

## RESEARCH ARTICLE

# Species provenance and traits mediate establishment and performance in an invaded grassland

Lachlan S. Charles<sup>1</sup>  | John L. Maron<sup>2</sup>  | Lorelee Larios<sup>1</sup> 

<sup>1</sup>Department of Botany and Plant Sciences, University of California, Riverside, CA, USA

<sup>2</sup>Division of Biological Sciences, University of Montana, Missoula, MT, USA

## Correspondence

Lachlan S. Charles

Email: [lachlan.charles@uqconnect.edu.au](mailto:lachlan.charles@uqconnect.edu.au)

## Funding information

National Science Foundation, Grant/Award Number: DEB-1553518; NSF Postdoctoral Research Fellowship in Biology, Grant/Award Number: 1309014

Handling Editor: Laura Yahdjian

## Abstract

1. In many invaded grasslands, dominant exotic species can produce large amounts of litter that modify local abiotic conditions and species' interactions. These novel conditions can reduce native species abundance and promote the persistence of exotic species, yet the strength of this disparity may be influenced by how consumer pressure interacts with litter accumulation. Consumers may exacerbate this disparity by preferentially targeting native species or by promoting heterogeneity in microhabitats due to their movement and small-scale ground disturbances that favours fast growing exotic species. How species respond to litter accumulation and consumer pressure may depend on either evolutionary differences, whereby exotics species may benefit from a lack natural predators, or by functional differences, in which species' physiological traits may confer fitness advantages to low-light conditions or herbivory or granivory pressure.
2. We examined the impact of litter presence and small mammal herbivory on the establishment and reproduction of functionally diverse exotic versus native species seeded across sites that naturally vary in resource availability in an annual invaded California grassland. We assessed whether seed mass and leaf nitrogen content (LNC) were predictive of successful establishment and reproduction.
3. Litter accumulation affected exotic and native species differently, with litter significantly decreasing native recruitment and reproduction, while exotics were largely unaffected. Small mammals had a slight positive effect on the establishment of native species when litter was present but did not influence exotic species. Regardless of species provenance, larger seeded species established at a higher density while species with lower leaf nitrogen content had a higher density of reproductive individuals. Native species that successfully established and reproduced were functionally different in LNC than the resident community, while successful exotic species were functionally more similar to the resident community in LNC.
4. Our study demonstrates that exotic species outperformed native species regardless of the presence of litter or herbivory pressure. Without the removal or thinning of litter, it is likely that exotic species will continue to dominate, resulting in positive feedback that further favours the persistence of exotic species within this invaded grassland system.

## KEYWORDS

context dependency, exotic species, functional traits, grasslands, invasion, leaf nitrogen, litter, seed mass

## 1 | INTRODUCTION

Invasion success is often determined by multiple interactions between invading and resident species within recipient communities (Seabloom et al., 2003; Thebaud et al., 1996). The strength and frequency of these interactions, however, can change as the composition of a community shifts towards greater exotic dominance, creating conditions that feed back to disproportionately favour the establishment of other exotic species over native species (e.g. invasional meltdown; Richardson et al., 2000; Simberloff & Von Holle, 1999). This is a common scenario in invaded annual grasslands, where dominant fast-growing exotic species produce large quantities of litter that create a novel low light/resource environment (Facelli & Pickett, 1991; Loydi et al., 2013) that inhibits native species recruitment, growth and biomass (Molinari & D'Antonio, 2020), reinforcing exotic dominance (Mariotte et al., 2017).

The positive feedback between litter accumulation and invasion may be driven by two key mechanisms. First, native and exotic species can differ in their responses to litter accumulation due to intrinsic differences in their evolutionary history (Cadotte et al., 2010). Dominant exotic species responsible for litter accumulation, as well as newly colonizing exotics, may be adapted to high litter environments, whereas native species may be poorly adapted to these conditions and therefore suffer under high litter (Mariotte et al., 2017; Simberloff & Von Holle, 1999). Second, differences among species in life-history strategies can also influence how litter filters species. These differences in performance are underpinned by functional traits (or combinations of traits) that provide distinct trade-offs between survival and growth in a given environment (Larson & Funk, 2016; Violle et al., 2007). Trait variation among species, therefore, may mediate how species respond to litter accumulation, independent of their provenance. For instance, low light conditions under litter may benefit the germination of both exotic and native large-seeded, slow-growing resource conservative species (Fynn et al., 2011; Leishman et al., 2000; Letts et al., 2015; Moles & Westoby, 2004). These dynamics may interact with other ecological processes that mediate successful establishment such as small mammal herbivory to differentially impact exotic versus native colonization.

Abundant small mammals such as voles may promote or inhibit the effects of litter accumulation, through granivory and/or herbivory (Batzli & Pitelka, 1971; Mittelbach & Gross, 1984; Olff & Ritchie, 1998; Pearson et al., 2011). These interactive effects may similarly be a function of evolutionary history, whereby small mammals may preferentially consume native species, reducing their establishment and reproduction more than exotic species (Pearson

et al., 2011). Alternatively, generalist consumers may promote heterogeneity in microhabitats due to their movement and small-scale ground disturbances (i.e. runways or burrow entrances for voles or mounds for gophers) that can either promote the colonization of less abundant native species (Fehmi & Bartolome, 2002; Questad & Foster, 2007) or the colonization of ruderal exotic species (Hobbs & Mooney, 1991). The net effect of consumers and litter on establishment may ultimately be mediated by specific traits. For instance, while litter may favour the recruitment of large-seeded, slow-growing species, the seeds of these species are often preferred by small mammals due to their high energy content (Germain et al., 2013; Howe & Brown, 2000; Howe et al., 2002). Thus, the combined effect of litter and herbivory might result in limited establishment across all seed sizes (Reader, 1993).

The effect of litter accumulation and consumer pressure on establishment may be further mediated by underlying variation in resource availability. High-resource areas are often more vulnerable to invasion (Huenneke et al., 1990) yet are also areas where the positive effects of herbivory on diversity are more pronounced (Eskelinen et al., 2016; Hillebrand et al., 2007; Larios & Maron, 2021). Litter accumulation is often promoted in high-resource areas because they favour productive, resource acquisitive species (Eskelinen et al., 2012; Facelli & Pickett, 1991; Pyšek & Richardson, 2007). Copious litter accumulation can in turn promote small mammal activity (Larios & Maron, 2021; Liu et al., 2018; Ostfeld et al., 1997), because some small mammals predominately forage in areas of high litter cover to decrease predation risk (Batzli & Pitelka, 1970; Pusenius & Ostfeld, 2000). Taken together, litter accumulation, consumer preference and resource availability may influence species differently, with responses depending on species provenance or functional strategies.

Although many studies in natural systems (i.e. not planted assemblages) have examined the influence of these factors on rates of natural colonization of exotics versus natives (Hejda et al., 2009; Lemoine et al., 2016), few control for species' propagule pressure. This limits our ability to tease apart the mechanisms whereby litter accumulation influences native versus exotic establishment and reproduction (Godoy, 2019). Likewise, few studies assess species' responses to experimentally manipulated litter and herbivory from a trait perspective (but see Korell et al., 2017; Maron et al., 2012 for perennial grasslands). Therefore, teasing apart the relative contribution of evolutionary history versus species' traits in mediating species responses to litter and herbivory and whether this dictates successful establishment into an invaded system is key for identifying strategies for reintroduction of native species. Given that successful establishment of species within a community is the

cumulative effect of multiple biotic and abiotic filters over the life cycle of the plant, assessing how species respond to these filters at different life stages may help explain why some species and which traits are more successful at establishing within a community than others (Laughlin, 2014).

Here we examine the individual and interactive effects of invader litter and small mammals on native and exotic species establishment across sites that naturally vary in resource availability. To do this, we added seeds of either native or exotic species into plots where we manipulated both litter and rodent presence across annual invaded grassland sites with varying resource availability. Species in both native and exotic seed mixes were selected to encompass a broad range of seed mass that span the continuum of resource conservative or acquisitive life-history strategies, with similar seed mass distributions in each seed mix. Importantly, assessing colonization success and subsequent performance of native and exotic species with similar trait distributions allows us to determine the relative contribution of species provenance and functional traits in explaining species responses to litter and consumer pressure. We predict that if both exotic and native species display a similar suite of traits (or axes of functional specialization) that confer advantages to particular biotic and abiotic filters, then we would expect provenance is less likely to drive species establishment. Alternatively, if the presence of litter and/or consumer pressure benefit exotic species over natives, regardless of functional strategies, then provenance may be an important predictor of species success in invaded systems. Lastly, to provide some insight as to whether the successfully colonizing species either have similar or different traits to the resident community, we also evaluated the extent trait differences between the added species and resident community impacted species fitness. Here in accordance with limiting similarity (MacArthur & Levins, 1967), we expect that large trait differences may confer fitness advantages to introduced species over those species with similar traits to the dominant invaded community.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

This study was conducted in annual grasslands at the University of California Sierra Foothill Research and Extension Center (SFREC), located in Browns Valley, California, USA (39°15'N, 121°17'W). The site has a Mediterranean climate, with a cool wet growing season (September–May) and host dry summers (June–August). Temperature and precipitation over the course of the experiment varied over the three growing seasons: 2014–2015, 2015–2016 and 2016–2017, with 454 mm (mean 15.5°C), 625mm (mean 14.9°C) and 978 mm (mean 14°C) recorded, respectively (PRISM Climate Group, 2004). Vegetation at the site is dominated by exotic annual species, with low abundances of native annual species. The most abundant exotic species, *Elymus caput-medusae*, produces large amounts of litter, which remains on the landscape due to slow

