

RESEARCH ARTICLE

# Seed predator preferences are associated with seed traits but an unlikely mechanism of local extinction

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Certain traits, including those that make species more vulnerable to consumption by predators, may make species inherently susceptible to population declines and local species loss (i.e. extirpation). To examine whether small mammal and arthropod granivory is a mechanism of community change via association with extirpation events, we studied seed predation on six phylogenetically paired extirpated and extant species from Kalamazoo, Michigan, using a seed removal experiment in a restored prairie. We also examined differences in granivore preferences for seed traits (seed mass, water content, C:N content) and differences in seed traits between extirpated and extant taxa. Granivory was independent of extirpation status but was affected by seed traits. Small mammals consumed more seeds than arthropods and preferentially consumed large seeds, while arthropods consumed small seeds and those with higher C:N ratios (lower nitrogen content). Extirpated and extant taxa did not differ in seed traits, perhaps explaining why they did not differ in granivory. Granivory was phylogenetically conserved, suggesting that certain plant families are more susceptible to granivores than others. This study indicates that granivory varies across species and seed traits in a prairie restoration, but does not likely influence extirpation in this system. Understanding granivore preferences may help managers predict establishment success for rare or extirpated species with particular traits being introduced into prairie restorations.

**Key words:** arthropods, extirpation, granivory, prairie, seed traits, small mammals

## Implications for Practice

- To counteract the effects of small mammal granivory on large-seeded and nitrogen-rich species in restorations with large small mammal populations, practitioners might want to selectively apply granivore deterrents, add additional seeds of these species to seed mixes, or sow seeds during seasons with the least granivore activity.
- Granivores equally consumed common extant species and extirpated species, suggesting that restorations aiming to reintroduce rare or threatened species may not need to compensate for higher seed predation on rare species.

## Introduction

Contemporary plant extinctions exceed historical rates of species loss (Le Roux et al. 2019). Although local species losses (i.e. extirpations) often reflect global extinction risks (Davies 2019), we still have a limited understanding of mechanisms underlying extirpation events, which are ultimately a series of reductions in plant population performance (Collen et al. 2010). Consumers, which can damage plant performance via tissue and seed loss, can fundamentally alter plant population dynamics and abundance (Maron & Crone 2006). Granivory, or seed predation, influences plant community composition (Howe & Brown 2001; Pellish et al. 2017) and population abundance (Bricker et al. 2010; Chen & Valone 2017) by increasing seed limitation (Orrock et al. 2006; Combs et al. 2013) and reducing seedling establishment (Orrock et al. 2009; Pellish et al. 2017; Lucero & Callaway 2018).

Granivores can also negatively affect plant population growth rates (Bricker & Maron 2012; Kurkjian et al. 2017), potentially contributing to population declines and eventual extirpation. Rare species in particular have the potential to be driven to extirpation by seed predators (Kurkjian et al. 2017). Seed predation is higher in rare species than common congeners (i.e. species in the same genus) in a shrub-steppe ecosystem, leading to lower seed production in the rare species (Combs et al. 2013) and suggesting that seed predation could contribute to rarity and population decline. Comparative approaches between closely related extirpated and extant species could elucidate potential mechanisms underlying differences in abundance (or extirpation) between species (Bevill & Louda 1999). Specifically, comparing granivory on closely-related extirpated versus extant taxa could allow us to investigate whether differences in granivore preferences correlate with local species extinctions, independently of differences in phylogeny or ecology (Combs et al. 2013).

Granivore preferences and subsequent effects on plant populations likely vary depending on consumer identity and plant

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traits. Small mammals and arthropods often differ in their seed preferences (Pulliam & Brand 1975; Mittelbach & Gross 1984; Linabury et al. 2019). Seed size is an important seed quality that can influence consumer preference: while small mammals often prefer large-seeded species (Abramsky 1983; Celis-Diez et al. 2004; Connolly et al. 2014; Chen & Valone 2017; Dylewski et al. 2020), arthropods tend to consume smaller seeds (Mittelbach & Gross 1984; Pearson et al. 2014). Granivores may also consume seeds with particular nutritional and morphological features such as seeds with high calorie, carbohydrate (Kelrick et al. 1986), water (Frank 1988), fat (Xiao et al. 2006), nitrogen (Gong et al. 2015), or oil content (Clause et al. 2017), although few studies have distinguished between small mammal versus arthropod preferences for these traits.

Seed traits that influence vulnerability to granivores may differ between extirpated and extant taxa. For example, seed size is often related to seed production and competitive ability (Westoby et al. 2002), which may be lower in extirpated relative to extant species. If granivory contributed to local species declines, extirpated species might also have traits that make them more or less susceptible to certain seed predators. For instance, if extirpated species generally have smaller seeds, they might be more vulnerable to arthropods than small mammals. Trait-based approaches allow us to generalize plant responses to specific factors (McGill et al. 2006). If elevated granivory is associated with extirpation, identifying seed traits that affect species' susceptibility to seed predation could be useful for predicting extirpation risk.

Understanding granivore preferences in threatened habitats, such as native tallgrass prairies, could help us understand the role of seed predators in the decline of taxa once predominantly found in such habitats. Additionally, habitat restoration is a way to return lost biodiversity to an area (Suding 2011). Understanding patterns of seed predation in restored populations may help us predict species' success and design management strategies accounting for seed predation rates on specific species or for species with traits correlated with high granivory (Pearson et al. 2018; Taylor et al. 2020). Moreover, seed predators can cost \$180–250 per hectare in restorations (Pellish et al. 2017), so understanding seed removal rates for species included in restoration mixes could help ameliorate costs due to seed predation (Linabury et al. 2019), particularly for threatened species that are being reintroduced.

