

RESEARCH ARTICLE

Does increasing the diversity of seeds broadcast for restoration alter post-dispersal seed predation and its community-determining effects?

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Abstract

1. Native seeds broadcast for restoration are often consumed by predators before they can germinate. However, it is unclear how the composition of a seed mix affects seed predation.
2. We excluded vertebrates from small plots seeded with native grassland plants to evaluate how seed diversity affects predation. There were two seeding treatments: a less diverse mix with a focal cohort of eight species on which we focused our analyses, and a more diverse mix that consisted of the focal cohort plus eight additional species.
3. The focal cohort experienced greater predation when dispersed with the additional species, but this effect was unevenly distributed throughout the focal cohort.
4. The species of the focal cohort that experienced the greatest increase in predation when in the high-diversity treatment were also the ones favoured by predators when in the treatment without additional species. This suggests that when more species of palatable seed are available in a dispersed seed patch, predators may exert a stronger community-filtering effect on such a seed patch.
5. Increasing the number of species dispersed together for land stewardship efforts may increase predation of these seeds, which is a concern if their dispersal is intended to restore native plant diversity. We recommend strategies to minimize this potential detriment, such as staggering seed dispersal over time, for practitioners who seek to disperse a high diversity of seeds for native restoration.

KEYWORDS

annual forbs, associational susceptibility, California grasslands, community assembly, consumer effects, granivory, neighbour effects, seed addition, seed neighbourhood, small vertebrates

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1 | INTRODUCTION

The success of ecological restoration is often predicated on the reintroduction of native plant species, but establishing plants is also one of the biggest challenges faced by restoration practitioners. Ecological restoration is recognized as one of the most direct ways humans can reverse land degradation and promote the conservation of native species (Dobson et al., 1997; Pearson et al., 2022). Although the motivation behind ecological restoration projects can vary in scope (Perring et al., 2015), reestablishing native species that were lost from a site or augmenting populations that have declined due to degradation is almost always a goal (Gann et al., 2019). Sites targeted for restoration are often similar to early successional habitats in that desired native species tend to be seed limited (Turnbull et al., 2000) and are dependent on the addition of propagules or seedlings to establish new populations (Perring et al., 2015). One of the most common ways to reintroduce native species is through the addition of seeds ('direct seeding') to the restoration site because it is cost-efficient and easy to implement (Florentine & Westbrooke, 2004; Merritt & Dixon, 2011; Rinella & James, 2017). However, when compared to other more cost-intensive strategies, direct seeding generally provides lower plant survivorship and slower recovery at the degraded site (Palma & Laurance, 2015). The widespread difficulty with establishing native species through direct seeding in restoration (Bakker et al., 1996; James et al., 2011) highlights a need to better understand what constrains plant establishment from seed during restoration.

Loss or destruction of seeds before they can emerge as seedlings is one factor likely contributing to low native plant establishment after direct seeding for restoration. In particular, there is mounting evidence that seed loss to seed predators ('granivores') could be constraining habitat restoration efforts (Archer & Pyke, 1991; Orrock et al., 2009; Pearson et al., 2019) and in some cases be the primary determinant of the plant community that establishes from dispersed seeds (Germain et al., 2013; Howe & Brown, 2001; Maron et al., 2012; Pearson et al., 2018). Rodents, birds and ants have been shown to suppress the establishment of many plants post-seed dispersal (Pérez et al., 2006) and can influence the assembly of plant communities (e.g. Guo et al., 1995; Hulme, 1994; Inouye et al., 1980). However, most studies have indicated that vertebrate granivores exert a greater effect on these processes than invertebrates, in general (Borchert & Jain, 1978; Brown & Heske, 1990; Brown & Human, 1997; Bricker et al., 2010; Larios et al., 2017; Maron & Simms, 2001; Orrock et al., 2009; Peters et al., 2005; Suazo et al., 2013).

We also understand that granivore foraging behaviour, and subsequently their impact on plant communities, is determined by plant traits and spatial relationships (Pyke et al., 1977; Vickery, 1984). These include seed spatial density (Orrock et al., 2009; Ostojka et al., 2013; Price & Heinz, 1984), seed size (Hay & Fuller, 1981; Pérez et al., 2006; Petry et al., 2018; Radtke, 2011) and the chemical and nutritional content of seeds (Henderson, 1990;

Ríos et al., 2012). By having a preference for certain species, granivores can select for plants that have undesirable seeds to become more abundant than those with desirable seeds (Inouye et al., 1980; Samson et al., 1992; Soholt, 1973). However, it is also possible for post-dispersal seed predation to influence community assembly in a density-dependent manner, where granivores simply consume seeds relative to their abundance until all seeds are equally present (Larios et al., 2017). Furthermore, Podolsky and Price (1990) found that heteromyid granivores preferentially forage from patches with greater sum mass (greater 'profitability') when selecting between two patches that differ in individual seed size.

Previous investigations of how selective seed predation influences community structure have mostly focused on seed patches with few species or no seed addition whatsoever (see, e.g. Borchert & Jain, 1978; Guo et al., 1995; Hay & Fuller, 1981; Lucero & Callaway, 2018; Pellish et al., 2018; Radtke & Wilson, 2015; but see, e.g. Germain et al., 2013; Howe & Brown, 1999, 2001; Maron et al., 2018; Pearson et al., 2019). However, many undisturbed native plant communities naturally cast a diverse seed rain, and restoration efforts often disperse many species of seed together because increasing species diversity is a common goal (Perrow & Davy, 2002; Ruiz-Jaen & Aide, 2005). Diverse communities are desired in restoration because evidence suggests that they reduce reinvasion of the restored site, enhance ecosystem functioning and increase resilience to disturbance events such as drought or wildfire (Alexander et al., 2016; Allen & Meyer, 2014; Benayas et al., 2009; Elmquist et al., 2003). Understanding how the diversity of dispersed seeds might influence the behaviour and impact of granivores would benefit such restoration efforts.