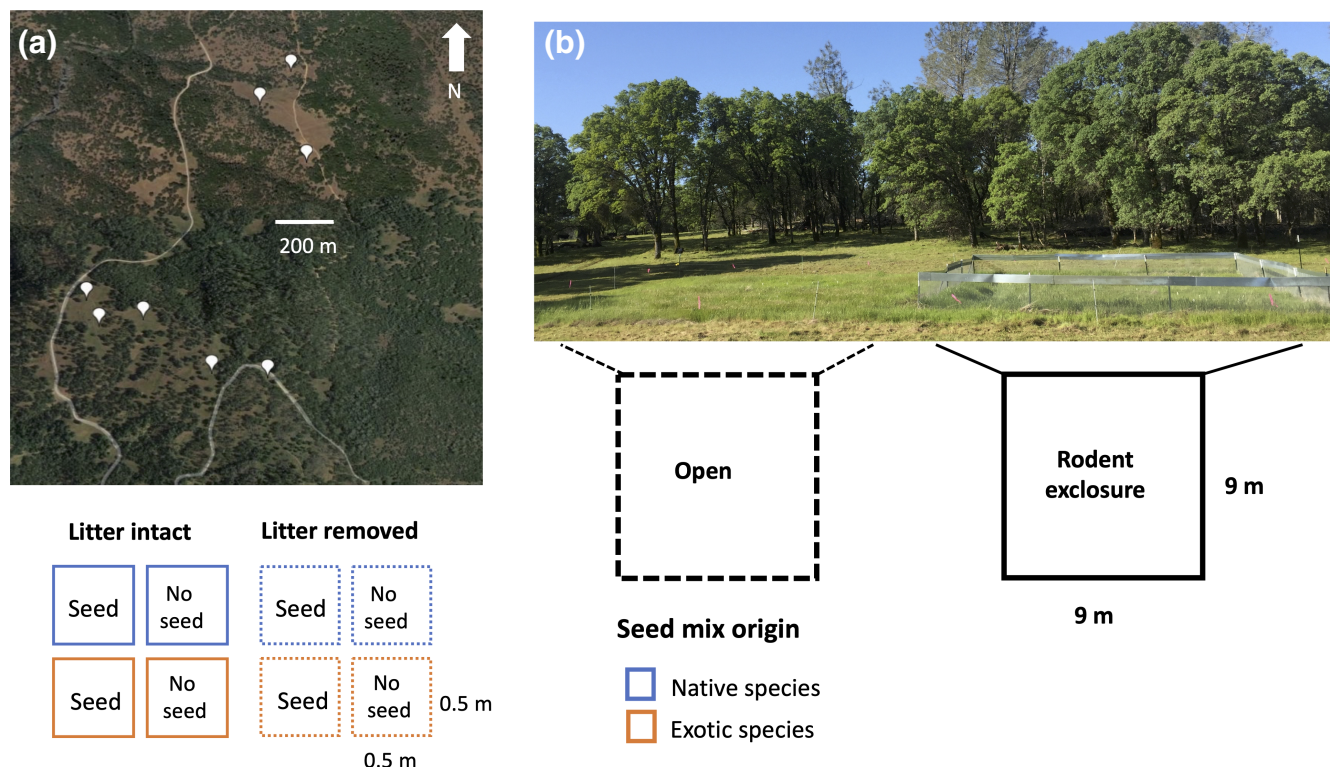
decomposition and low palatability (Nafus & Davies, 2014). Other dominant exotics species include *Avena barbata*, *Bromus hordeaceus* and *Erodium botrys* (nomenclature follows Baldwin et al., 2012). Plant consumers in this system include mule deer *Odocoileus hemionus* and small mammals such as field voles *Microtus californicus* and gophers *Thomomys bottae* (Block & Morrison, 1990).

### 2.2 | Experimental design

To assess the influence of litter, small mammals and resources on native and exotic species recruitment and reproduction, in the summer of 2014, we established experiments at eight sites at either end of a productivity/soil resource gradient. Four sites were characterized by low soil nitrogen and low plant productivity (but high micro-nutrients), whereas the remaining four sites had high soil nitrogen and greater plant productivity (please see Larios & Maron, 2021 for details on how site productivity was quantified). Sites were separated by at least 150 m to avoid spatial autocorrelation and to ensure we were sampling separate small mammal communities (Figure 1A). Within each site, we either excluded rodents or not within paired 9 m × 9 m plots, one of which was fenced to exclude small mammals and the other which remained unfenced to allow small mammal access (Figure 1B). Electric fences enclosed both paired plots to prevent herbivory or disturbance from cattle. Enclosures were checked monthly, to ensure no rodent disturbance was present. To assess small mammal activity within the treatment subplots (see below for details), percent visual cover estimates of small mammal burrowing activity and runway construction were conducted in 2016.

Within each pair of plots, we established 16 subplots (0.5 m × 0.5 m) that were randomly assigned to one of eight unique treatments (Figure 1). The eight treatments represented a factorial combination of (a) litter treatment (removed or left intact), (b) seed addition (yes or no) and (c) Origin of species in seed mix (native or exotic). The first set of 8 subplots were seeded in each site in summer 2014 for a total of 64 subplots. The second set of 8 subplots were seeded in the summer of 2015 and provided a replicate over time (total of 128 subplots sampled over 2 years).

Species within the seed mix (Table 1) all occurred on the SFREC reserve. We did not include the dominant litter producing *E. caput-medusae* in the exotic seed mix due to its high invasive status. The seed mixes were constructed to represent a similar trait distribution for seed mass with similar community-weighted means and functional diversity. Initial trait values for species were obtained from published sources (Anacker & Harrison, 2012; Fernandez-Going et al., 2013; Harrison & Grace, 2007), with missing seed mass data obtained from the Kew database (Royal Botanic Gardens Kew, 2017) and scientific literature. We added 75 seeds for each species within each seed mix, for a total of either 1,275 or 1,200 seeds per 0.5 m × 0.5 m for the native ( $n = 17$ ) and exotic ( $n = 16$ ), respectively. While we did not assess germination rates of species prior to seeding, 13 of the 17 commercially sourced species in the native mix have germination and viability rates higher than 45% and



**FIGURE 1** (A) Location of eight experimental plots within the University of California Sierra Foothill Research and Extension Center (SFREC). (B) Schematic of experimental design for a single replicate (block). Within each block, two 9 m × 9 m plots were established either allow (black dashed line) or exclude (solid black line) rodent herbivory/granivory. Within each pair of plots, 16 subplots (0.5 m × 0.5 m) were assigned one of 8 unique treatments: litter left intact (solid line) or removed (dotted line), crossed with either a seed mix (seed mix type denoted by different colours)

67%, respectively. Seed mixes were added in July and August for the subsequent growing season (e.g. August 2014 for Spring 2015 sampling). This mid-summer timing ensured that we were accurately capturing summer granivory.

We assessed the colonization of each species in every subplot by counting the number of individuals of each added species that established at peak biomass in April–May 2015 and 2016. We assessed reproduction by counting the number of reproductive stems of added species. To capture differences in phenology among species, we sampled all plots once a week between April and May. We estimated the total number of seeds produced by individuals of each added species by first randomly selecting 2–4 individuals per species within four different subplots (two subplots in the rodent exclusion and two subplots in the open plot), to obtain a total of 8–16 individuals per species per site. For each individual, we then estimated per capita seed production by counting all viable seeds. If seeds were not yet present, we counted the total number of spikelets or inflorescences for an individual and multiplied this number by an estimated number of seeds per spikelet/inflorescence. This multiplier was either obtained by field estimates of fecundity of individuals outside of plots that produced seed or extracted from a published source. If species did not have at least eight individuals within seed addition subplots, we sampled all individuals that were present.

To evaluate species responses based on functional traits, we measured functional traits that are known to impact germination

and growth, which included seed mass (Moles & Westoby, 2004), specific leaf area (SLA), leaf water content (LWC), maximum plant height, leaf nitrogen concentration (LNC) and carbon to nitrogen ratio (C:N) (Navas & Violle, 2009). Although we used an initial published trait dataset to assemble our seed mixes, we took field measurements of traits from our study site to investigate trait-based responses to our experiment. We measured traits on 5–10 individuals of most species outside the treatment plots, avoiding trait estimations in experimental plots where treatments could influence trait expression. However, of the total 33 seeded species, six species could not be found outside of the treatment plots, and for these species we had to sample individuals from plots representing each of the treatment combinations. For each species, we calculated a mean trait value (see Larios & Maron, 2021 for full methodology and trait data). Species mean values were used as predictor variables in models described below. To assess the extent that trait differences between the added species and the resident community impacted the fitness of added species, we calculated community-weighted mean trait indices of the resident community. First, we estimated the percent cover of resident species (species that were not included in the seed mix but recruited naturally) within all seed addition subplots in 2015 and 2016. Species cover was visually estimated for each species in every subplot, and total cover was allowed to go over 100 to allow for multiple canopy layers. Second, we sampled traits for resident species, following the methodology to that of the seeded



Seed size	Native	Exotic
Small <0.00051 g	<i>Achillea millefolium</i> *	<i>Petrorhagia dubia</i> *
	<i>Clarkia purpurea</i> *	<i>Trifolium dubium</i> *
	<i>Lasthenia californica</i> *	<i>Festuca bromoides</i> *
	<i>Clarkia gracilis</i> *	<i>Briza minor</i> *
	<i>Gilia tricolor</i> *	<i>Senecio vulgaris</i> *
Medium <0.00051 g < X < 0.004 g	<i>Elymus glaucus</i>	<i>Bromus hordeaceus</i>
	<i>Trifolium microcephalum</i>	<i>Festuca perennis</i>
	<i>Trifolium willdenovii</i>	<i>Trifolium hirtum</i> *
	<i>Amsinckia menziesii</i>	<i>Briza maxima</i>
	<i>Plantago erecta</i>	<i>Hordeum murinum</i>
	<i>Uropappus lindleyi</i>	
Large <0.004 g	<i>Galium aparine</i> *	<i>Avena barbata</i>
	<i>Lupinus bicolor</i>	<i>Bromus diandrus</i>
	<i>Stipa pulchra</i>	<i>Carduus pycnocephalus</i>
	<i>Achyraea mollis</i>	<i>Avena fatua</i>
	<i>Asclepias fascicularis</i>	<i>Erodium botrys</i> *
	<i>Lupinus succulentus</i>	<i>Trifolium subterraneum</i>
Functional dispersion	0.725	0.728
Seed mass community	0.0041	0.0048

**TABLE 1** Summary information of seed mixes used in the seed addition experiment, including functional trait metrics (CWM, community weighted mean; FDis, functional dispersion). \* Indicate species that were excluded from the analysis (see methods). Note that the diversity of the seed mixes varied due to seed availability

species (see above). Third, we calculated the resident community-weighted mean for seed mass, SLA, LWC, LNC and C:N within all seed addition subplots spanning each treatment combination and year. Plant sampling did not require permits or licences within the SFREC reserve.