Here, we use a seed removal experiment to examine the roles of seed consumer, extirpation status, and seed traits in granivory patterns in a restored prairie. We addressed the following questions: (1) Do extirpated and extant prairie species differ in their seed traits? (2) Do extirpated and extant prairie species differ in seed removal rates by small mammals versus arthropods? (3) Do small mammals and arthropods demonstrate different preferences for seed traits, and do these patterns differ between extirpated and extant species?

## Methods

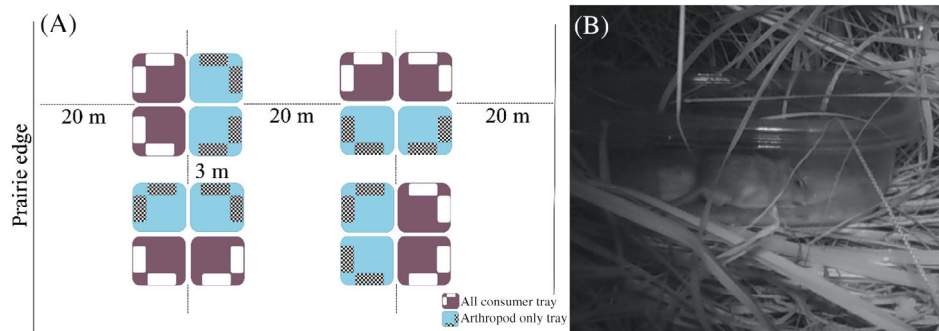
Kalamazoo County, Michigan, U.S.A., supports only 0.0006% of its historic prairie acreage (Zettlemoyer & Srodes 2019) and

lost 14.01% of its native prairie species between 1890 and 2004 (Hanes & Hanes 1947; McKenna 2004; Zettlemoyer et al. 2019). Using historical botanical records, we identified all the extirpated, native, long-lived perennial, prairie specialist (i.e. were not recorded in any other habitat type in Kalamazoo) forbs once found in Kalamazoo's prairies and savannas. For each extirpated species, we selected the most closely related (same plant family, or confamilial) extant species that was also a native, perennial, and prairie specialist forb. We then selected six of these confamilial pairs that ranged in seed size (Table 1). For more details on historical datasets and extirpation in Kalamazoo County, see Zettlemoyer et al. (2019). Although habitat loss and other anthropogenic changes (e.g. invasion, nutrient addition, climate change; ongoing experiments are testing several of these potential drivers) likely influence species loss in this area, seed predation can also contribute to population declines in grasslands (Bricker & Maron 2012). We also note that although these species became extirpated in the last 100 years, they may have experienced differential seed predation for much longer; however, we do not know how long these species have been declining or if seed predation influenced their extirpation. These extirpated and extant species were experimentally reintroduced into a circa 20-year-old restored prairie at the Boudeman Farm, Richland, Michigan, in 2017. Seeds were sourced from Midwestern nurseries, as local to Michigan as possible, including Michigan Wildflower Farm (Portland, Michigan), Naturally Native Nursery (South Bend, Indiana), Agrecol (Edgerton, Wisconsin), and Prairie Moon (Winona, Minnesota). In spring 2017, we transplanted seedlings of all 12 species into an experiment manipulating two common drivers of species loss in prairies, nitrogen addition and deer herbivory ( $n = 10$  seedlings/species  $\times 20$  plots  $\times 12$  species = 2,400 seedlings); we surveyed populations annually.

To test whether extirpated and extant species differ in seed predation by small mammal versus arthropod granivores, we set up granivore sampling stations at Boudeman Farm in July 2019. We elected to use Boudeman Farm, despite its age, because populations of the extirpated species had established there (see above). However, this study assumes that ongoing seedling establishment by perennial species contributes to community composition in this established prairie. We set out 40 sampling stations across two transects placed 20 m apart. Transects were placed 20 m from the edge of the prairie to control for edge effects (Donoso et al. 2003; Germain et al. 2013). Each transect had 20 sampling stations, each 3 m apart. Each station contained four seed trays ( $n = 4$  seed trays  $\times 20$  stations  $\times 2$  transects = 160 trays; Fig. 1A). Two types of seed trays were constructed from Glad Tupperware containers (15 cm<sup>2</sup>, 5.5 cm deep) with holes (4  $\times$  7 cm) cut into two adjacent sides to either (1) allow arthropods and small mammals to enter and consume seeds ("All Consumer" trays) or (2) had hardware mesh (0.5 cm<sup>2</sup> opening) adhered across the holes to permit arthropods but exclude mammals ("Arthropod Only" trays) (following Linabury et al. 2019). Lids were placed on the containers to prevent seeds from washing away with rain and to prevent seed predation by birds, another seed predator (Kelt et al. 2004) but not a focus of this study. Although we did not identify granivores in this study, likely seed predators

**Table 1.** Species (abbreviation) and plant family for the six confamilial pairs included in this study. Superscript LE indicates an extirpated species. We provide the mean proportion of arthropod granivory, small mammal granivory, and total granivory on each species, mean granivory for extant and extirpated species overall, and mean total granivory by each consumer group. Values are least square means  $\pm$  standard error.