However, very few studies have investigated the selectivity of granivores among multiple complex seed mixes (Howe & Brown, 1999; Pearson et al., 2011). There is consensus that the presence of a palatable neighbour seed can increase 'associational susceptibility', that is, the predation of other close-by seeds (Barbosa et al., 2009; Caccia et al., 2006; Germain et al., 2013; Ostojka, 2008; Veech, 2000, 2001; but see, Hulme & Hunt, 1999), but, to our knowledge, no studies have investigated such associational effects in a seed mixture of more than two species (e.g. Ostojka et al., 2013). How this rule of thumb may work when the diversity of a seed patch increases is unclear, but it could be an important factor that contributes to the community-determining role that granivores play, especially in the context of native plant restoration.

Here, we focus on how selective predation of seed mixes with different diversity may affect the species common to all the seed mixes offered. To do so, we describe a field experiment in an invaded California grassland. We chose this ecosystem because California grasslands rarely revert back to native communities without intervention after disturbances are removed (D'Antonio & Vitousek, 1992; Stromberg & Griffin, 1996), and there are many small vertebrates that live in and rely on this diverse ecosystem. However, the effect of these animals on the assembly and

restoration of California grasslands in particular is relatively understudied (Espeland et al., 2003; Gurney et al., 2015; Orrock et al., 2009). This line of research could be especially key for restoration efforts in California because direct seeding is often used due to budget constraints and the isolated nature of most restoration sites. In this field experiment, we crossed small vertebrate exclosure treatments with two native seed addition treatments that consisted of a diverse suite of species native to California grasslands to address the following questions: (1) In a diverse grassland system, does vertebrate granivory significantly reduce post-dispersal seedling emergence ('recruitment')? (2) How does the intensity of granivory differ between grassland species? (3) Does the addition of palatable species to a dispersed seed cohort (increasing seed diversity) affect the predation of the original seeds? (4) If predation is altered by seed diversity, does altered seed predation affect all species in the focal cohort equally?

2 | MATERIALS AND METHODS

2.1 | Study system

The research was carried out in the University of California Sedgwick Reserve; a 2358-hectare reserve in the foothills of the Santa Ynez Mountains in Santa Barbara County, California, USA (34°41'34" N, 120°02'26" W; 370–730 m a.s.l.; UC Natural Reserve System, 2023), which is unceded territory of the indigenous Chumash people (Santa Ynez Band of Chumash Indians, 2023). Because this is a research reserve, we did not need permits for any aspect of this field experiment. The climate is typical of the Mediterranean climate of California with warm, dry summers and a cool, wet growing season during the winter months (approximately between November and April). Between 1991 and 2020, the mean annual precipitation was 541.12 mm with growing season temperatures ranging from 6.0°C to 22.2°C and summer temperatures ranging from 8.2°C to 31.3°C (PRISM Climate Group, 2021). During the 2018/2019 growing season, Sedgwick Reserve received 578 mm of rain. The experiment was carried out in two soils, Botella clay loam and Salinas silty clay loam. Both are fine-loamy, mixed, superactive, thermic Pachic Argixerolls (Shipman, 1972). The plant communities at both sites are dominated (>95% cover) by European annual grasses and forbs such as *Avena fatua* and *Brassica nigra*, with moderate cover of native grassland species. *Reithrodontomys megalotis* are the primary small mammalian granivore encountered at this location, although *Mus musculus* are also common (John L. Orrock, unpublished data, 2005). We observed that birds are the most active granivores in our seed-baited camera surveys (Appendix S1). *Junco hyemalis* was the most frequently observed predator of herbaceous seeds, followed by *Haemorhous mexicanus*, *Spinus pinus* and *Haemorhous purpureus*. We expect that there were also many invertebrate species that consumed dispersed seed at the site, but at minimal levels compared to birds and rodents. For example, *Veromessor andrei* occurs

at high densities elsewhere in the reserve but is uncommon at our specific study locations (Petry et al., 2018; William K. Petry, pers. comm.).

2.2 | Species selection and seed collection

In this experiment, we focused on four perennial grass species, three perennial forb species and nine annual forb species (Table 1). All seeds were collected within the Sedgwick Reserve between 2017 and 2019. For a given species, we applied a standard quantity, in mg, of seed to every seeded plot, regardless of mixture treatment. We estimated the number of seeds per plot using the mean seed mass of each species (Table 1). To determine each species' mean seed mass, we counted seven samples of approximately 25 or more seeds and weighed each sample to the nearest 0.1 mg.

2.3 | Experimental treatments

To explore how the composition of the seed patch affected granivory, there were three seeding treatments: (1) a low-diversity mix of eight species (the focal cohort), (2) a high-diversity mix of 16 species (the focal cohort plus eight additional species) and (3) a control treatment where no seeds were added (Table 1). We use the terms 'focal cohort' and 'focal species' because we evaluated the differences between seeding treatments (Questions (3) and (4)) by focusing on these species, and because previous literature uses the terms 'focal species' and 'neighbour species' to describe associational interactions (Barbosa et al., 2009).

Species were selected so that the focal cohort represents native annual forbs that are commonly found among invasive annual grasses, while the eight additional species represent a remnant or restored native community that is more diverse. Importantly, additional species in the high-diversity treatment include four grass species and *Lupinus succulentus*, which are species that may be sought after by granivores, as suggested in previous research (Borchert & Jain, 1978; Clark & Stratton, 2020; Espeland et al., 2003; Gurney et al., 2015; Orrock et al., 2009). The low-diversity treatment received 1405 ± 186 seeds per plot, on average, and the high-diversity treatment received an average of 9488 ± 931 seeds per plot. The average number of seeds in a single plot for any given species was 593 ± 58 (Table 1). Our seed inventory and research budget precluded an additional seeding treatment consisting of the low-diversity treatment seeded at a density equivalent to the high-diversity treatment. Subsequently, we chose to keep the seed density for each species consistent across seeding treatments in order to best assess our second question.