## 2.3 | Analysis

### 2.3.1 | Native and exotic species responses to litter, small mammals and site resource availability

We assessed the individual and interactive effects of litter and small mammals on native and exotic species performance, quantified as (a) the probability of species establishment, (b) establishment density of a species, (c) number of reproductive stems and (d) seed output. We modelled these variables as a function of site resource availability (low or high), small mammal presence (present or excluded), litter (litter or litter removed) and seed mix origin (native or exotic). Four-way interactions between species origin, small mammals, litter and site productivity were included as fixed effects in all models. Plot, nested within site along with sampling year, was included as random effect in all models to account for the split-plot design. To evaluate how species traits mediated these responses, we additionally included seed mass and LNC as predictor variables within the establishment and reproduction models, respectively. We did not include other traits in our models due to the high correlation among plant traits variables (i.e. height was correlated to SLA ( $p = -0.47$ )

and LWC ( $p = -0.58$ ), while LNC and C:N ratio were also correlated ( $p = -0.89$ )). We were not able to include interactions terms between our experimental treatments and plant traits due to statistical limitations (i.e. our sample size was not large enough to accurately fit such a complex model). To summarize the overall effects of our seed addition treatment, we used a Wilcoxon test to assess how native and exotic species recruitment, density and seed output differed across the study. We used the Wilcoxon test to account for the non-normal distribution of species recruitment, density and seed output, with species origin used as a fixed factor in all tests.

Probability of species recruitment (binary response, 1 = recruited, 0 = did not recruit) was modelled using a generalized linear mixed-effect model with logit-link function and binomial error distribution, using the *LME4* package in R (Bates et al., 2011). Due to the presence of zero values for recruitment density (59%), number of reproductive stems (15%) and seed output (15%), potential zero inflation was assessed by comparing recruitment density, number of reproductive stems and seed output models with different error distributions: negative binomial with log-link function and zero inflation parameter, negative binomial with log-link function and Poisson with a log-link function, respectively, using the *GLMMADMB* package in R (Skaug et al., 2016). AICc values indicated that negative binomial models with zero-inflated parameters were best for all response variables.

We used our no seed added plots to account for natural establishment. First, for subplots where our no seed plot had greater stem counts for a species than the seed addition plot, we set establishment to 0 stems to be conservative about natural recruitment.

Second, for several exotic species ( $n = 7$ ), natural establishment was consistently high, and we could not accurately determine colonization. These species were predominantly small seeded species; therefore, to keep a balanced comparison between the added native and exotic species, we dropped native species that exhibited similar seed size. Our resulting models reflected the response of eleven native and nine exotic added species, although models with the full set of species generated similar results (not reported). Seed mass and LNC were all log transformed to meet the assumptions of linear regression. Full models containing all relevant explanatory variables were simplified by backward stepwise selection.

### 2.3.2 | Trait differences between colonizing species and resident invaded communities

To assess whether the traits of colonizing species that successfully recruited were similar to or differed from the resident invaded communities, we first calculated trait differences of seed size and LNC between each species present in the reduced seed addition groups from the community-weighted mean (CWM) of resident invaded communities (i.e. trait difference = species mean trait value – CWM value; thus, a negative trait difference indicates higher trait values of the added species compared to the resident community and vice versa for positive trait differences). The resident community consisted of species that were not present in the reduced seed mix (i.e. species that established either from the soil seed bank or from dispersal events). Resident CWM for each trait was calculated for each subplot using `FD` package in `R` (Laliberté & Legendre, 2010; Laliberté et al., 2014). We modelled the trait difference of LNC between invading species and the resident community as a function of site resource availability (high or low), small mammal presence (present or absent), litter (litter or removed) and seed mix origin (native or exotic), using linear mixed-effect models. We did not model the trait difference of seed mass between the invading species and the resident community, as we excluded small seeded species from the seed addition group (see above). Excluding the smaller seed species may lead to inflated differences between seed mass of the added and resident community, with small seeded species being dominant in the resident community. Three-way interactions between species origin, small mammals and litter were included as fixed effects in all models. Plot nested within site was also included as a random effect (Bates et al., 2011). Differences between significant explanatory variables within all best supporting models were assessed using post-hoc pairwise Tukey test using the `ghlt` function in the `MULTCOMP` `R` package (Hothorn et al., 2008). To determine whether LNC trait differences ultimately impacted the seed output of an added species in the experiment, we modelled average species seed output as a function of small mammal presence (present or absent), litter (litter or litter removed), and seed mix origin (native or exotic) and the trait difference for LNC. The trait difference of

LNC was selected as a predictor variable as variation in LNC was important in explaining reproduction responses of added species (see below). As above, we used a generalized linear mixed model with log-link function. To assess whether the resident community composition differed between treatments, we modelled resident species cover as a function of site resource availability (high or low), small mammal presence (present or absent) and litter (litter or litter removed) using a perMANOVA using the `VEGAN` `R` package (Oksanen et al., 2020). All data analysis was conducted using the `R` statistical software package version 3.3.3 (R Development Core Team, 2010).

