

## RESEARCH ARTICLE

# A non-native earthworm shifts seed predation dynamics of a native weed

Emilie E. Regnier<sup>1</sup>  | Stephen M. Hovick<sup>2</sup>  | Jianyang Liu<sup>3</sup>  |  
Steven Kent Harrison<sup>1</sup>  | Florian Diekmann<sup>4</sup> 

<sup>1</sup>Department of Horticulture & Crop Science, Ohio State University, Columbus, Ohio, USA

<sup>2</sup>Department of Evolution, Ecology and Organismal Biology, Ohio State University, Columbus, Ohio, USA

<sup>3</sup>School of Plant and Environmental Sciences, Virginia Tech, AHS Jr. Agricultural Research and Extension Center, Winchester, Virginia, USA

<sup>4</sup>Food, Agricultural, and Environmental Sciences Library, Columbus, Ohio, USA

**Correspondence**

Emilie E. Regnier

Email: regnier.1@osu.edu

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**Abstract**

1. Introduced seed dispersers can shift seed predation dynamics in native species, impacting native plant establishment and spread. We studied the effect of the non-native earthworm, *Lumbricus terrestris*, on seed loss dynamics in the large-seeded native annual, *Ambrosia trifida* (giant ragweed), an expanding agricultural weed whose seeds are heavily predated by mice. *Lumbricus terrestris* may protect seeds against rodent predation by caching them in its burrows from which seedlings can emerge unharmed; however, little is known about the ability of earthworms to compete with rodents for seeds. We investigated this interaction and how environmental factors affected the competitive outcome.
2. In a 2-year field study, we analysed relative rates of seed removal by earthworms and mice for seeds dispersed at various times in habitats that varied in vegetative cover.
3. Species-specific responses to environmental conditions drove variation in the share of seeds taken by earthworms versus mice, with earthworms gaining relatively more seeds under warmer, wetter conditions and in low plant cover habitats, and mice obtaining more seeds under colder, drier conditions and in high cover habitats.
4. Environmental factors also determined which competitor accessed seeds first, and this conferred a competitive advantage that was compounded over time.
5. Earthworms cached some seeds under all experimental conditions, suggesting that *L. terrestris* can act mutualistically with giant ragweed in diverse environments.
6. *Synthesis and applications.* Our results support the hypothesis that the non-native earthworm *Lumbricus terrestris* behaves as a seed dispersal mutualist for the native annual giant ragweed by caching its seeds in its burrows, thereby reducing their availability to rodent seed predators. The data also support the view that interactions among the environment and competing seed predators determine the fate of seed pools in response to species-specific environmental preferences. In crop fields where *L. terrestris* is abundant, additional efforts to prevent giant ragweed seed return may be warranted due to the likelihood that earthworms will increase

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giant ragweed soil seed pools. *Lumbricus terrestris* is expanding its range throughout temperate regions and may similarly affect secondary seed dispersal and seed predation dynamics of large-seeded species in other plant communities.

#### KEYWORDS

*Ambrosia trifida*, giant ragweed, *Lumbricus terrestris*, non-native earthworm, rodent seed predator, secondary seed dispersal, seed dispersal mutualism, seed predation dynamics

## 1 | INTRODUCTION

Seed predators can influence plant population dynamics and community composition through their impacts on seed pools (Larios et al., 2017). An understanding of seed predation dynamics can therefore guide ecologically based weed and invasive plant management (Davis & Raghu, 2010; Westerman et al., 2003). However, seed predation rates can vary widely, depending on interactions among seed predators and environmental factors (Crawley, 2014; Perea et al., 2013). When predators with different seed consumption behaviours co-occur, seed pool sizes are influenced by the proportion of seeds handled and seed mortality exerted by each predator (Tamura et al., 2005; Theimer, 2005). Seed predators that exert lower mortality may act as plant mutualists in the presence of more destructive competitors, but as antagonists in their absence (Bronstein, 1994; Siepielski & Benkman, 2008). The introduction of non-native species that interact with seeds in novel ways can alter seed predation dynamics, with implications for seed survival and seedling establishment (Sawaya et al., 2018; Shiels & Drake, 2015; Theimer, 2005).

Deer mice (*Peromyscus maniculatus bairdii*, *P. leucopus*) are the principal vertebrate seed predators in Midwestern US row-crop agriculture (Berl et al., 2017) and play an important role in weed seed losses, particularly for large-seeded species whose seeds are readily detected by rodents. Mice exert high seed mortality by eating many seeds in situ, and also by consuming most of the seeds they cache for winter use (Abbott & Quink, 1970; Den Ouden et al., 2005; Howard & Evans, 1961). The introduction of the anecic earthworm *Lumbricus terrestris* into North America by European settlers (Edwards & Bohlen, 1996) represents the addition of an evolutionarily novel seed disperser that may affect seed pools. The earthworm collects and stores plant litter, including seeds, inside its vertical burrows, consuming the organic matter as it decomposes (Edwards & Bohlen, 1996; Regnier et al., 2008). Many weed seeds are resistant to microbial decomposition in soil and are too large for earthworms to ingest (>2 mm; Shumway & Koide, 1994). Earthworm burial of these seeds may protect them from detection and consumption by rodents, increasing soil seed pools available for seedling recruitment.