Species	Family	Proportion Arthropod Granivory	Proportion Small Mammal Granivory	Proportion Total Granivory
<i>Baptisia tinctoria</i> (L.) Vent. (BT)	Fabaceae	0.124 $\pm$ 0.042	0.137 $\pm$ 0.043	0.277 $\pm$ 0.042
<i>Baptisia bracteata</i> Nuhl. Ex Elliott (BB) <sup>LE</sup>	Fabaceae	0.137 $\pm$ 0.043	0.085 $\pm$ 0.043	0.248 $\pm$ 0.042
<i>Eryngium yuccifolium</i> Michx. (EY)	Apiaceae	0.225 $\pm$ 0.043	0.385 $\pm$ 0.043	0.612 $\pm$ 0.042
<i>Thaspium trifoliatum</i> (L.) A. Gray (TT) <sup>LE</sup>	Apiaceae	0.240 $\pm$ 0.043	0.307 $\pm$ 0.043	0.561 $\pm$ 0.042
<i>Liatris aspera</i> Michx. (LA)	Asteraceae	0.321 $\pm$ 0.042	0.439 $\pm$ 0.042	0.760 $\pm$ 0.041
<i>Liatris punctata</i> Hook. (LP) <sup>LE</sup>	Asteraceae	0.192 $\pm$ 0.043	0.517 $\pm$ 0.044	0.714 $\pm$ 0.043
<i>Monarda fistulosa</i> L. (MF)	Lamiaceae	0.416 $\pm$ 0.043	0.150 $\pm$ 0.043	0.571 $\pm$ 0.042
<i>Pycnanthemum tenuifolium</i> Schrad. (PT) <sup>LE</sup>	Lamiaceae	0.354 $\pm$ 0.043	0.103 $\pm$ 0.043	0.464 $\pm$ 0.042
<i>Ratibida pinnata</i> (Vent.) Barnhart (RP)	Asteraceae	0.297 $\pm$ 0.043	0.247 $\pm$ 0.043	0.559 $\pm$ 0.042
<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl. (RC) <sup>LE</sup>	Asteraceae	0.253 $\pm$ 0.042	0.194 $\pm$ 0.043	0.450 $\pm$ 0.043
<i>Silphium perfoliatum</i> L. (SP)	Asteraceae	0.032 $\pm$ 0.043	0.950 $\pm$ 0.043	0.975 $\pm$ 0.043
<i>Silphium terebinthinaceum</i> Elliot non. Jacq. (ST) <sup>LE</sup>	Asteraceae	0.025 $\pm$ 0.043	0.915 $\pm$ 0.043	0.927 $\pm$ 0.042
Extant species overall mean		0.233 $\pm$ 0.024	0.381 $\pm$ 0.024	0.624 $\pm$ 0.023
Extirpated species overall mean		0.198 $\pm$ 0.024	0.351 $\pm$ 0.024	0.561 $\pm$ 0.024
Mean granivory by each consumer		0.218 $\pm$ 0.017	0.369 $\pm$ 0.017	0.593 $\pm$ 0.017



**Figure 1.** (A) Experimental design. Stations (sets of four trays, each separated by 3 m; four stations shown here) were set out along two transects, each 20 m from each other and from the edges of the prairie. Within each station, two trays were “All Consumer” trays (lavender), whose entrances (white panels) allowed arthropods and small mammals to enter and consume seeds, and another two trays were “Arthropod Only” trays (light blue), which had hardware mesh (gray panels) adhered across entrances to permit arthropods but exclude mammals. (B) Camera trap image of a field mouse in an “All Consumer” granivore tray.

in this system include beetles (unknown spp.), ants (including *Myrmica lobicornis*), *Peromyscus maniculatus* (field mouse), *Zapus hudsonius* (meadow jumping mouse), and *Microtus pennsylvanicus* (meadow vole) (Mittelbach & Gross 1984; Linabury et al. 2019). We used a field camera placed over six randomly selected stations for a week each to observe small mammals (Fig. 1B).

We placed two of each tray type at each station, facing outward from each other, and covered the base of the containers with a fine layer of sand. Because seeds from confamilial pairs were similar in appearance, we could not place seeds from the same pair into the same seed tray. We, therefore, separated each confamilial pair between the two replicate trays of each consumer type at each station (i.e. each tray contained 6/12 species). Species were randomly assigned to trays, although species from within each confamilial pair were always placed in separate trays as described above ( $n = 20$  seeds/species  $\times$  12 species  $\times$  2 tray types  $\times$  40 stations = 19,200 seeds). We deployed seed trays on 9 July 2019 and collected the remaining

seeds 6 weeks later (five trays were destroyed by deer and not collected). Removal rates for “All Consumer” and “Arthropod Only” trays were calculated by subtracting the number of seeds for each species that remained in the trays from the 20 seeds that were originally deposited. We estimated small mammal granivory as seed removal in “All Consumer” minus “Arthropod Only” trays (following Linabury et al. 2019).

We measured three species-level seed traits hypothesized to influence granivore preferences: seed mass, water content, and carbon to nitrogen (C:N) ratio. To estimate seed mass (mg), we weighed 20 seeds per species and averaged their mass. To estimate water content, we weighed 20 seeds per species (“wet weight”), dried the seeds at 70°C for 48 hours, then reweighed the seeds (“dry weight”). We estimated water content as wet weight minus dry weight, then estimated percent water content as water content/wet weight  $\times$  100. To estimate seed C:N ratio, triplicate samples of ground seeds (2–5 mg of seed material/sample;  $n = 3$  samples/species  $\times$  12 species = 36 samples) were dried, finely ground, and packed in tin capsules. C:N ratio was measured

using C:N combustion analysis (Carlo Erba NA1500 Series II Combustion Analyzer; Kellogg Biological Station Long-Term Ecological Research; <https://lter.kbs.msu.edu/protocols/147>).