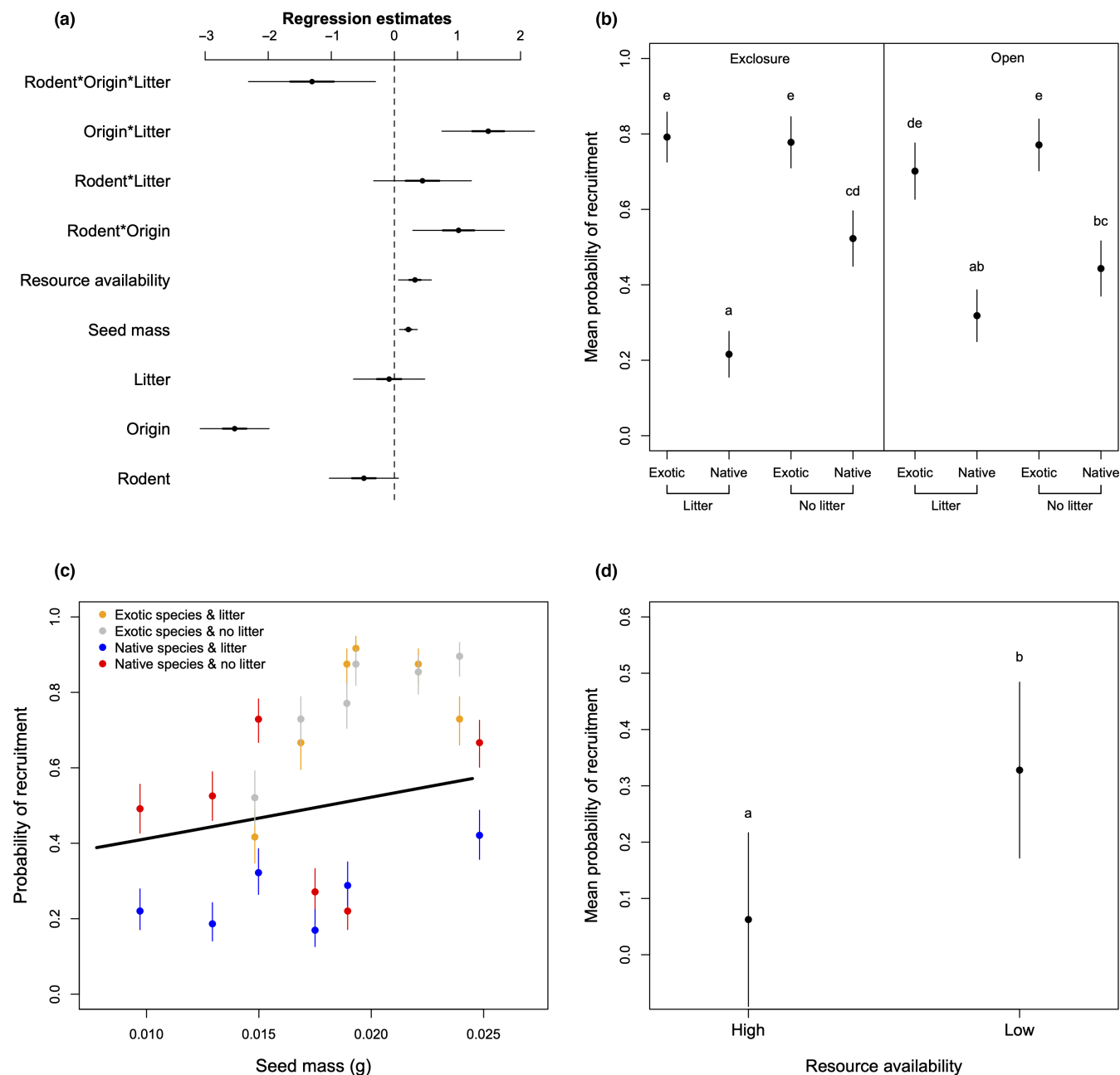
## 3 | RESULTS

Establishment and reproduction varied widely among added species and differed considerably based on species' provenances (Table S1). The proportion of species that established in each seed mix was significantly higher for exotics (76%) compared with natives (37%, Wilcoxon Signed Rank Test  $p > 0.0001$ ) as were mean stem densities, 14 stems per 0.25 m<sup>2</sup> for exotics compared to 2 stems per 0.25 m<sup>2</sup> for natives (Wilcoxon Signed Rank Test  $p = 0.00063$ ). The percentage of species that established and produced seed was significantly higher for exotic species (87%), compared with native species (64%, Wilcoxon Signed Rank Test  $p > 0.0001$ ). Of the species that did reproduce, exotic species produced significantly more seed (mean 382 seeds per 0.25 m<sup>2</sup>) than native species (mean 39 seeds per 0.25 m<sup>2</sup>, Wilcoxon Signed Rank Test  $p > 0.0001$ ). Surveys of small mammal activity conducted in open subplots in 2016 revealed that vole activity was greater in plots with litter compared to bare plots (Tukey's Post-hoc test,  $p = 0.033$ ). There was no vole activity recorded in the rodent enclosure plots.

### 3.1 | Species establishment responses

Probability of establishment was best explained by seed mass, site resource availability and the interaction between species origin, litter and rodent presence (Table S2, Figure 2A). Exotic species displayed higher establishment probabilities regardless of litter or rodent treatments, while the probability of establishment for native species decreased significantly in the presence of litter and in the absence of rodents (Tukey's Post-hoc test,  $p > 0.001$ , Figure 2B). The probability of establishment increased with increasing seed mass (Figure 2C). Native and exotic species establishment was greater in low-resource sites compared to high-resource sites (Tukey's Post-hoc test,  $p = 0.003$ , Figure 2D).

Establishment density was best explained by the interaction between species origin, litter and rodent presence (Table S3, Figure 3A). All species, regardless of origin, established at higher densities in the absence of litter (Figure 3B). Exotic species had significantly higher establishment density compared to native

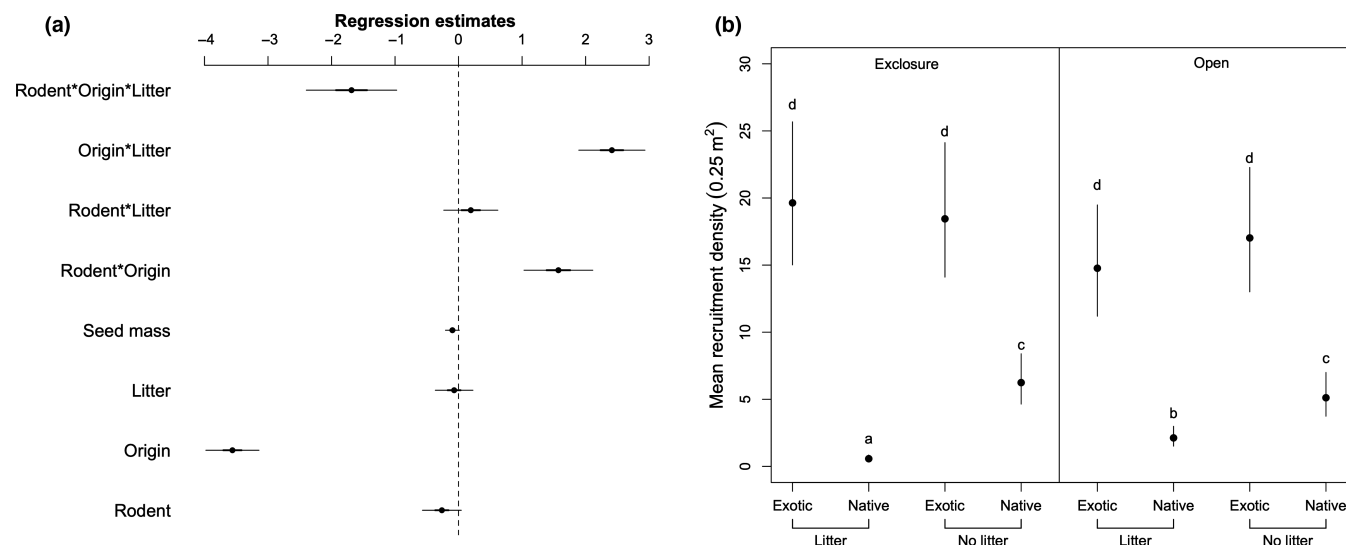


**FIGURE 2** (A) Coefficient plot for the probability of recruitment model. Points are standardized coefficient estimates. Thick, inner bars represent  $\pm 1$  standard error and thin, outer bars  $\pm 2$  standard errors. (B) Probability of seedling recruitment in relation to the interaction of species origin (Native/Exotic), litter treatment (litter /litter removed) and small mammal treatment (excluded/present). (C) Probability of seedling recruitment in relation to the seed mass (g) and the interaction between species origin and litter treatment. Points for the interaction between species origin and litter treatments are mean probabilities calculated from eight bins of ordered binary values. All bars are associated standard errors on the probability scale. (D) Mean probability of seedling recruitment in relation to site productivity. All bars are associated standard errors on the probability scale. Letters denote significantly different groups ( $p < 0.05$ ), based on pairwise post-hoc tests

species (Tukey's Post-hoc test,  $p < 0.001$ , Figure 3B). While the presence of rodents did not influence establishment density of exotic species, native species density increased in the presence of rodents, but only in plots with litter present (Tukey's Post-hoc test,  $p < 0.001$ ; Figure 3B). Unlike establishment probability, both native and exotic species recruitment density were not influenced by seed mass.

### 3.2 | Species reproduction responses

The number of reproductive stems and seed output was best explained by leaf nitrogen content (LNC) and the interaction between species origin and litter (Tables S4 and S5, Figure 4A and Figure S1a, respectively). Exotic species had a higher number of reproductive stems and seed output than native species but were not influenced



**FIGURE 3** (A) Coefficient plot for recruitment density model. Points are standardized coefficient estimates. Thick, inner bars represent  $\pm 1$  standard error and thin, outer bars  $\pm 2$  standard errors. (B) Mean stem density in relation to the interaction of species origin, small mammal and litter treatments. All bars are associated standard errors on the probability scale. Letters denote significantly different groups ( $p < 0.05$ ), based on pairwise post-hoc tests

by litter treatment (Figure 4B, Figure S1b). Native species displayed a small, but significant increase in the number of reproductive stems and seed output in the absence of litter (Tukey's Post-hoc test,  $p < 0.0036$ , and  $p < 0.0037$ , respectively). There was a negative relationship between LNC and the number of reproductive stems and seed output, with species with higher LNC experiencing decreased reproductive stems and seed output (Figure 4C and Figure S1c, respectively). The presence of small mammals did not influence the number of reproductive stems or seed output for either native or exotic species.

