterns of species abundances have been found in other studies (Cornwell & Ackerly, 2009; Díaz, Cabido, & Casanoves, 2009; Garnier et al., 2004; Laughlin et al., 2015; Shipley, 2010). Consistent with our experimental results and theory, at less productive sites, less competitively tolerant small-seeded species had advantages by dint of their higher fecundity. However, at more productive sites, these species were disadvantaged due to their poor competitive tolerance (Figure 3). We also found that CWMs for seed size and adult height also increased across the productivity gradient, in a manner congruent with how they increased between plots without versus with bunchgrass competition. However, CWM for LMA was not significantly changed

across the productivity gradient. The trade-off between seed size, fecundity and competitive tolerance was not simply manifest at the recruitment stage, but magnified over time. These results indicate an important link between functional traits and the demography of species (Adler et al., 2014; Rüger et al., 2018; Violle et al., 2007; Visser et al., 2016), as well as the importance of trade-offs involving spatial environmental variation.

4.4 | Effects of bunchgrass competition and seed predation on equalizing adult abundance

Three years after seed addition, adult abundance strongly correlated with fecundity, but only in plots without bunchgrass competition (Figure 5a). In plots with bunchgrass, target species abundance was strongly equalized, erasing the significant effect of fecundity on final abundance (Figure 5b). We interpret these impacts on abundance as equalizing fitness differences because they affected the extent to which fecundity translates to longer-term patterns of abundance. We acknowledge, however, that these equalizing effects are unlikely to perfectly equilibrate fitness differences among species (Chesson, 2000; Turnbull, Rees, & Purves, 2008). Yet, given these effects, it may be that only small stabilizing mechanisms may be needed to ensure coexistence. This interpretation, however, hinges on whether our experimental seed addition accurately mimicked natural variation in plant fecundity. In other words, could the positive fecundity–abundance relationship we found in plots without bunchgrass be a product of an experimental treatment (i.e. varied number of seeds added across species) as opposed to true differences among species in fecundity? It is likely that we added seeds to plots at densities higher than the natural density of dispersed seeds because large differences in abundance among species could greatly affect the density of dispersed seeds. Our goal, however, was not to try to mimic interspecific differences in seed density on the landscape in our seed addition plots. Instead, we sought to examine the effects of interspecific variation in fecundity per se so that we could determine whether higher fecundity small-seeded species had inherent recruitment and establishment advantages over lower fecundity larger-seeded species. These differences in fecundity could help drive differences in abundance, as opposed to differences in abundance dictating fecundity (as measured by dispersed seed density). Importantly, the natural recruitment around focal plants that occurred across our sites strongly correlated with their fecundity (Maron et al., 2019). We recognize, however, that unknown differences in longevity and lifetime fecundity among focal species could also play an important role.

In sum, our results suggest that the processes influencing the maintenance of seed size diversity in perennial systems might be different than what occurs in annual systems, where most previous empirical tests of trade-offs between seed size and number for coexistence have been performed (Ben-Hur, Fragman-Sapir, Hadas, Singer, & Kadmon, 2012; Leishman, 2001; Rees, 1995; Turnbull, Coomes, Hector, & Rees, 2004; Turnbull, Rees, & Crawley, 1999; but

see Turnbull, Manley, & Rees, 2005). In particular, although subordinate species may compete with each other as adults, as is common in annual systems, trade-offs involving tolerance to competition from dominant foundation species may be most important in influencing the maintenance of seed size diversity, and hence coexistence.

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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 AVAILABILITY STATEMENT

Data used in this study are archived with Dryad Digital Repository: <https://doi.org/10.5061/dryad.6djh9w0zj> (Maron, Hahn, Hajek, & Pearson, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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