**Data Analysis**

To test whether extirpated and extant species differ in seed traits, we performed three linear mixed models (Gaussian distributions), one for each trait. We included seed mass (mg), percent water content, and C:N ratio as three separate response variables, status as the predictor variable, and species (nested within status) as a random factor. To further investigate how extirpated versus extant taxa differ in seed traits, we examined differences in seed traits within each confamilial pair. We included the three seed traits as separate response variables and status as the predictor in separate models for each species pair.

To test whether consumer preferences varied between extant and extirpated species, we conducted a linear mixed model using the “lmer” function in the lme4 package in R (Bates et al. 2015; R Core Team 2019) with status, consumer type (Small Mammal [estimated as All Consumer – Arthropod Only] vs. Arthropod Only), and their interaction as predictor variables, and proportion seeds removed as the response variable. We included species

(nested within genus nested within pair) (species is included because it is the unit of replication for tests of status; pair is included to ensure comparisons are within each phylogenetic contrast) and station (to control for spatial variation) as random factors.

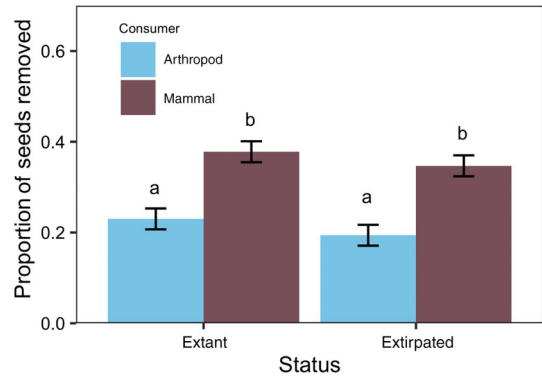


Figure 3. Proportion of extant versus extirpated species’ seeds removed (least square means ± SE) by arthropods (light blue) versus small mammals (lavender; estimated as the difference in seed predation between “All Consumer” and “Arthropod Only” trays). Letters represent differences at the  $\alpha = 0.05$  level (Tukey tests).

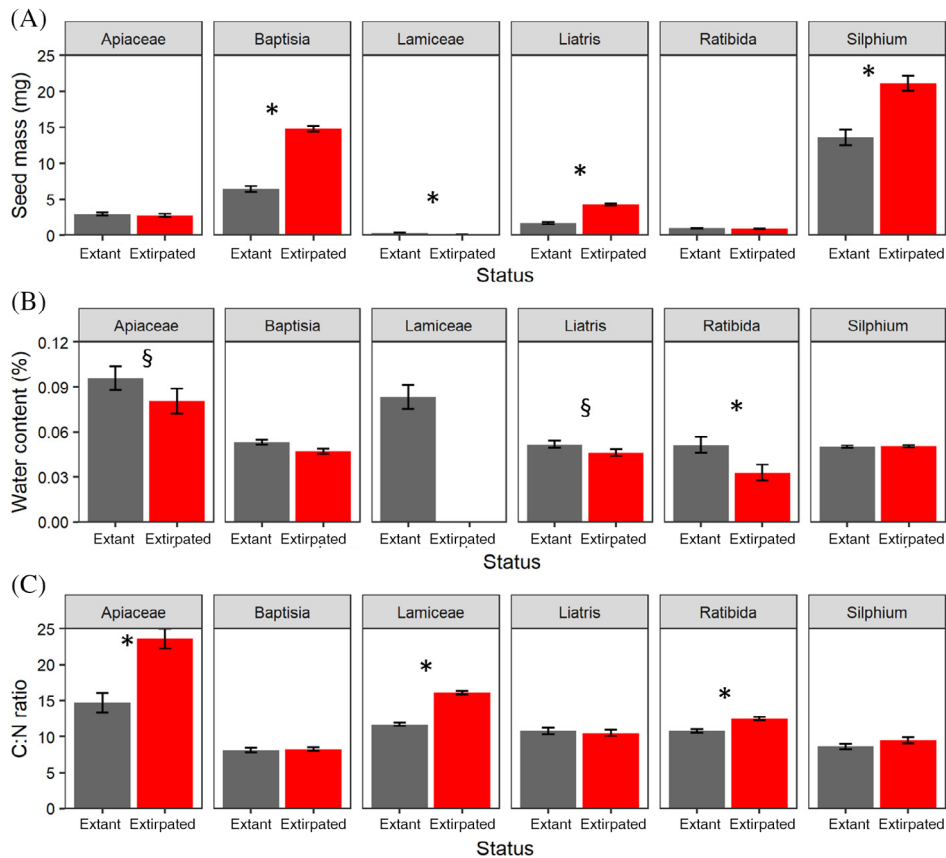


Figure 2. Mean species trait values (least square means ± SE) for (A) seed mass (mg), (B) water content (% of mass), and (C) C:N ratio. Red indicates extirpated species; gray indicates extant species. Symbols indicate that extirpated and extant species within a confamilial pair differed in their trait value, where \* $p < 0.05$  and § $p < 0.1$ .

To test whether differences in trait values between extant and extirpated species contribute to differences in consumer preferences between extant and extirpated species, we conducted two linear mixed models. Because traits were measured at the species level, we used species mean estimates of granivory by each consumer type for this analysis (i.e. one model for mean mammal and another for mean arthropod granivory). Species-level mean mammal or arthropod granivory were included as the two separate response variables. We included status, each species' mean trait values (mean seed mass [mg], mean percent water content, and

mean C:N ratio), and two-way interactions between status  $\times$  each trait as predictor variables in both models.