### 3.3 | Trait differences between added species and resident communities

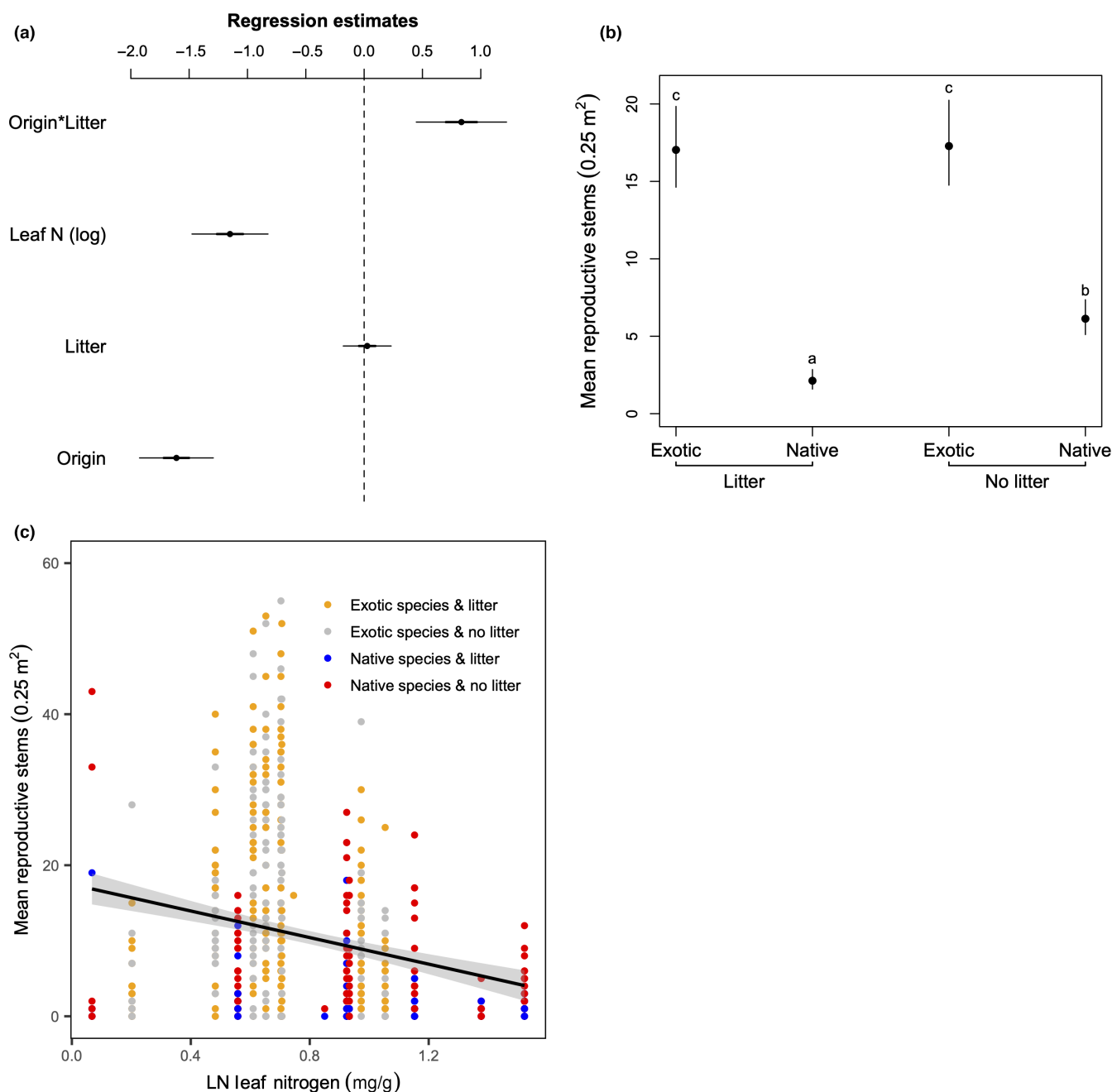
Overall, we recorded 50 resident species across all seed addition subplots. Resident species mean cover varied between species (Table S6) and was significantly different between litter treatments and site available resources (both  $p < 0.0001$ , Table S7). The average difference in LNC of added native and exotic species that reproduced varied widely from the resident community and each other. Native species displayed a larger average difference in LNC than the resident community regardless of litter treatment ( $p < 0.001$ ), while exotic species displayed lower or marginally larger average difference in LNC than the resident community ( $p = 0.006$ ) in the presence or absence of litter, respectively (Figure 5A, Table S8). LNC differences between added species and the resident community also explained seed output and varied by species origin, regardless of the presence of litter. Exotic species with mean LNC similar or marginally lower than the resident community displayed higher fecundity. In contrast, native species with higher mean LNC than the resident community displayed lower fecundity (Figure 5B, Table S9).

## 4 | DISCUSSION

Our results demonstrate that successful colonization into a invaded annual grassland is influenced by multiple processes that disproportionately favour exotic species. Controlling for propagule pressure via seed addition, we found that the establishment and reproduction of added native species significantly decreased in the presence of exotic litter, as has been previously documented in other systems (Johnson et al., 2018; Molinari & D'Antonio, 2020). However, this was not the case for added exotic species, which were not sensitive to the presence of exotic litter. Small mammals had a slight positive effect on the establishment of added native species when litter was present. These colonization dynamics were mediated by the functional traits of the species—seed mass for establishment and leaf nitrogen for reproduction. The degree to which a species' trait overlapped with the resident community was a strong predictor of mean seed output for added species, where species that had more similar LNC to the resident community produced more seeds. Together, these results suggest that invaded annual grassland can favour the establishment of exotic over native species and that while plant traits do mediate colonization dynamics, exotic species tend to outperform native species regardless of these traits.

Litter from the invaded community negatively affected native species performance but had no effect on exotic species performance. The negative effects of litter on native species were observed at multiple life stages, including the probability of establishment and the density of established and reproductive individuals. Negative litter effects on colonization and growth are often due to litter acting as a physical barrier that can reduce light availability (Johnson et al., 2018; Molinari & D'Antonio, 2020). While we observed that native establishment decreased in the presence of litter, the low density of individuals across the study



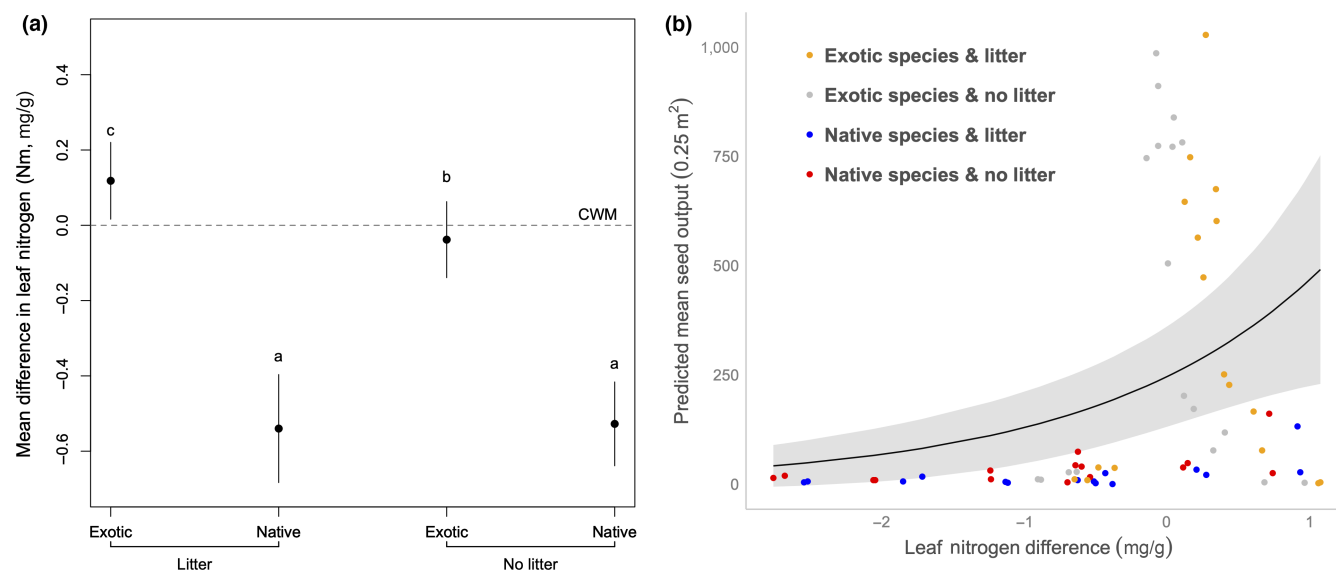


**FIGURE 4** (A) Coefficient plot for the number of reproductive stems model. Points are standardized coefficient estimates. Thick, inner bars represent  $\pm 1$  standard error and thin, outer bars  $\pm 2$  standard errors. (B) Species mean number of reproductive stems in relation to the interaction to species origin and litter treatments. Bars represent standard error. Letters denote significantly different groups ( $p < 0.05$ ), based on pairwise post-hoc tests. (C) Species mean number of reproductive stems in relation to leaf Nitrogen (mg/g). Coloured points denote and treatment group combinations of species origin and competitive environment. Shaded band represents 95% confidence interval

suggest that the successful natural establishment of these species may be constrained by other factors such as low germination rates (Wainwright & Cleland, 2013) or propagule limitation (Aicher et al., 2011; Loydi et al., 2013; Meisner et al., 2012). For example, we observed low seed output by native species in our study. The influence of litter on species performance is bolstered by the fact that we found higher establishment probability at low-resource sites where litter accumulation is much less than at high-resource, high litter sites. Low-resource sites often coincide with lower rates

of litter accumulation, thus improving germination and recruitment (Tilman, 1993).

We found that small mammals provided a small reprieve from the negative effects of litter for native species at the establishment phase. When litter was present, small mammals increased both the probability and density of native species establishment. We speculate that this was due to increased small mammal foraging activity in high litter areas, causing disturbance, that increased light availability for native species (Borer et al., 2014; Korell et al., 2017). High litter



**FIGURE 5** Difference in (A) leaf Nitrogen (Nm, mg/g) between the community-weighted mean of resident communities (naturally recruiting species that were not seeded in experimental plots, grey dashed line) and both exotic and native species that were seeded into litter treatments. Data are for all species that recruited and reproduced. Letters denote significantly different groups ( $p < 0.05$ ), based on pairwise post-hoc tests. (B) Predicted mean seed output in relation to differences in leaf Nitrogen content (mg/g) of seeded exotic and native species to the community-weighted mean (CWM) of resident communities (naturally recruiting species that were not seeded in experimental plots). Shaded band represents 95% confidence interval

areas with greater cover can be attractive to small mammals seeking to avoid predators (Pusenius & Ostfeld, 2000). We concomitantly observed the lowest native establishment in rodent exclosures, suggesting that litter effects are exacerbated in the absence of small mammals, likely as a result of resident exotic biomass and therefore litter being greater in the absence of small mammals (Figure S3).

In contrast, exotic species establishment was not constrained by the presence of litter or small mammals. Exotic species often have more plastic germination cues (Wainwright & Cleland, 2013), allowing them to still recruit in the high litter microclimates, which have been characterized as having lower soil temperatures and light availability and higher soil moisture (Warren et al., 2013). The lack of influence of litter on exotic species performance is not always species specific and can be independent of litter type. For example, Mariotte et al. (2017) observed an increase in exotic species germination, recruitment and fecundity with increasing litter depth, regardless of litter origin. Within our study site, exotic species may benefit from the prevalence of the co-occurring Medusahead *Elymus caput-medusae*, which has formed dense patches of litter, due to slow decomposition and low palatability (Nafus & Davies, 2014). This appears to produce a positive feedback between litter and exotic species, whereby continual litter accumulation can increase exotic species performance (Mariotte et al., 2017; Wolkovich et al., 2009), which, in turn, promotes both increased litter production and abundance of exotic species (Simberloff & Von Holle, 1999). Over time, this cycle may be reinforced by subsequent changes in the soil chemistry (Farrer & Goldberg, 2009; Hawkes et al., 2005) and microbial communities in grassland systems, further supporting the persistence of exotic species. For example, in California grasslands,

dominant annual exotic grass species can promote species-specific soil microbial communities (Hawkes et al., 2006) and can alter arbuscular mycorrhizal fungi communities colonizing native plant roots (Hausmann & Hawkes, 2009).