Giant ragweed *Ambrosia trifida*, a native allergenic annual, has shifted from a predominantly ruderal weed of field, forest and stream margins to one of the most economically destructive and difficult to control weeds of row-crop agriculture in the US Corn Belt

and Canada (Page & Nurse, 2015; Regnier et al., 2016). *Lumbricus terrestris* buries seeds of giant ragweed, with seedlings often emerging from burrow openings (Schutte et al., 2010). Burial of giant ragweed seeds by earthworms can decrease seedling emergence due to burial of some seeds below emergence depth limits; however, as the seeds (approximately 1 cm in length) cannot be directly ingested by earthworms and can persist several years when buried, initial reductions in seedling emergence may be compensated by reduced predation losses and higher seed numbers in soil (Harrison et al., 2007; Regnier et al., 2008).

While shifts in cropping systems and the evolution of adapted giant ragweed biotypes undoubtedly contribute to giant ragweed population increases (Liebman & Nichols, 2020; Page & Nurse, 2015; Regnier et al., 2016), shifts in seed predation dynamics may have also played an important role. This view is supported by documentation of giant ragweed increases before the appearance of herbicide-resistant biotypes (Page & Nurse, 2015). Giant ragweed seeds are highly vulnerable to seed predation, with mice being the principal predator (Harrison et al., 2003). Seed predation losses can reach 80% during the interval from dispersal through emergence (Harrison et al., 2003), and models predict that seed predation losses reduce giant ragweed population densities and the need for weed control (Liebman & Nichols, 2020).

A recent survey in the United States and Canada indicated that giant ragweed abundance in crop fields was strongly associated with its abundance in ruderal habitats, as well as with the presence of *L. terrestris* in crop fields and reduced-tillage practices (Regnier et al., 2016). *Lumbricus terrestris* can attain high population densities in reduced-tillage fields and field margins where soil disturbance is minimal (Edwards & Bohlen, 1996; Holden et al., 2019). Such habitats also favour foraging by rodents because the presence of vegetative cover reduces their own predation risk (Lichti et al., 2017). Thus, *L. terrestris* may decrease giant ragweed seed losses in crop fields and bordering habitats, playing direct and indirect roles in giant ragweed establishment in crop fields.

*Lumbricus terrestris* is considered beneficial in agricultural soils due to its favourable effects on soil fertility and physical properties, but detrimental in North American forests where it disrupts ecosystem functioning by removing surface plant litter and altering soil physico-chemical characteristics (Craven et al., 2017; Hendrix & Bohlen, 2002). The potential for *L. terrestris* to impact seed pools is important to understand given its expanding range

and low likelihood of eradication from ecosystems once established (Hendrix & Bohlen, 2002). Non-native earthworms compete for seeds with vertebrate seed predators in forests and open habitats (Cassin & Kotanen, 2016; McTavish & Murphy, 2020); however, little is known about *L. terrestris* competition with rodent seed predators. Earthworm–rodent interactions may vary with plant cover or other factors that favour seed detection by one species over the other. In no-tillage crop fields, a stronger spatial association of giant ragweed seedlings and *L. terrestris* burrows was observed when weather conditions during the previous fall were moist with mild temperatures, which favour earthworm foraging (Schutte et al., 2010). Such responses could influence the proportion of seeds handled by each species and hence the size of the surviving seed pool (Den Ouden et al., 2005; Heithaus, 1981). The goal of this research was to expand our understanding of *L. terrestris*–rodent competition for giant ragweed seeds as a function of environmental context. We hypothesized that variation in vegetation cover and seed dispersal time would influence seed foraging by *L. terrestris* and mice, and that *L. terrestris* would be likely to detect and forage seeds before mice due to its greater population densities (Edwards & Bohlen, 1996).

## 2 | MATERIALS AND METHODS

### 2.1 | Experimental design

This study was conducted at the Waterman Agricultural and Natural Resources Laboratory in Columbus, Ohio, USA (40°00'N, 83°02'W), a 106-ha research farm comprised of annual crop fields, grass pastures and a forested area. Air temperature and precipitation were recorded continuously by a nearby weather station. In each of our two study years, we selected 10 sites with the goal of establishing five sites each of lower and greater vegetative cover (see Table S1 in Supporting Information). Plant cover was rated through visual evaluation of per cent ground cover by living plants, structural complexity (e.g. woody debris and/or shrubs), canopy height and proximity to neighbouring vegetation. Each year, the five sites with greatest vegetative cover were classified as high cover and the five sites with lowest vegetative cover as low cover. High cover sites included forest edges, creek borders, standing crops and weedy fallow fields; low cover sites included harvested crop fields, fallowed fields with low weed cover and tree alleys. Fields ranged from 0.2 to 1.8 ha and border habitats (e.g. forest edges, creek borders) ranged from 5 to 10 m wide and from 20 to 500 m long. Sites were separated by at least 40 m and different sites were selected each year.