We also tested for phylogenetic signal in extirpation status, seed traits, and granivory by small mammals and arthropods. We obtained a phylogenetic tree from Phylomatic (phylodiversity.net/phyloomatic), using the Zanne et al. (2014) tree (Fig. S1). We tested for phylogenetic conservatism with Blomberg's  $K$ , which compares the observed phylogenetic signal in a trait with the signal under a Brownian motion model of trait evolution ("phylosignal" function in the package "picante" v.1.3-0; Kembel et al. 2010).

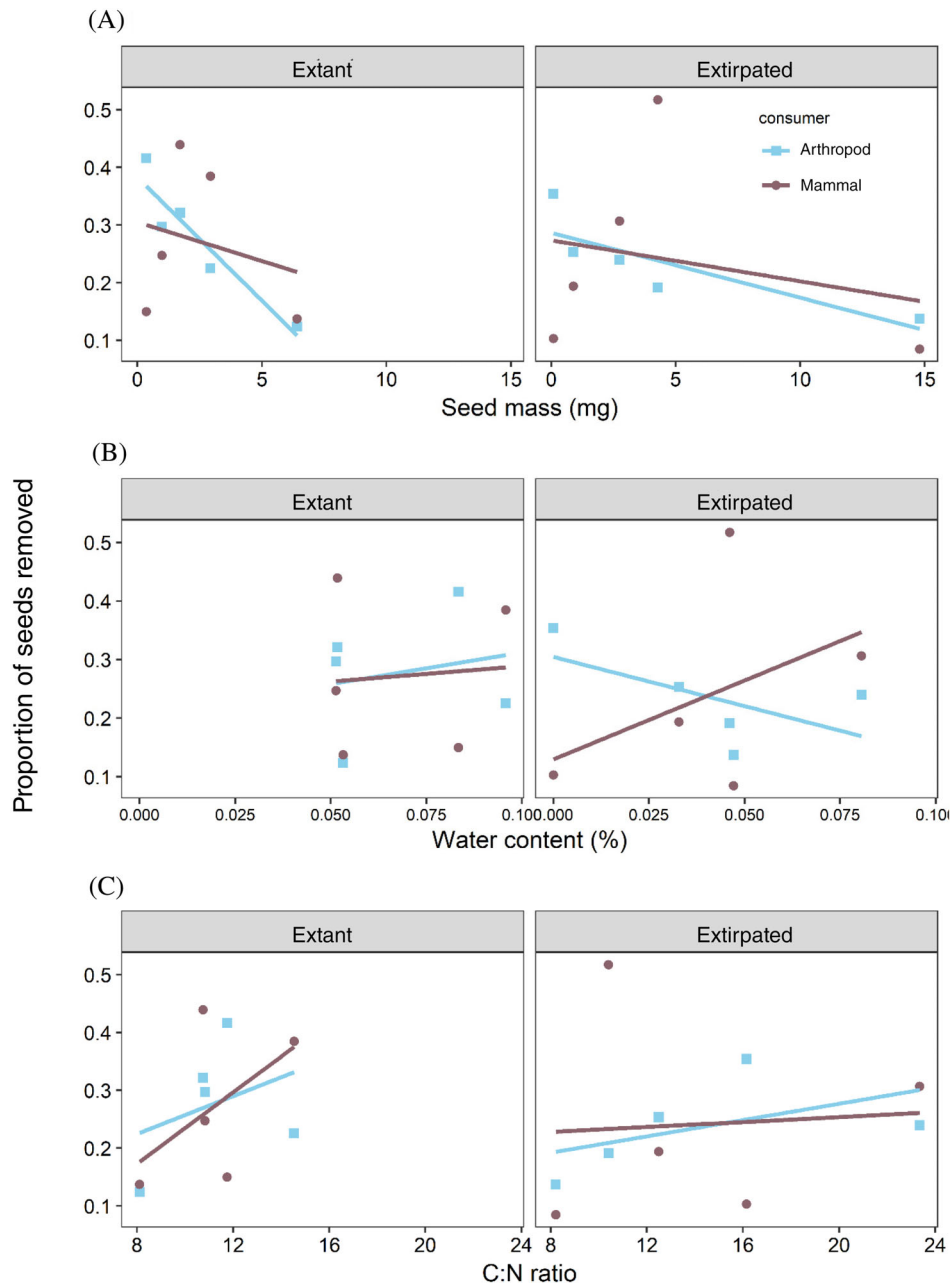


Figure 4. Proportion of seeds removed by arthropods (light blue squares) versus and small mammals (lavender circles; estimated as the difference in seed predation between "All Consumer" and "Arthropod Only" trays), depending on (A) seed mass (mg), (B) water content (% of mass), (C) C:N ratio. Granivory and traits are estimated at the species level. The left and right columns show removal rates for extant and extirpated species, respectively. See Figure S2 for error estimates.