Despite the overall differences in establishment between native and exotic species, for both groups of species we found that seed mass was a good predictor of establishment success, with larger seeded species displaying increased recruitment probability. Because of sampling challenges, we were not able to explore the relationship between provenance and seed mass across the full range of the seed mix; however, we additionally re-analysed all recruitment models just for native species, including all seed sizes. The results of these models support our findings that seed mass is a good predictor of species recruitment, with the probability of recruitment increasing for larger seeded species (Figure S3, Table S10). The strong response of larger seeded species indicates an alternate strategy that could be successful in this invaded grassland. Larger seed species provide more resources to newly germinated seedlings, allowing an advantage in low light conditions (Jensen & Gutekunst, 2003; Westoby et al., 1996). Larger seeds may also produce seedlings that may be better adapted to penetrating a thick layer of litter compared to small seeded species (Amatangelo et al., 2008; Carson & Peterson, 1990; Chen et al., 2018; Loydi et al., 2013). However, the benefits that larger seeded species have in recruiting into sites with more stressful conditions may not readily translate to greater adult abundance at these sites because larger seeded species also experience greater seed predation. Within the same study system, Larios and Maron (2021) observed that CWM seed mass decreased over time in the

presence of voles, suggesting that voles are disproportionately consuming larger seeds. Importantly, like many annual systems (Leishman et al., 2000), our grassland system was dominated by small-seeded species (average CWM seed mass = 0.003), so while we observed that larger seeded species increased in establishment, small-seeded species do well in this system.

The differences in establishment between native and exotic added species persisted through reproduction where we observed that exotic species had a greater number of reproductive individuals and thus greater seed output, consistent with past observations that exotic species produce significantly more seed on average than native species in Californian grasslands (D'Antonio et al., 2007; DiVittorio et al., 2007; Young & Evans, 1989). We continued to observe a strong effect of litter on the number of reproductive native individuals. Contrary to establishment dynamics, species reproduction dynamics were correlated with LNC, with both the number of reproductive stems and seed output decreasing for both exotic and native species with increasing LNC. Although this result is consistent with studies finding that targeted herbivory upon species with high nitrogen concentrations can reduce performance (Howe et al., 2002; Zorn-Arnold et al., 2006), we did not detect differences in abundances in species with high LNC between small mammal treatments. Indeed, within the same study system, Larios and Maron (2021) observed over longer term sampling that in the absence of voles, CWM leaf Nitrogen increased, indicating the occurrence of preferential herbivory of high Nitrogen species. The decrease in the number of reproductive stems and seed output for species with high LNC may be an artifact of the negative relationship between seed mass and seed production (Moles & Westoby, 2006), with many nitrogen-fixing forbs typically exhibiting large seed mass due to their thick seed coats (Russi et al., 1992; Smýkal et al., 2014). We observed this relationship, with seed production significantly decreasing with seed mass for high LNC species ( $F_{1,21} = 10.1, p = 0.0017$ ), indicating that seed production per stem may negatively covary with seed mass for these species.

The success of an added species may not rest on its traits alone but also on the differences between the species' traits to those of the resident community (Funk et al., 2016; Gallien & Carboni, 2017; Hooper & Dukes, 2010). We observed that having differing LNC was important for native species reproduction but was not as important for exotics, suggesting that native and exotic performance within these invaded communities may be driven by niche differentiation (Leibold & McPeck, 2006; MacArthur & Levins, 1967). These results show that while niche differences may be influencing the reproductive potential of native species, exotic species that were functionally similar to the resident community may have a competitive advantage in reproduction, indicating that competitive trait hierarchies involving LNC may be more important during this life stage (Fried et al., 2019; Herben & Goldberg, 2014). In combination, these ecological mechanisms impact native and exotic species entering the community differently, with successful native species having to be

functionally diverse in LNC than the resident community for improved reproduction, while exotic species do not need to differ.

The relative lack of rodent influence on establishment or reproductive output for either native and exotic species was unexpected and suggests that foraging behaviour may be more stochastic or frequency dependent, reducing their impact on rarer or newly invading species (Howe & Brown, 2000). This result contrasts with the commonly observed consumer driven changes in reducing plant productivity and biomass of dominant species in grassland systems (Hulme, 1996; Maron et al., 2014; Pearson et al., 2012). While limited effects of rodent herbivory on plant performance have been recorded (Gibson et al., 1990), this may be contingent on temporal variation in abiotic conditions (Norrdahl et al., 2002) and site productivity (Bakker et al., 2006). However, in our study, the relative lack of consumer pressure was evident in both high- and low-resource sites. Additionally, the relative lack of rodent influence may be explained in part by the fact that our study corresponded with the culmination of an extended multi-year drought in California (Griffin & Anchukaitis, 2014), which as a result of limiting resources, may have reduced local vole populations and their subsequent influence. An increase in vole activity was observed in surveys conducted in 2017 (Larios & Maron, 2021), indicating that vole populations had yet to fully recover during the duration of our study.

## 5 | CONCLUSIONS

The results of this study highlight that both species provenance and functional traits are important factors mediating the establishment of species in response to multiple biotic and abiotic filters in an invaded grassland. Here we provide evidence that litter accumulation affects exotic and native species differently, with litter significantly decreasing native recruitment and reproduction, while exotics were largely unaffected. We also show that seed mass and LNC are key functional traits in explaining species recruitment probability and reproduction, respectively. Lastly, for enhanced reproduction and persistence within this system, native species need to vary greatly in LNC than that of the resident community. To enhance native species performance in this system, seed addition of larger seeded species would be needed to minimize seed limitation, however, without the removal or thinning of litter, it is likely that exotic species will continue to dominate, resulting in positive feedback that further favours the persistence of exotic species.

## ACKNOWLEDGEMENTS

We thank Julia Battisti, Elin Crockett, Lauren Hallett, Christine Parisek, Marko Spasojevic and Caitlin White for help in the field and processing samples. We additionally thank the staff at the Sierra Foothills Research Extension Center for their logistical support. We would also like to thank the members of the Larios research group and two anonymous reviewers for providing feedback on the manuscript. L.L. was supported by the NSF Postdoctoral Research

Fellowship in Biology Award #1309014. J.L.M. was supported by NSF grant DEB-1553518.

## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## AUTHORS' CONTRIBUTIONS

L.L. and J.L.M. designed the experiment; L.L. collected the data; L.S.C. analysed the data; L.S.C. led the writing. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <http://doi.org/10.5061/dryad.rjdfn2zcv> (Charles et al., 2022).