To explore whether seed predation differed between treatments, we used three exclosure treatments: (1) a full cage (closed) that kept out vertebrate animals, (2) a partial cage (sham) that controlled for the effect of the cage without excluding vertebrates and (3) a treatment without a cage (open). Cages were 0.25 m² and 0.3 m

TABLE 1 Seeding treatment compositions and species characteristics. Colour shading highlights the seed cohorts and seeding treatments. The dark orange colour that frames the interior cells illustrates that the high-diversity treatment consisted of both seed cohorts, whereas the low-diversity treatment (blue) consisted only of the focal cohort. Cells that detail the totals for the high-diversity treatment are light orange in colour, and cells that detail the totals for the added cohort are very light orange. The label cell for the focal cohort is light blue. The totals for the focal cohort are the same as the totals for the low-diversity treatment, and we highlight these data in cells that are a darker shade of blue. Seed size (third column) was measured for seven samples for each species, and we measured the total mass of each seed species to be dispersed onto every plot (fourth column). We used these two numbers to calculate the number of seeds dispersed (fifth column). We estimate the standard error for the number of seeds dispersed (fifth column) as the result of the standard error of the mean seed size of each species ('SEM seed size', third column). The sixth (furthest right) column lists species presence as the per cent of all plots seeded with each species in which at least one seedling of that species was found. In this column, the cells that detail the 'totals' are not true totals for each cohort and seeding treatment, but instead these cells detail the per cent of all plots seeded with the respective cohort and/or seeding treatment in which at least one seedling of any of its contingent species was present^{a,b}.

Species	Species code	Seed size (average \pm SEM mg/seed)	Mass dispersed (average \pm SD mg/plot)	Number dispersed (average \pm SE number seeds/plot)	Seedling presence (% of seeded plots)
Focal cohort					
<i>Amsinckia menziesii</i>	AMME	3.0 \pm 0.1	250.1 \pm 0.4	82 \pm 3.5	93%
<i>Asclepias eriocarpa</i>	ASER	27.9 \pm 1.2	251.5 \pm 0.8	9 \pm 0.4	20%
<i>Croton setiger</i>	CRSE	6.0 \pm 0.5	250.0 \pm 0.3	41 \pm 3.7	88%
<i>Eschscholzia californica</i>	ESCA	1.3 \pm 0.1	251.9 \pm 0.5	192 \pm 9.9	58%
<i>Plantago erecta</i>	PLER	2.2 \pm 0.1	252.1 \pm 0.5	117 \pm 3.7	20%
<i>Salvia columbariae</i>	SACO	0.7 \pm 0.1	504.1 \pm 0.6	676 \pm 133.0	0%
<i>Sisyrinchium bellum</i>	SIBE	1.9 \pm 0.3	251.5 \pm 0.6	131 \pm 19.8	0%
<i>Uropappus lindleyi</i>	URLI	1.6 \pm 0.1	251.8 \pm 0.5	157 \pm 12.0	43%
Focal cohort total = low-diversity treatment total:					
		5.6 \pm 0.3	2263.0 \pm 4.2	1405 \pm 186.0	100%
Added cohort					
<i>Chlorogalum pomeridianum</i>	CHPO	7.4 \pm 0.2	250.7 \pm 0.4	34 \pm 0.8	45%
<i>Chorizanthe staticoides</i>	CHST	1.2 \pm 0.1	249.8 \pm 0.5	208 \pm 23.4	5%
<i>Elymus glaucus</i>	ELGL	3.3 \pm 0.1	501.2 \pm 0.7	150 \pm 6.1	55%
<i>Eriogonum fasciculatum</i>	ERFA	0.7 \pm 0.1	4231.1 \pm 16.2	5963 \pm 451.2	80%
<i>Lupinus succulentus</i>	LUSU	31.0 \pm 0.3	3268.3 \pm 3.6	105 \pm 1.0	0%
<i>Melica californica</i>	MESPP ^b	1.5 \pm 0.1	502.9 \pm 1.5	337 \pm 20.6	60% ^b
<i>Melica imperfecta</i>		0.2 \pm 0.0	250.1 \pm 0.4	1252 \pm 241.0	
<i>Stipa pulchra</i>	STPU	7.4 \pm 0.1	251.7 \pm 0.5	34 \pm 0.3	85%
Added cohort total:					
		6.6 \pm 1.0	9505.9 \pm 23.8	8082 \pm 744.5	100%
Focal + added cohorts = high-diversity treatment total:					
		6.1 \pm 0.2	1,1768.8 \pm 28.1	9488 \pm 930.5	100%

^aSpecies present in 5% or less of all seeded plots were excluded from data analysis. Additional data that further detail species presence are listed in the expanded version of this table, Appendix S1: Table S1.

^bBecause *Melica* species were indistinguishable, we counted these species together and use 'MESPP' to refer to their data.

tall and constructed using four rebar posts fully enclosed with ¼" mesh hardware cloth. The sham cages were identical to closed cages except that they had two adjacent open walls without hardware cloth.

2.4 | Experimental design and data collection

The seed mix treatment was crossed with the enclosure treatment in a partial factorial design for a total of eight treatments. We used a partial factorial design due to budgetary and logistic constraints: we minimized the number of cage-control plots by reducing the 'sham + seed' and 'closed + no seed' plots. Plots were 0.25 m² and were randomly placed at each site in a series of eight clusters of four plots (Figure 1). The plots in each cluster were 0.5–1 m apart and clusters were 1–5 m apart. We randomly designated half of the clusters to be low-diversity clusters and the other half to be high-diversity clusters. Every cluster included one open plot and one closed plot that both received the same seed mix, as well as one open plot that received no seeds. To complete the partial factorial design described above, the fourth plot was either a sham cage that received the same designated seed mix or a full cage that received no seed (Figure 1). We used open plots without seed addition to measure natural recruitment from the local seed bank, and closed plots without seed addition to assess whether cages affected natural recruitment (results in Appendix S3). We randomly organized plots within each cluster.