$K = 0$  indicates random evolution;  $K = 1$  indicates trait conservatism;  $K > 1$  indicates species being more similar than expected (Blomberg et al. 2003). “PhyloSignal” also tests for greater phylogenetic signal (“PIC.variance”) than expected; traits with PIC.variance  $p \leq 0.05$  show non-random phylogenetic signal. Since our estimates of granivory by both small mammals and arthropods were phylogenetically conserved (Table S1), we performed phylogenetic generalized least squares (PGLS) analyses for granivory estimates with Brownian motion models of trait evolution (Garland et al. 1993; Martins & Hansen 1997). We incorporated the constructed phylogeny (Fig. S1) into the covariance structure using the “ape” package (v.5; Paradis & Schliep 2019). Small mammal and arthropod granivory were included as two separate response variables, and status, seed mass, water content, C:N, and two-way interactions of status  $\times$  each trait were included as predictor variables. Models were fit using the “gls” function in the “nlme” package (v.3.1-119; Pinheiro et al. 2015).

To examine species variation in consumer preferences, we used a linear mixed model with proportion seeds removed as the response variable, consumer type, species, and their interaction as predictor variables, and station as a random factor. We also examined whether proportion seeds removed differed within each confamilial pair; these models included consumer type, status, and their interaction as predictors and station as a random factor.

## Results

### Differences in Seed Traits and Predation Between Extirpated and Extant Species

Extirpated and extant taxa did not differ in their seed traits (Table S2). Species varied in seed mass ( $F_{11,228} = 215.82, p < 0.0001$ ) and water content ( $F_{10,205} = 5.99, p < 0.0001$ ; Table S2; Fig. 2). The *Baptisia*, *Liatis*, and *Silphium* demonstrated higher seed mass in extirpated than extant species (the only exception was the Lamiaceae, which demonstrated the opposite pattern) (Table S3;

Fig. 2A). In the Apiaceae, *Baptisia*, *Liatis*, and *Ratibida*, extant species had higher water content than extirpated species (Fig. 2B). Finally, in the Apiaceae, Lamiaceae, and *Ratibida*, extirpated species had a higher C:N ratio than extant species (Fig. 2C). Seed traits were not phylogenetically conserved (Table S1).

Granivory did not differ between extirpated versus extant species (status  $\chi^2_{1,14.85} = 0.35, p > 0.5$ ; Table S4).

### Different Seed Preferences Between Small Mammals and Arthropods

Mammals consumed almost twice as many seeds as arthropods, regardless of extirpation status (consumer  $\chi^2_{1,856.4} = 81.96, p < 0.0001$ ; mammals =  $45.2 \pm 3.14\%$  vs. arthropods =  $21.3 \pm 3.13\%$  seeds removed; Table S4; Fig. 3). Mammals also tended to consume larger-seeded species (mass  $\chi^2_{1,4} = 4.01, p = 0.11$ ), while arthropods consumed small-seeded species (mass  $\chi^2_{1,4} = 13.72, p = 0.02$ ) (although this pattern tended to be more pronounced among extant species; status  $\times$  mass  $\chi^2_{1,4} = 4.38, p = 0.10$ ; Table S5; Fig. S2; Fig. 4A). This pattern was similar when controlling for phylogeny. When controlling for phylogeny, small mammal herbivory tended to be higher on larger seeds ( $t = 2.49, p = 0.06$ ) while arthropods tended to consume smaller seeds ( $t = -2.47, p = 0.06$ ; Table S5). Small mammal and arthropod preferences did not differ for water content or C:N ratio (Table S5; Fig. 4B & 4C). However, when controlling for phylogeny, arthropods tended to consume seeds with higher C:N (lower nitrogen content), especially among extant species’ seeds (status  $\times$  C:N  $t = -2.43, p = 0.07$ ) (Table S5).

Consumers preferentially consumed certain species (consumer  $\times$  species  $\chi^2_{11,845.21} = 490.08, p < 0.0001$ ; Fig. 5; Tables S7B & S9). Arthropods consumed more *Lamiaceae* species while mammals consumed more *Liatis* species, *Silphium* species, and *Eryngium yuccifolium* (Table S6). Mammals and arthropods did not differ in their consumption of *Ratibida*, *Baptisia*, or *Thaspium trifoliatum*.