## ORCID

Lachlan S. Charles  <https://orcid.org/0000-0003-0055-2510>

John L. Maron  <https://orcid.org/0000-0002-4066-3322>

Loralee Larios  <https://orcid.org/0000-0002-9740-8111>

## REFERENCES

- Aicher, R. J., Larios, L., & Suding, K. N. (2011). Seed supply, recruitment, and assembly: Quantifying relative seed and establishment limitation in a plant community context. *The American Naturalist*, 178, 464–477. <https://doi.org/10.1086/661900>
- Amatangelo, K. L., Dukes, J. S., & Field, C. B. (2008). Responses of a California annual grassland to litter manipulation. *Journal of Vegetation Science*, 19, 605–612. <https://doi.org/10.3170/2008-8-18415>
- Anacker, B. L., & Harrison, S. P. (2012). Historical and ecological controls on phylogenetic diversity in Californian plant communities. *The American Naturalist*, 180, 257–269. <https://doi.org/10.1086/666650>
- Bakker, E. S., Ritchie, M. E., Olff, H., Milchunas, D. G., & Knops, J. M. H. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters*, 9, 780–788. <https://doi.org/10.1111/j.1461-0248.2006.00925.x>
- Baldwin, B. G., Goldman, D. H., Keil, D. J., Patterson, R., Rosatti, T. J., & Wilken, D. H. (2012). *The Jepson manual: Vascular plants of California*. University of California Press.
- Bates, D., Maechler, M., & Bolker, B. (2011). *lmer4: Linear mixed-effects models using Eigen and Eigen++*.
- Batzli, G. O., & Pitelka, F. A. (1970). Influence of meadow mouse populations on California grassland. *Ecology*, 51, 1027–1039. <https://doi.org/10.2307/1933629>
- Batzli, G. O., & Pitelka, F. A. (1971). Condition and diet of cycling populations of the California vole, *Microtus californicus*. *Journal of Mammalogy*, 52, 141–163. <https://doi.org/10.2307/1378438>
- Block, W. M., & Morrison, M. L. (1990). Wildlife diversity of the central Sierra foothills. *California Agriculture*, 44, 19–22. <https://doi.org/10.3733/ca.v044n02p19>
- Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., Adler, P. B., Alberti, J., Anderson, T. M., Bakker, J. D., Biederman, L., Blumenthal, D., Brown, C. S., Brudvig, L. A., Buckley, Y. M., Cadotte, M., Chu, C., Cleland, E. E., Crawley, M. J., ... Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, 508, 517–520. <https://doi.org/10.1038/nature13144>
- Cadotte, M. W., Borer, E. T., Seabloom, E. W., Cavender-Bares, J., Harpole, W. S., Cleland, E., & Davies, K. F. (2010). Phylogenetic patterns differ for native and exotic plant communities across a richness gradient in Northern California. *Diversity and Distributions*, 16, 892–901. <https://doi.org/10.1111/j.1472-4642.2010.00700.x>
- Carson, W. P., & Peterson, C. J. (1990). The role of litter in an old-field community: Impact of litter quantity in different seasons on plant species richness and abundance. *Oecologia*, 85, 8–13. <https://doi.org/10.1007/BF00317337>
- Charles, L. S., Maron, J. L., & Larios, L. (2022). Data from: Species provenance and traits mediate establishment and performance in an invaded grassland. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.rjdfn2zcv>
- Chen, B.-M., D'Antonio, C. M., Molinari, N., & Peng, S.-L. (2018). Mechanisms of influence of invasive grass litter on germination and growth of coexisting species in California. *Biological Invasions*, 20, 1881–1897. <https://doi.org/10.1007/s10530-018-1668-5>
- D'Antonio, C., Malmstrom, C., Reynolds, S., & Gerlach, J. (2007). Ecology of invasive non-native species in California grassland. In M. R. Stromberg, J. D. Corbin, & C. M. D'Antonio (Eds.), *California grasslands: Ecology and management* (pp. 67–83). University of California Press.
- DiVittorio, C. T., Corbin, J. D., & D'Antonio, C. M. (2007). Spatial and temporal patterns of seed dispersal: An important determinant of grassland invasion. *Ecological Applications*, 17, 311–316. <https://doi.org/10.1890/06-0610>
- Eskelinen, A., Harrison, S., & Tuomi, M. (2012). Plant traits mediate consumer and nutrient control on plant community productivity and diversity. *Ecology*, 93, 2705–2718. <https://doi.org/10.1890/12-0393.1>
- Eskelinen, A., Saccone, P., Spasojevic, M. J., & Virtanen, R. (2016). Herbivory mediates the long-term shift in the relative importance of microsite and propagule limitation. *Journal of Ecology*, 104, 1326–1334. <https://doi.org/10.1111/1365-2745.12592>
- Facelli, J. M., & Pickett, S. T. A. (1991). Plant litter: Its dynamics and effects on plant community structure. *The Botanical Review*, 57, 1–32. <https://doi.org/10.1007/BF02858763>
- Farrer, E. C., & Goldberg, D. E. (2009). Litter drives ecosystem and plant community changes in cattail invasion. *Ecological Applications*, 19, 398–412. <https://doi.org/10.1890/08-0485.1>
- Fehmi, J. S., & Bartolome, J. W. (2002). Species richness and California voles in an annual and a perennial grassland. *Western North American Naturalist*, 62, 73–81.
- Fernandez-Goñi, B. M., Harrison, S. P., Anacker, B. L., & Safford, H. D. (2013). Climate interacts with soil to produce beta diversity in Californian plant communities. *Ecology*, 94, 2007–2018. <https://doi.org/10.1890/12-2011.1>
- Fried, G., Carboni, M., Mahaut, L., & Violle, C. (2019). Functional traits modulate plant community responses to alien plant invasion. *Perspectives in Plant Ecology, Evolution and Systematics*, 37, 53–63. <https://doi.org/10.1016/j.ppees.2019.02.003>
- Funk, J. L., Standish, R. J., Stock, W. D., & Valladares, F. (2016). Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. *Ecology*, 97, 75–83. <https://doi.org/10.1890/15-0974.1>
- Fynn, R., Morris, C., Ward, D., & Kirkman, K. (2011). Trait–environment relations for dominant grasses in South African mesic grassland support a general leaf economic model. *Journal of Vegetation Science*, 22, 528–540. <https://doi.org/10.1111/j.1654-1103.2011.01268.x>
- Gallien, L., & Carboni, M. (2017). The community ecology of invasive species: Where are we and what's next? *Ecography*, 40, 335–352. <https://doi.org/10.1111/ecog.02446>
- Germain, R. M., Johnson, L., Schneider, S., Cottenie, K., Gillis, E. A., & MacDougall, A. S. (2013). Spatial variability in plant predation determines the strength of stochastic community assembly. *The American Naturalist*, 182(2), 169–179. <https://doi.org/10.1086/670928>
- Gibson, D. J., Freeman, C. C., & Hulbert, L. C. (1990). Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. *Oecologia*, 84, 169–175. <https://doi.org/10.1007/BF00318268>



- Godoy, O. (2019). Coexistence theory as a tool to understand biological invasions in species interaction networks: Implications for the study of novel ecosystems. *Functional Ecology*, 33, 1190–1201. <https://doi.org/10.1111/1365-2435.13343>
- Griffin, D., & Anchukaitis, K. J. (2014). How unusual is the 2012–2014 California drought? *Geophysical Research Letters*, 41, 9017–9023. <https://doi.org/10.1002/2014GL062433>
- Harrison, S., & Grace, J. B. (2007). Biogeographic affinity helps explain productivity–richness relationships at regional and local scales. *The American Naturalist*, 170, S5–S15. <https://doi.org/10.1086/519010>
- Hausmann, N. T., & Hawkes, C. V. (2009). Plant neighborhood control of arbuscular mycorrhizal community composition. *New Phytologist*, 183, 1188–1200. <https://doi.org/10.1111/j.1469-8137.2009.02882.x>
- Hawkes, C. V., Belnap, J., D'Antonio, C., & Firestone, M. K. (2006). Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. *Plant and Soil*, 281, 369–380. <https://doi.org/10.1007/s11104-005-4826-3>
- Hawkes, C. V., Wren, I. F., Herman, D. J., & Firestone, M. K. (2005). Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. *Ecology Letters*, 8, 976–985. <https://doi.org/10.1111/j.1461-0248.2005.00802.x>
- Hejda, M., Pyšek, P., & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, 97, 393–403. <https://doi.org/10.1111/j.1365-2745.2009.01480.x>
- Herben, T., & Goldberg, D. E. (2014). Community assembly by limiting similarity vs. competitive hierarchies: Testing the consequences of dispersion of individual traits. *Journal of Ecology*, 102, 156–166.
- Hillebrand, H., Gruner, D. S., Borer, E. T., Bracken, M. E. S., Cleland, E. E., Elser, J. J., Harpole, W. S., Ngai, J. T., Seabloom, E. W., Shurin, J. B., & Smith, J. E. (2007). Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 10904–10909. <https://doi.org/10.1073/pnas.0701918104>
- Hobbs, R. J., & Mooney, H. A. (1991). Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology*, 72, 59–68. <https://doi.org/10.2307/1938902>
- Hooper, D. U., & Dukes, J. S. (2010). Functional composition controls invasion success in a California serpentine grassland. *Journal of Ecology*, 98, 764–777. <https://doi.org/10.1111/j.1365-2745.2010.01673.x>
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363. <https://doi.org/10.1002/bimj.200810425>
- Howe, H. F., & Brown, J. S. (2000). Early effects of rodent granivory on experimental forb communities. *Ecological Applications*, 10, 917–924. [https://doi.org/10.1890/1051-0761\(2000\)010\[0917:EEORG\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0917:EEORG]2.0.CO;2)
- Howe, H. F., Brown, J. S., & Zorn-Arnold, B. (2002). A rodent plague on prairie diversity. *Ecology Letters*, 5, 30–36. <https://doi.org/10.1046/j.1461-0248.2002.00276.x>
- Huenneke, L. F., Hamburg, S. P., Koide, R., Mooney, H. A., & Vitousek, P. M. (1990). Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology*, 71, 478–491. <https://doi.org/10.2307/1940302>
- Hulme, P. E. (1996). Herbivores and the performance of grassland plants: A comparison of arthropod, mollusc and rodent herbivory. *Journal of Ecology*, 84, 43–51. <https://doi.org/10.2307/2261698>
- Jensen, K., & Gutekunst, K. (2003). Effects of litter on establishment of grassland plant species: The role of seed size and successional status. *Basic and Applied Ecology*, 4, 579–587. <https://doi.org/10.1078/1439-1791-00179>
- Johnson, D. P., Catford, J. A., Driscoll, D. A., & Gibbons, P. (2018). Seed addition and biomass removal key to restoring native forbs in degraded temperate grassland. *Applied Vegetation Science*, 21, 219–228. <https://doi.org/10.1111/avsc.12352>
- Korell, L., Lang, B. R., Hensen, I., Auge, H., & Bruehlheide, H. (2017). Interactions count: Plant origin, herbivory and disturbance jointly explain seedling recruitment and community structure. *Scientific Reports*, 7, 8288.
- Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305. <https://doi.org/10.1890/08-2244.1>
- Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD: Measuring functional diversity from multiple traits, and other tools for functional ecology*. R package version 1.0-12.
- Larios, L., & Maron, J. L. (2021). Voles mediate functional trait diversity along a resource gradient. *Functional Ecology*, 35, 205–215. <https://doi.org/10.1111/1365-2435.13686>
- Larson, J. E., & Funk, J. L. (2016). Regeneration: An overlooked aspect of trait-based plant community assembly models. *Journal of Ecology*, 104, 1284–1298. <https://doi.org/10.1111/1365-2745.12613>
- Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, 102, 186–193. <https://doi.org/10.1111/1365-2745.12187>
- Leibold, M. A., & McPeck, M. A. (2006). Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, 87, 1399–1410. [https://doi.org/10.1890/0012-9658\(2006\)87\[1399:COTNAN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1399:COTNAN]2.0.CO;2)
- Leishman, M. R., Wright, I. J., Moles, A. T., & Westoby, M. (2000). The evolutionary ecology of seed size. In M. Fenner (Ed.), *Seeds: The ecology of regeneration in plant communities* (pp. 31–57). CABI International.
- Lemoine, N. P., Burkepile, D. E., & Parker, J. D. (2016). Quantifying differences between native and introduced species. *Trends in Ecology & Evolution*, 31, 372–381. <https://doi.org/10.1016/j.tree.2016.02.008>
- Letts, B., Lamb, E. G., Mischkolz, J. M., & Romo, J. T. (2015). Litter accumulation drives grassland plant community composition and functional diversity via leaf traits. *Plant Ecology*, 216, 357–370. <https://doi.org/10.1007/s11258-014-0436-6>
- Liu, Y., Ma, G., Zan, Z., Chen, A., Miao, Y., Wang, D., & Miao, R. (2018). Effects of nitrogen addition and mowing on rodent damage in an Inner Mongolian steppe. *Ecology and Evolution*, 8, 3919–3926. <https://doi.org/10.1002/ece3.3949>
- Loydi, A., Eckstein, R. L., Otte, A., & Donath, T. W. (2013). Effects of litter on seedling establishment in natural and semi-natural grasslands: A meta-analysis. *Journal of Ecology*, 101, 454–464. <https://doi.org/10.1111/1365-2745.12033>
- MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101, 377–385. <https://doi.org/10.1086/282505>
- Mariotte, P., Spotswood, E. N., Farrer, E. C., & Suding, K. N. (2017). Positive litter feedbacks of an introduced species reduce native diversity and promote invasion in Californian grasslands. *Applied Vegetation Science*, 20, 28–39. <https://doi.org/10.1111/avsc.12291>
- Maron, J. L., Auge, H., Pearson, D. E., Korell, L., Hensen, I., Suding, K. N., & Stein, C. (2014). Staged invasions across disparate grasslands: Effects of seed provenance, consumers and disturbance on productivity and species richness. *Ecology Letters*, 17, 499–507. <https://doi.org/10.1111/ele.12250>
- Maron, J. L., Pearson, D. E., Potter, T., & Ortega, Y. K. (2012). Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. *Journal of Ecology*, 100, 1492–1500. <https://doi.org/10.1111/j.1365-2745.2012.02027.x>
- Meisner, A., de Boer, W., Cornelissen, J. H. C., & van der Putten, W. H. (2012). Reciprocal effects of litter from exotic and congeneric native plant species via soil nutrients. *PLoS ONE*, 7, e31596. <https://doi.org/10.1371/journal.pone.0031596>
- Mittelbach, G. G., & Gross, K. L. (1984). Experimental studies of seed predation in old-fields. *Oecologia*, 65, 7–13. <https://doi.org/10.1007/BF00384455>