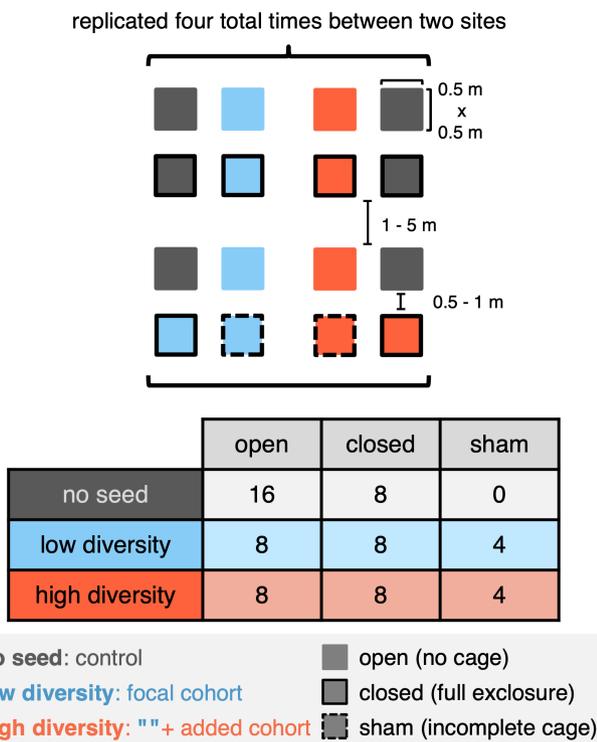


FIGURE 1 A symbolic illustration of the experimental design. The table details the total number of plots for each combination of enclosure+seeding treatment among the two sites.

This experimental design was replicated at two sites that were approximately 0.25 km apart.

Before seeding the plots, we removed all residual above-ground biomass and scraped the top 5 cm of soil from the plots with a hard rake to remove as many exotic seeds as possible. The native seeds were hand-casted and raked into the plots on 30 January 2019. There was a thorough cloud cover with approximately 2.6 cm of precipitation in the first 24 h after seed dispersal, approximately 5 cm of precipitation in the first week, and approximately 12.7 cm of precipitation in total during the first month (Weather Underground, 2020).

The plots were counted for seedlings 70 days after the plots were seeded. During this census, individual forb seedlings were identified to species. Individual grass seedlings were identified to genus 33 days later. (*Stipa pulchra* and *Elymus glaucus* were distinguished from the two *Melica* species, but *M. californica* and *M. imperfecta* were indistinguishable at the time of the census.)

2.5 | Data analysis

Species that were present in 5% of the seeded plots or fewer were excluded from data analysis. The low germination rates of these species likely contributed to their low recruitment (Appendix S3: Table S3). To determine the impact of granivores on the establishment of the remaining native grassland species, we calculated the recruitment rate of each species and then averaged them to calculate the mean recruitment rate for each plot. For the high-diversity treatment, we also calculated the collective mean recruitment rate for just the focal cohort within each plot.

When calculating each species' recruitment rate, we controlled for local seed bank recruitment rates and plot surface damage from gopher holes. For gopher damage, we used the undamaged area of each plot as the denominator for seedling density (Appendix S2: Equation S1). Of the 64 total plots, 18 had gopher damage. Of these, the average area damaged by gopher cavitation was 13 ± 12% of the plot.

To account for natural recruitment from the seed bank, for each species we subtracted the seedling density counted in the nearest no seed plot, regardless of enclosure treatment (Appendix S2: Equation S2). We then calculated the recruitment rate to be the ratio of each species' adjusted seedling density relative to the estimated number of seeds applied to each plot using Equation (1).

$$G = \frac{D_2}{(S \times W^{-1})} \quad (1)$$

For each species, G is the recruitment rate, calculated as the adjusted seedling density of the species, D_2 , divided by the estimated number of seeds applied to each plot, $(S \times W^{-1})$. The estimated number of seeds per plot is the measured quantity of seeds (in mg) broadcast on a given plot, S , multiplied by the inverse of the mean mass per seed, W^{-1} , of that species (Table 1).

All statistical analyses were implemented in R version 4.2.2. We used the adjusted boxplot method (Hubert & Vandervieren, 2008)

using the *R* package *robustbase* v.0.95-0 to distinguish outliers in terms of their seedbank-controlled recruitment rate (Maechler et al., 2022). We excluded two outlier values for *Croton setiger* for all statistical analyses (Appendix S3). To support statistical power, we did not block data by site as recruitment rates did not differ according to site (Appendix S3).