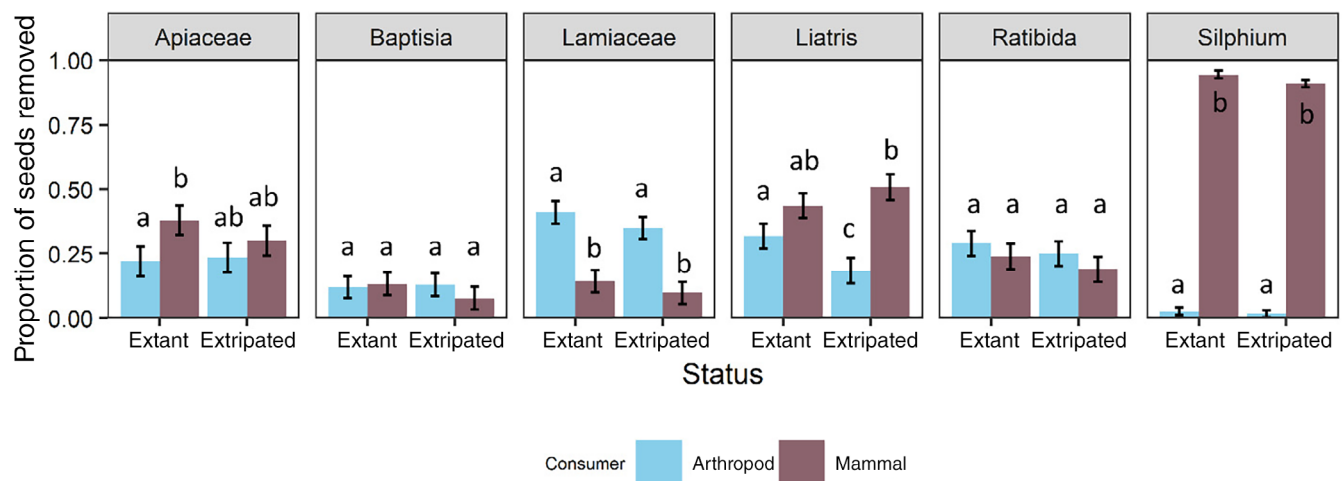


Figure 5. Proportion of seeds removed (least square means  $\pm$  SE) by arthropods (light blue squares) versus small mammals (lavender circles; estimated as the difference in seed predation between “All Consumer” and “Arthropod Only” trays) across the six confamilial pairs (12 extirpated vs. extant species) included in this study. Letters represent differences in consumer preference within a genus (e.g. mammals consumed significantly more extant *Eryngium yuccifolium* [Apiaceae] seeds than arthropods did) at the  $\alpha = 0.05$  level (Tukey tests).

## Discussion

Seed removal in a restored prairie depended on granivore identity and seed size but not extirpation status. Most seed removal occurred via small mammals. Small mammals preferred larger seeds while arthropods consumed smaller seeds and seeds with high C:N (less nitrogen content). Preferences for these traits likely have ecological consequences for plant and granivore communities in restored prairies, as seed consumption can affect seedling emergence and community composition (Howe & Brown 2001). Additionally, extant and extirpated species experienced similar granivory, likely due to the similarity in their seed traits, suggesting that seed predation on rare species may not be a critical management consideration in prairie restorations whose goal is to restore rare or threatened species.

### No Differences in Seed Traits or Granivory Between Extirpated and Extant Species

Overall, locally extinct and extant species did not differ in their seed traits. However, within phylogenetic pairs, extirpated species' seeds tended to have lower nitrogen content (higher C:N) and be heavier than extant species. High seed nitrogen content has been linked to increased germination and seedling establishment (Hara & Toriyama 1998; Naegle et al. 2005). Here, lower seed nutritional resources could correlate with extirpation events. Seed mass is a key fitness-related trait (Adler et al. 2014), as species with large seeds may demonstrate reduced seed production (Venable 2007; Cochrane et al. 2015) but higher seedling survival (Moles & Westoby 2004) (although seed size does not correlate with greater germination or establishment in this system; Fig. S3). Demographic studies on these species reveal that extirpated species produce significantly fewer seeds than extant species (M. Zettlemoyer, 2021, unpublished data), supporting a potential trade-off between large seed size and reduced seed production in some plant families.

We detect no evidence that granivory differed between the extirpated and extant species studied here. Similarly, perennial plants can be robust to <50% seed harvest rates (Meissen et al. 2017), and 30% seed removal (via caging 70% of reproductive plants) leads to a relatively low (0.2–31.7%) probability of extinction in a rare herb (Kurkjian et al. 2017), suggesting that the low rates of granivory detected here may not correlate with high extinction risk. Future work should compare extinction risk (i.e. population growth rates) with and without granivory estimates incorporated into population models.

### Differences in Granivore Preferences for Seed Traits

Similar to previous studies, small mammals preferred large seeds (Abramsky 1983; Celis-Diez et al. 2004; Connolly et al. 2014; Chen & Valone 2017; Dylewski et al. 2020; but see Kollmann et al. 1998; Gong et al. 2015). This relationship was independent of extirpation status. In most mammals, a positive relationship exists between granivore body size and seed size preference (Chen & Moles 2015). We also detected a preference for smaller seeds among arthropods, similarly to Mittelbach and Gross (1984) and Pearson et al. (2014). These

seed size preferences are consistent with optimal foraging theory (Dylewski et al. 2020) as consumer differences likely correlate with differences between seed-handling ability (e.g. mouth size, time to tear seed apart) and optimal net rate of energy intake (Kerley & Erasmus 1991). However, consumers not considered here (e.g. smaller seed predators or fungi) could also have consumed smaller-seeded species. Altogether, our data are consistent with the idea that body size filters what seeds are suitable for granivores, although other seed traits will inform diverse seed predator preferences.

Arthropods also tended to consume seeds with higher C:N ratios, or seeds with lower nitrogen content, while mammals favored seeds with higher nitrogen content (lower C:N ratio) (although this pattern was only true when controlling for phylogenetic relationships). This may be due to different nutritional needs between small mammals and arthropods. Nutritional needs (e.g. nitrogen/protein; Mariotti et al. 2008) are often higher in larger-bodied animals due to higher metabolic rates, which often scale with body size (Reichle 1968; Nagy 1994). Although small mammals preferred seeds with high nitrogen content, they did not consume large quantities of the two legumes (nitrogen-fixing species) in our study, *Baptisia tinctoria* and *B. bracteata*. This could be because some granivores can distinguish structural strength of seeds (Lundgren & Rosentrater 2007), and these *Baptisia* have hard seed coats; because *Baptisia* contain secondary chemicals, especially alkaloids, that can deter herbivores (Cranmer & Turner 1967); or due to high pre-dispersal predation in *Baptisia* (Petersen et al. 1998). This finding again supports optimal foraging theory wherein body size correlates with nutrients needed for energy gain (Pyke 1984).