- Moles, A. T., & Westoby, M. (2004). Seedling survival and seed size: A synthesis of the literature. *Journal of Ecology*, 92, 372–383. <https://doi.org/10.1111/j.0022-0477.2004.00884.x>
- Moles, A. T., & Westoby, M. (2006). Seed size and plant strategy across the whole life cycle. *Oikos*, 113, 91–105. <https://doi.org/10.1111/j.0030-1299.2006.14194.x>
- Molinari, N. A., & D'Antonio, C. M. (2020). Where have all the wildflowers gone? The role of exotic grass thatch. *Biological Invasions*, 22, 957–968. <https://doi.org/10.1007/s10530-019-02135-1>
- Nafus, A. M., & Davies, K. W. (2014). Medusahead ecology and management: California annual grasslands to the Intermountain West. *Invasive Plant Science and Management*, 7, 210–221. <https://doi.org/10.1614/IPSM-D-13-00077.1>
- Navas, M. L., & Violle, C. (2009). Plant traits related to competition: How do they shape the functional diversity of communities? *Community Ecology*, 10, 131–137. <https://doi.org/10.1556/ComEc.10.2009.1.15>
- Norrdahl, K., Klemola, T., Korpimäki, E., & Koivula, M. (2002). Strong seasonality may attenuate trophic cascades: Vertebrate predator exclusion in boreal grassland. *Oikos*, 99, 419–430. <https://doi.org/10.1034/j.1600-0706.2002.12025.x>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2020). *vegan: Community ecology package*.
- Olf, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution*, 13, 261–265. [https://doi.org/10.1016/S0169-5347\(98\)01364-0](https://doi.org/10.1016/S0169-5347(98)01364-0)
- Ostfeld, R. S., Manson, R. H., & Canham, C. D. (1997). Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology*, 78, 1531–1542. [https://doi.org/10.1890/0012-9658\(1997\)078\[1531:EOROSO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1531:EOROSO]2.0.CO;2)
- Pearson, D. E., Callaway, R. M., & Maron, J. L. (2011). Biotic resistance via granivory: Establishment by invasive, naturalized, and native asters reflects generalist preference. *Ecology*, 92, 1748–1757. <https://doi.org/10.1890/11-0164.1>
- Pearson, D. E., Potter, T., & Maron, J. L. (2012). Biotic resistance: Exclusion of native rodent consumers releases populations of a weak invader. *Journal of Ecology*, 100, 1383–1390. <https://doi.org/10.1111/j.1365-2745.2012.02025.x>
- PRISM Climate Group. (2004). *Prism climate data*. Oregon State University. Retrieved from <http://prism.oregonstate.edu>
- Pusenius, J., & Ostfeld, R. S. (2000). Effects of stoat's presence and auditory cues indicating its presence on tree seedling predation by meadow voles. *Oikos*, 91, 123–130. <https://doi.org/10.1034/j.1600-0706.2000.910111.x>
- Pyšek, P., & Richardson, D. M. (2007). Traits associated with invasiveness in alien plants: Where do we stand? In W. Nentwig (Ed.), *Biological invasions* (pp. 97–125). Springer Berlin Heidelberg.
- Questad, E. J., & Foster, B. L. (2007). Vole disturbances and plant diversity in a grassland metacommunity. *Oecologia*, 153, 341–351. <https://doi.org/10.1007/s00442-007-0734-y>
- R Development Core Team. (2010). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Reader, R. J. (1993). Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology*, 81, 169–175. <https://doi.org/10.2307/2261232>
- Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, S. J., & Rejmánek, M. (2000). Plant invasions—The role of mutualisms. *Biological Reviews*, 75, 65–93. <https://doi.org/10.1017/S0006323199005435>
- Royal Botanic Gardens Kew. (2017). *Seed Information Database (SID), Version 7.1*. Retrieved from <http://data.kew.org/sid/>
- Russi, L., Cocks, P. S., & Roberts, E. H. (1992). Seed bank dynamics in a Mediterranean grassland. *Journal of Applied Ecology*, 29, 763–771. <https://doi.org/10.2307/2404486>
- Seabloom, E. W., Borer, E. T., Boucher, V. L., Burton, R. S., Cottingham, K. L., Goldwasser, L., Gram, W. K., Kendall, B. E., & Micheli, F. (2003). Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecological Applications*, 13, 575–592. [https://doi.org/10.1890/1051-0761\(2003\)013\[0575:CSLDA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0575:CSLDA]2.0.CO;2)
- Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, 1, 21–32.
- Skaug, H. J., Fournier, D. A., Bolker, B., Magnusson, A., & Nielsen, A. (2016). *Generalized linear mixed models using 'AD model builder'*. R package version 0.8.3.3.
- Smýkal, P., Vernoud, V., Blair, M. W., Soukup, A., & Thompson, R. D. (2014). The role of the testa during development and in establishment of dormancy of the legume seed. *Frontiers in Plant Science*, 5, 351. <https://doi.org/10.3389/fpls.2014.00351>
- Thebaud, C., Finzi, A. C., Affre, L., Debussche, M., & Escarre, J. (1996). Assessing why two introduced conyza differ in their ability to invade mediterranean old fields. *Ecology*, 77, 791–804. <https://doi.org/10.2307/2265502>
- Tilman, D. (1993). Species richness of experimental productivity gradients: How important is colonization limitation? *Ecology*, 74, 2179–2191. <https://doi.org/10.2307/1939572>
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Wainwright, C. E., & Cleland, E. E. (2013). Exotic species display greater germination plasticity and higher germination rates than native species across multiple cues. *Biological Invasions*, 15, 2253–2264. <https://doi.org/10.1007/s10530-013-0449-4>
- Warren, R. J., Bahn, V., & Bradford, M. A. (2013). Decoupling litter barrier and soil moisture influences on the establishment of an invasive grass. *Plant and Soil*, 367, 339–346. <https://doi.org/10.1007/s11104-012-1477-z>
- Westoby, M., Leishman, M., Lord, J., Poorter, H., & Schoen, D. (1996). Comparative ecology of seed size and dispersal [and discussion]. *Philosophical Transactions: Biological Sciences*, 351, 1309–1318.
- Wolkovich, E. M., Bolger, D. T., & Cottingham, K. L. (2009). Invasive grass litter facilitates native shrubs through abiotic effects. *Journal of Vegetation Science*, 20, 1121–1132. <https://doi.org/10.1111/j.1654-1103.2009.01110.x>
- Young, J. A., & Evans, R. A. (1989). Seed production and germination dynamics in California annual grasslands. In L. F. Huenneke & H. A. Mooney (Eds.), *Grassland structure and function: California annual grassland* (pp. 39–45). Springer.
- Zorn-Arnold, B., Brown, J. S., & Howe, H. F. (2006). Obvious and cryptic vole suppression of a prairie legume in experimental restorations. *International Journal of Plant Sciences*, 167, 961–968. <https://doi.org/10.1086/505719>

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Charles, L. S., Maron, J. L., & Larios, L. (2022). Species provenance and traits mediate establishment and performance in an invaded grassland. *Functional Ecology*, 36, 1528–1541. <https://doi.org/10.1111/1365-2435.14044>