For each experimental question, we first tested for a general trend in the data with appropriate parametric considerations, and then we tested the specific comparisons that would precisely answer each question. We used the Benjamini–Hochberg method to adjust tests involving multiple comparisons (Benjamini & Hochberg, 1995). For Question (1), we first used the *rstatix* package v.0.7.2 for a pairwise Mann–Whitney–Wilcoxon (MWW) test of the differences in the mean plot recruitment rates between the three enclosure treatments (Kasambara, 2023). We then performed pairwise *t*-tests of the differences in this response metric between sham, closed and open plots particular to each seeding treatment to elucidate the effect of the cage. For Question (2), we first conducted an analysis of similarity test (ANOSIM) on a dissimilarity matrix derived from the recruitment rate for each species in all ‘open + high diversity’ and ‘closed + high-diversity’ plots. We used the *vegan* package v.2.6-4 to derive the dissimilarity matrix and to conduct the ANOSIM (Oksanen et al., 2022). Because a removed outlier value of *C. setiger* would have made the matrix problematically incomplete, we substituted the average germination rate of *C. setiger* in ‘open + high-diversity’ plots in place of that missing value. We used the Bray–Curtis distance index and 9999 permutations for ANOSIM. We then conducted an indicator species test using the *indicspecies* package v.1.7.1 to determine which species were most significantly affected by vertebrate exclusion, again with 9999 permutations (De Cáceres & Legendre, 2009). We also used pairwise tests of the recruitment rate in all closed versus open plots, regardless of seeding treatment, for each species, to characterize the species as very palatable ($p\text{-adj} < 0.05$), palatable ($p\text{-adj} < 0.1$), moderately palatable ($p\text{-adj} < 0.2$), unpalatable ($p\text{-adj} > 0.5$, with a 95% confidence interval centred on zero) or neutral/uncertain ($0.5 > p\text{-adj} > 0.2$). We chose to do so because this characterization might provide helpful information for restoration practitioners working in California grasslands. For Question (3), we evaluated the recruitment rate of the focal cohort in a two-way crossed ANOVA including all exclusion treatments, and then calculated four pairwise *t*-tests for the four specific combinations relevant to our Question (Table 3), with Benjamini–Hochberg’s adjustment using the *rstatix* package. For Question (4), we used Mantel’s test to compare dissimilarity matrices for each of the two seeding treatments: each matrix used the Bray–Curtis distance index to compare the recruitment rate of focal species in closed versus open plots within each seeding treatment. We did this using the *vegan* package, and substituted the mean germination rate of *C. setiger* particular to the treatment type (‘open + low-diversity’ or ‘open + high diversity’) for each of the two outlier values excerpted from that species’ data. This test also has relevant implications for Question (3) as well: rather than assessing a difference in the magnitude of predation, we infer a difference between the two seeding treatments in terms of the change in community composition due to enclosure. Finally, we conducted an indicator species test on

the focal species’ recruitment rates in open plots of the two seeding treatments to determine which, if any, of the focal species showed a significantly pronounced effect from association, that is, if predation was increased or decreased for these indicator species when in the high-diversity treatment (De Cáceres et al., 2010; R Core Team, 2017).

3 | RESULTS

3.1 | Emergence

At the time of census, the seeded plots had an average of 35.3 ± 33.2 seedlings/plot (0.25 m^2). Closed plots had an average of 51.0 ± 42.4 seedlings/plot, open plots had an average of 21.8 ± 18.7 seedlings/plot and sham plots had an average of 30.7 ± 23.2 seedlings/plot. Plots seeded with the low-diversity treatment had an average of 15.8 ± 10.5 seedlings/plot. The plots seeded with the high-diversity treatment had an average of 54.7 ± 36.9 seedlings/plot, of which 15.7 ± 9.4 seedlings/plot were focal cohort species. *Chorizanthe staticoides*, *L. succulentus*, *Salvia columbariae* and *Sisyrinchium bellum* were each present in only two or fewer plots, so we excluded these species from analyses (Table 1). *Croton setiger*, *Amsinckia menziesii*, *S. pulchra*, *Melica* spp., *Eriogonum fasciculatum* and *E. glaucus* recruited at the highest rates. We detail the mean seedling density of each species in open and closed plots in Table 2.

3.2 | Preliminary analyses

We did not find a significant site effect when comparing only closed plots per site (*t*-test: $p = 0.46$, $t = 0.77$), nor when assessing the interaction of site with enclosure treatments using ANOVA (site factor: $p = 0.58$, $F_1 = 0.31$; Treatment:Site interaction: $p = 0.88$, $F_{2,1} = 0.13$). In our assessment of the caging effect, we found that open plots

TABLE 2 Species mean seedling density in open and closed plots.

Species code	Seedling density in closed plots (mean \pm SD seedlings 0.25 m^{-2})	Seedling density in open plots (mean \pm SD seedlings 0.25 m^{-2})
AMME	9.4 ± 4.5	4.1 ± 3.8
ASER	0.2 ± 0.4	0.3 ± 0.5
CRSE	4.1 ± 4.5	4.1 ± 4.9
ESCA	3.7 ± 3.9	1.5 ± 2.6
PLER	0.4 ± 0.8	0.1 ± 0.4
URLI	1.6 ± 2.0	0.6 ± 1.1
CHPO	1.3 ± 1.5	0.3 ± 0.5
ELGL	2.5 ± 1.7	0.9 ± 1.1
ERFA	17.7 ± 17.6	7.8 ± 8.7
MESPP	15.2 ± 10.5	2.8 ± 5.1
STPU	5.4 ± 3.0	2.0 ± 1.7

and sham plots differed from closed plots in a similar pattern within each seeding treatment (Appendix S3: Figure S1; Appendix S3: Table S1). Considering this, we chose to exclude sham cage data and not to block data by site to conserve statistical power and simplicity for all subsequent analyses.

3.2.1 | In a diverse grassland system, does vertebrate granivory significantly reduce seedling recruitment?

Vertebrate exclosures clearly altered recruitment rates, however, when assessing all three exclosure treatments, this effect was only statistically significant prior to adjustment for multiple comparisons (MWW test of closed vs. open exclosures, $p=0.086$, $W=174$, BH-adjusted $p=0.26$; Appendix S3: Figure S1). The closed plots had a mean recruitment rate of 0.041 ± 0.022 seedlings/seeds dispersed, compared to 0.028 ± 0.026 seedlings/seeds for the open plots and 0.030 ± 0.024 seedlings/seeds plot for the sham plots.

3.2.2 | How does the intensity of granivory differ between grassland species?

When we compare how each species responded to vertebrate predation, we found that the change in recruitment rate was not similar for all species ($p=0.0089$, ANOSIM $R=0.28$, 9999 permutations). In decreasing order, *A. menziesii*, *Melica* spp. and *S. pulchra* showed a significant decline in recruitment rate when exposed to vertebrates (indicator species test: BH-adjusted $p=0.051$, 0.051, 0.051 respectively; statistic=0.72, 0.63, 0.61 respectively; 9999 permutations; Figure 2).