Granivory by both small mammals and arthropods was phylogenetically conserved in this system, suggesting that other phylogenetically conserved traits might influence patterns of granivory. For example, the Lamiaceae seeds have a strong odor (M. Zettlemoyer, 2019, personal observation) that could serve as a deterrent or attractor (Taylor et al. 2020). Chemical defenses such as high phenol, tannin, or alkaloid content also result in lower predation (Gong et al. 2015) and can differ between congeners (Siemens et al. 1992), but were not measured here. Additionally, other traits like seed coat thickness are not accounted for by measurements like seed mass, which also likely impact feeding preferences (Blaney & Kotanen 2001; Sih & Christensen 2001). We note that the phylogenetic conservatism of granivory could also be due to the abundance of Asteraceae species included in this study.

### Importance of Small Mammals as Granivores

Small mammals contributed most to granivory in this restored prairie. This result mirrors previous studies in grasslands, which find that mammals are a prominent granivore (Klinkhamer et al. 1988; Hulme 1994; Reed et al. 2004; Pellish et al. 2017), although other studies in this area find that insects remove more seeds than small mammals in first-year prairie restorations (Linabury et al. 2019). This may be because arthropod communities likely differ between first-year prairie restoration and

older, established prairies (Woodcock et al. 2021). Small mammal granivory is also likely high in this older restored prairie due to its dense vegetation, as rodents often prefer high vegetation cover while foraging (Ahlgren 1966; Clark & Kaufman 1990; Hulme 1997). However, small mammal populations fluctuate both seasonally and across years (Merritt et al. 2003), so future studies might quantify small mammal granivory over multiple seasons and years. The presence of large predators (e.g. hawks and owls) could influence seed predation. Additionally, granivory by small mammals can decrease the number of seeds in a prairie (Heggenstaller et al. 2006), potentially resulting in reduced native seedling establishment, increased weed establishment, and lower native diversity (Schurr et al. 2004; Orrock et al. 2009; Abernathy et al. 2016; Pellish et al. 2017). Preferential consumption of certain species by small mammals (e.g. *Silphium* and *Liatris*) could alter local species composition (Kerley & Erasmus 1991; Chambers & MacMahon 1994). Future work might quantify how seed removal affects seedling establishment and community composition in this system. Understanding how small mammal consumption affects seed losses could aid conservation and restoration efforts for the native species examined here, which are used in tallgrass prairie restorations (Grman et al. 2015).

### Managing for Granivory in Restored Prairies

Here, we identify species with relatively high consumption rates (species with >50% of seeds removed included *Liatris punctata*, *Silphium perfoliatum*, *S. terebinthinaceum*) for which feeding deterrents could be developed and applied during restoration (e.g. vertebrate exclosures, feeding deterrents like capsaicin [Hemsath 2007; Pearson et al. 2018] or bergamot oil [Taylor et al. 2020], or the addition of sterilized birdseed to deter predation on native seeds [Riebkens et al. 2018]). We also find that seeds with particular characteristics are more at risk of predation, suggesting that seed traits could be used to characterize species' risk of consumption prior to establishment. This mirrors the growing evidence that plant traits can be used to generalize potential management effects (Clark et al. 2012; Zirbel et al. 2017). For example, in prairie restorations with large populations of small mammals such as meadow voles and field mice, it might be useful to compensate for seed removal of species with large seeds by tailoring seed mixes (e.g. doubling seeding density in the case of highly preferred species; Orrock et al. 2009) or protecting seeds by caging reproductive individuals (Kurkjian et al. 2017). The seed predation rates observed here were in an established, 20-year-old restoration, and seed predation on these same species might differ in more recent prairie plantings with different plant, small mammal, or arthropod communities. Finally, we find that granivory is similar on extant and extirpated species. This suggests that introductions of rare or extirpated species need not focus on a higher risk of seed predation for these species' establishment. For example, eight prairie species that had not been recorded in naturally occurring populations in Kalamazoo County since the 1940s were reintroduced into 29 restored prairies in southwestern Michigan (Grman et al. 2015); these restorations likely do not need to consider

additional management for granivory on reintroduced extirpated species.

This study shows that seed traits and species identities, but not extirpation status, influence the feeding preferences of granivores in established prairie restorations. Small mammals accounted for the majority of seed losses. Future work should link granivory to plant establishment and population growth rates in restored prairies as well as develop protocols to reduce the effects of small mammal granivory on seed predation in restorations. This research illustrates a prominent role of seed predation, particularly by small mammals, in older restored prairies, suggesting that understanding how plant traits affect species interactions may be important for predicting biodiversity outcomes in prairie restorations.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Phylogeny of the confamilial pairs of prairie species included in this study.

**Figure S2.** Proportion of seeds removed by arthropods (light blue squares) versus small mammals, depending on (A) seed mass (mg), (B) water content (% of mass), (C) C:N ratio.

**Figure S3.** Effect of seed mass (mg) on (A) proportion of seeds germinated and (B) proportion of seedlings established at the end of their first growing season.

**Table S1.** Phylogenetic signal of extirpation status, seed traits, and granivory.

**Table S2.** Results of linear mixed models testing whether (1) seed mass (mg), (2) percent water content, (3) C:N ratio differs between (A) extirpated versus extant species (status  $\chi^2$ ) or (B) among species (species F).

**Table S3.** Results of linear models testing whether (A) seed mass (mg), (B) percent water content, and (C) C:N ratio differ between extirpated versus extant species (status) within each confamilial pair.

**Table S4.** (A) Results of a linear mixed model testing the effects of consumer (arthropods vs. small mammals), status (extant vs. extirpated), and their interaction on the proportion of seeds removed.

**Table S5.** Effect of status and seed traits on granivory.

**Table S6.** Results of linear models testing whether granivory by small mammals versus arthropods differs between extirpated versus extant species within each confamilial pair.

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