This suggests that these may have been the most palatable species of those that recruited. Two additional species, *E. glaucus* and *Chlorogalum pomeridianum*, also showed a notable response to vertebrate exclosures, but without significance after adjustment for multiple comparisons (*E. glaucus* and *C. pomeridianum*: indicator species test: BH-adjusted $p=0.13$, 0.22 respectively; statistic=0.50, 0.44 respectively; Figure 2). After examining the response of each species to vertebrate exclosures throughout the experiment (rather than focusing only on the high-diversity treatment, as we did with the indicator species test), we ranked *A. menziesii* as 'very palatable', *S. pulchra* and *Melica* species as 'palatable' and *E. glaucus* as 'moderately palatable' (Appendix S3: Table S2). We gave *C. pomeridianum* a 'neutral/uncertain' palatability ranking, which is most likely a result of its low overall recruitment rate.

3.2.3 | Does the addition of palatable species to a dispersed seed cohort (increasing seed diversity) affect the predation of the original seeds?

The focal cohort experienced more predation when dispersed with additional species in the high-diversity treatment. Using ANOVA as a preliminary assessment for this pattern, we found a significant effect for the seeding treatment factor and marginally insignificant effects for the exclosure treatment factor and the interaction factor (seeding treatment, exclosure and interaction effects: $p=0.083$, 0.19, 0.23 respectively; $F=3.2$, 1.7, 1.5 respectively; $df=1$, 1, 2 respectively, Figure 3). Using pairwise *t*-tests for a more precise evaluation, we found that the focal cohort had a significant increase in mean recruitment rate in closed plots only in the high-diversity treatment. There was no significant change in recruitment due to exclosure for the focal

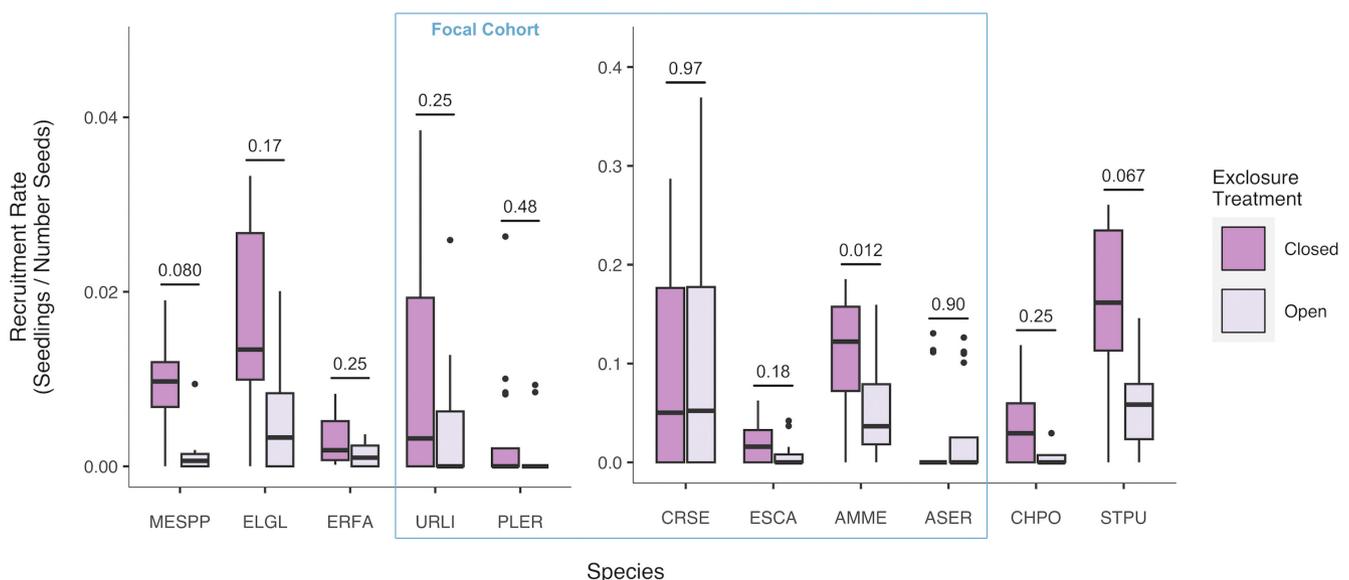


FIGURE 2 Species recruitment rates in closed plots (dark violet) and open plots (light violet), with the results of a two-sample test (*t*-test or MWW test) to detail significant or nonsignificant exclosure response. The significance values were adjusted for multiple comparisons using the Benjamini–Hochberg adjustment. Species are segregated into two y-axis scales. On the left are species with a relatively low recruitment rate, while species with a high recruitment rate are on the right. Species comprising the focal cohort are centred within a rectangular cyan outline.

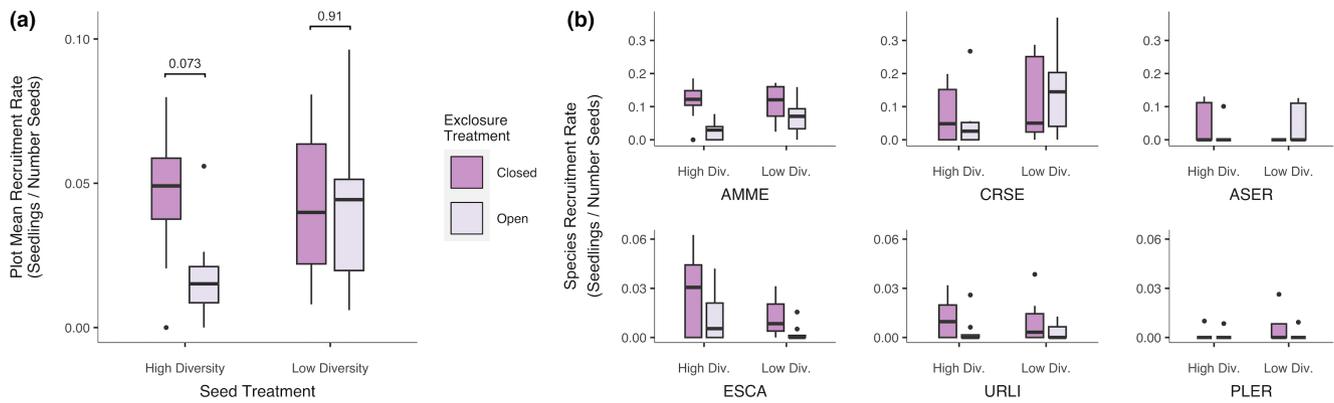


FIGURE 3 (a) (left): Recruitment rate of the focal cohort when alone (low-diversity treatment) and when in the presence of the added cohort (high-diversity treatment). The significance values are from pairwise Student's *t*-tests with adjustment for multiple comparisons, which we summarize in Table 3. (b) (right): Focal species recruitment rates in closed plots (dark violet) and open plots (light violet), with the results of a two-sample test (*t*-test or MWW test) to detail significant or nonsignificant enclosure response. Species are segregated into two *y*-axis scales. The bottom row shows species with a relatively low recruitment rate, while species with a high recruitment rate are in the top row.

TABLE 3 Results of pairwise Student's *t*-tests comparing the closed and open plots of high-diversity and low-diversity seeding treatments in terms of the mean recruitment rate of the focal cohort. The furthest right column lists the significance after the Benjamini–Hochberg adjustment for multiple comparisons.

Comparison	<i>t</i>	<i>p</i>	<i>p</i> -adj
(closed + high div.) versus (open + high div.)	3.06	0.02	0.07
(closed + low div.) versus (open + low div.)	0.12	0.91	0.91
(open + high div.) versus (open + low div.)	-1.80	0.11	0.23
(closed + high div.) versus (closed + low div.)	0.24	0.82	0.91

cohort (closed vs. open in high-diversity and low-diversity treatments: $p=0.07$, 0.91 respectively; $t=3.1$, 0.12 respectively; Table 3). When comparing the open plots of the two seeding treatments, we see a noticeable difference in the mean recruitment rate of the focal cohort; however, this difference was marginally insignificant (Table 3). These results suggest that the presence of the added cohort increased the proportion of seeds from the focal cohort that were lost to vertebrate consumers, which reduced the establishment rate of the focal cohort.

3.2.4 | If predation is altered by seed diversity, does altered seed predation affect all species in the focal cohort equally?

Not all species in the focal cohort experienced increased predation in the high-diversity treatment. When comparing focal species' response to enclosure in the two seeding treatments, we found that predation was unevenly distributed among these species ($p=0.044$; Mantel's $r=0.26$; 9999 permutations). According to the indicator species test, *A. menziesii* experienced a significantly pronounced response to association with the added species, ($p=0.054$; statistic=0.48; Figure 3b). No other focal species had the same magnitude of response as *A. menziesii*. However, *Eschscholzia californica* was the only other species in the focal cohort that was certainly palatable to granivores according to our characterization method (Appendix S3: Table S2). These results

suggest that, while the presence of additional species did alter predation, this was not the case for all focal species.

4 | DISCUSSION

4.1 | A more diverse cohort of seeds increases granivory and strengthens seed selection patterns

We found that increasing the diversity of a seed mix, without keeping the total seed density constant, increased predation, especially for large and palatable species. If this effect is consistent in a restoration context, changes in the composition of a seed mix could unintentionally affect the final composition of the plant community by altering predation patterns. Specifically, adding species to a seed mix could lead to increased predation on the more palatable species, especially if the total density of dispersed seeds is not reduced to account for the additional species. For example, in our study we found that *A. menziesii* experienced increased predation. However, we cannot say whether this effect will still occur if the total seed density is reduced. This is because our experiment used only two additive seeding treatments, so we cannot separate the effects of higher seed density from the effects of a greater seed diversity (Underwood et al., 2014). We focused our experiment on the common scenario in which restoration practitioners choose to increase the

diversity of seeds dispersed without reducing the total seed density. In our experiment, most of the members of the added cohort, namely grass species and *L. succulentus*, had equal or greater seed mass (and equal or greater palatability) than members of the focal cohort, and in the focal cohort, the two largest seeds (*Asclepias eriocarpa* and *C. setiger*) were characteristically unpalatable species with strong chemical defences (Cook et al., 1971; Seiber et al., 1983; Appendix S3: Table S2). This means that the high-diversity treatment had a greater proportion of palatable species, which was conferred mainly by the addition of grass species and perhaps also *L. succulentus*, but we cannot assume that this was the cause of increased predation.

Overall, our study suggests that the more diverse and dense seed mix appears to have amplified the community-filtering effect of granivores by increasing predation for a subset of species. This has important implications for land stewardship efforts that employ seed dispersal to support or restore native plant diversity.

4.2 | Implications for ecological restoration

In California grassland systems, restoring plant diversity is often the primary goal of the work, however, it is constrained by limited budgets and restricted amounts of native seed. Thus, choosing the correct seed mix composition that maximizes the establishment of native plants is critical. However, there is mounting evidence that seed loss to granivores could be constraining success by minimizing establishment rates of species introduced during restoration efforts (Archer & Pyke, 1991; Howe & Brown, 1999; Pearson et al., 2019). Our results suggest that an additional factor complicating direct seeding efforts is that to increase diversity could unintentionally increase the rate at which seed is lost to granivores. Previous research has shown that to increase the density of a seed patch increases seed predation rates (Bowers, 1990; Brown, 1988; Howe & Brown, 1999; Mitchell & Brown, 1990; Ostoja, 2008; Price & Heinz, 1984; Veech, 2001). Our study adds that if the density of dispersed seeds increases as a result of including additional species in a seed mix, the same effect occurs.

This consideration might be most applicable when the most active granivores at a restoration site are only moderately selective. In ecosystems similar to California grasslands, avian granivores (which were the primary granivores in our experiment) have been found to act as post-dispersal filters very weakly in short time-scales, (Howe & Brown, 1999), but can have a strong and persistent effect on plant community structure over longer time-frames (Guo et al., 1995). We might consider granivores that produce this community-filtering pattern to be granivores that forage with moderate to low selectivity. Such granivores may act more strongly as a community filter when presented with a seed mix that includes larger and more palatable seeds. Furthermore, our results suggest that the practice of mixing highly palatable seeds, such as sunflower seeds, with the native seeds to satiate granivores, is unlikely to prevent the consumption of the native seeds (Germain et al., 2013; Riebkes et al., 2018). Rather, this practice

could lead to granivores consuming native seeds at a greater rate than before.

Importantly, the species that were most heavily foraged from our seed mixes (Grass spp., *A. menziesii*, *E. californica*) happen to be some of the most common species being restored in California. Within California grasslands, native grasses are known to be strongly predated by granivores after direct seeding in restoration, even when the surrounding community is dominated by large-seeded and palatable invasive annual grasses such as *Avena* and *Bromus* species (Borchert & Jain, 1978; Espeland et al., 2003; Gurney et al., 2015; Orrock et al., 2009). Our results suggest that the presence of native grasses in a seed mix could also increase predation on other native species that are not otherwise strongly predated ('associational susceptibility'). Species may be more likely to experience increased predation when dispersed with a diverse and palatable suite of other species if they themselves are already at least somewhat palatable to granivores. These may include species that are frequently targeted in restoration for their cultural/aesthetic value (in this system: *E. californica*, *L. succulentus* and *S. columbariae*), for their strong competitive ability against dominant invasive species (in this system: native grasses; Corbin & D'Antonio, 2004), or for their low fecundity (in this system: perhaps bulb species such as *C. pomeridianum*) and/or endangered status (in this system: *A. menziesii* as a proxy for certain *Amsinckia* species; Espeland et al., 2003).

Overall, our research suggests a few considerations for practitioners when planning how to introduce species to a restoration site. One suggestion is that practitioners could temporally separate when palatable and less-palatable species are dispersed. Granivores may perhaps focus their search on the most recently dispersed seeds. To date, this is a presumption that has not been studied, but if it is true, dispersing a more palatable species several weeks after a low- and/or moderately palatable species may reduce the predation of one or all of the species. For example, in our study we would disperse a grass seed after a small-seeded forb species. Practitioners could then apply the same concept to cohorts of seeds rather than individual species. Sequentially dispersing several distinct cohorts of seed species over a series of weeks rather than dispersing all of them together at once may perhaps reduce seed consumption to the level of intensity and selectivity that would occur for each unique cohort under completely isolated dispersal conditions. To our knowledge, this tactic has not yet been studied, but perhaps it would be most effective if species/cohorts are dispersed in a staggered pattern of *low-high-low-high* palatability: First, disperse the *least* palatable species, then at least 1 week later, disperse the *most* palatable species, then the *second-least* palatable species, and then the *second-most* palatable species, followed by the moderately palatable species last. This tactic might be beneficial even when drill seeding equipment is available, as some granivore species dig up drilled-in seeds (Reynolds, 1950, 1958).

A second tactic would be to introduce the most palatable species as seedling plugs and disperse the rest of the intended species

as a cohort of seeds that are at most only moderately palatable. This might be a great tactic for California grasslands, because many of the most palatable species are grasses, which generally establish more reliably as out-planted seedlings rather than broadcast seeds. However, sometimes the most palatable species in a restoration cohort are species that either (a) do not grow well in the greenhouse, (b) do not often establish from seedling plugs or (c) are species whose seeds are available so abundantly and recruit after being broadcast so reliably that to grow them in the greenhouse would be an unwise investment. For these cases, this second tactic would not be preferable.

A third tactic would be to disperse all the intended species together, but with an overwhelming deterrent among the dispersed seeds. For example, including chilli flakes in dispersed seed has previously been shown to reduce granivory (see, e.g. Pearson et al., 2019). An alternative would be to include a very unpalatable species at a very high density in place of the chilli flakes. This tactic has not yet been studied, to our knowledge, but perhaps such a high density of a species readily avoided by granivores would have a strong deterring effect enough to overwhelm the attractive effects of a dense and diverse suite of palatable seeds. Including an overwhelming deterrent (seed or spice) among the dispersed seeds would most likely be the least expensive of the three tactics we offer here. However, more research is needed to determine how each of these options performs in different ecosystems, where different suites of seed species interact with different communities of granivores, in which different granivores express unique selective foraging behaviours.

Overall, our study suggests that practitioners might need to be more thoughtful about their plant restoration choices beyond just thinking about what they want to see at the end of their project timeline. Seed dispersal deserves to be given as much thought as other aspects of restoration planning. The natural rhythm of most plant communities does not often involve a synchronous dump of all species' seeds on the same day—in most communities, even in communities with seed-masting species, the members of the community have a somewhat-sequential timing of seed dispersal throughout the season, just as the flowering times in a plant community are quasi-sequential. Practitioners can mimic this when planning the composition and timing of seeds to be dispersed for restoration. Essentially, we are advocating for an approach to plant restoration that seeks to understand and incorporate the subtle and complex dynamics of any given ecosystem while acting as a steward.

AUTHOR CONTRIBUTIONS

Benny J. Drescher designed and conducted the field experiment and data analysis and drafted all portions of the manuscript except the introduction, which he revised following Madeline Nolan's first draft. Madeline Nolan was the primary editor and collaborator in the drafting of the manuscript and contributed to all parts of the research. Benny J. Drescher created the graphical abstract using Dream by WOMBO artificial intelligence through the website interface (Wombo Studios, Inc., 2023). This research was carried out in

our home country; however, we are settlers of stolen land. Although we did discuss our research with some of the local stakeholders, we failed to discuss our research with the indigenous Chumash people until after its completion and we strive to correct this failing for future endeavours.

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CONFLICT OF INTEREST STATEMENT

We have no conflict of interest related to this work.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and analytical R script are available from the Figshare Digital Repository: <https://doi.org/10.6084/m9.figshare.19194962.v4> (Drescher, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Experimental methods supplement.

Appendix S2. Analytical methods supplement.

Appendix S3. Additional results supplement.

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