At each site, we established two 10 × 3 m treatment plots, one of which was the undisturbed vegetation and the other of which served as a control with no living vegetation. Control plots were located 5–10 m away from their paired vegetated plots and were established in a mowed tall fescue *Festuca arundinacea* roadway sprayed with glyphosate (1.0 kg/ha) 2 weeks before seeds were first dispersed. Control plots provided conditions lacking living vegetation across all sites for comparison with the vegetated plots, thereby providing

some statistical control over the variability occurring across the wider area as well as a broader range of habitat conditions in which to test our hypotheses.

We monitored seed removal over time from a 10-m transect established within each plot. Seed removal by *L. terrestris* and mice was determined by tagging giant ragweed seeds with 40-cm long polyester sewing threads. The dispersal unit of giant ragweed (referred to here as 'seed') is an achene enclosed within a spiny lignified involucre. To secure the thread, we made a small incision in the terminal spine with a razor blade, inserted the thread and glued the spine back together with a small drop of cyanoacrylate glue. Seeds were harvested from a nearby giant ragweed population each fall. Twenty tagged seeds were dispersed along each transect at two different dates each year (3 November and 17 November 2005 [year 1]; 26 October and 7 November 2006 [year 2]) to simulate natural seed dispersal, which occurs from September through November (Harrison et al., 2001). Seeds from the first dispersal batch were spaced 0.5 m apart along the transect, and seeds from the second dispersal batch were interspersed equidistantly between them. Seeds were secured in place by tying the free end of the thread to a stake at that position. To simulate a matrix of natural seed distribution on the soil surface near the transect, additional giant ragweed seeds were distributed at each site at a density of approximately 240 seeds/m<sup>2</sup> at each dispersal date in a 1-m band around the transect (Baysinger & Sims, 1991). The additional seeds also served to standardize any potential differences among sites in endemic giant ragweed seed dispersal; however, only one site had giant ragweed plants present (see Table S1).

Due to unanticipated disturbance of two of the high cover sites in year 1 immediately before the second seed batch was distributed, these sites were reclassified from high to low vegetative cover for the second dispersal batch and an additional high cover site was added. Thus, for the second batch in year 1, we had seven low and four high cover sites.

### 2.2 | Data collection and statistical analysis

The condition of tagged seeds was noted approximately every 2 days after dispersal during the first 2 weeks, every 3 to 5 days for the following 2 weeks, and once in the following spring (March) of each year. Seeds were categorized as intact (intact involucre remaining on the thread), buried by earthworms (thread protruding from a burrow opening) or predated by mice (damaged, empty involucre attached to the thread or involucre detached from the end of the thread). All empty involucres had holes with teeth-marked margins consistent with mouse predation—this damage is easily distinguished from that caused by other giant ragweed seed predators (Harrison et al., 2003). Of the seeds classified as predated by mice, the proportion consumed in situ was 68 ± 4% in year 1 and 47 ± 6% in year 2. Seeds removed from threads may have been consumed elsewhere or cached. We assessed variation in the percentage of seeds removed by earthworms or, in a separate model, removed by mice, within the first 4–6 days after seed dispersal as a function of

Year, Dispersal Batch and their interaction. These models included the random effect of Treatment nested within each Year-Site combination, to account for spatial non-independence of the vegetated plots and paired control plots. Mouse species observed in the study area included *Peromyscus maniculatus*, *P. leucopus* and *Mus musculus*. We did not attempt to quantify mouse population densities. As small mammal densities are mainly driven by food availability (Prevedello et al., 2013), dramatic changes in mouse populations seemed unlikely over the 2-year period at our experimental sites due to the relatively stable cropping and management history of the surrounding fields.

*Lumbricus terrestris* population densities were estimated by counting middens (mounds of castings and debris). This earthworm establishes a permanent burrow capped by a midden that remains spatially stable for several years (Potvin & Lilleskov, 2017). Midden densities were estimated by different means each year: in year 1, middens were counted within a 20-cm band centred on the transect on 1 February; and in year 2, the presence or absence of a midden at each 0.25-m increment along the transect (i.e. at each dispersal point) was recorded on 14 November. To combine these two different measures of earthworm population density in models where data from both years were used, we standardized the observed earthworm density values to range from 0 to 1 within each year (by subtracting the minimum density from an observation and then dividing by the range). We used t-tests to test for differences in midden density by Treatment (vegetated or control plot) within a given year, after determining that site-level Cover did not influence midden densities.

A 'removal difference' metric was calculated as the proportion of the 20 seeds per dispersal batch removed by mice minus the proportion removed by earthworms. Batches that were removed primarily by mice thus have removal difference values approaching one and those removed primarily by earthworms have values approaching negative one. Our analyses are based primarily on removal difference values calculated from data recorded in March, which captures season-long trends in seed removal patterns. We ran statistical models as GLMMs in R version 4.0.1 using the package `lme4` (Bates et al., 2015). Our initial models included the effects of site-level Cover (high or low vegetation cover), Treatment (vegetated or control plot, paired within site), Dispersal Batch, Year and all interactions as fixed effects. We also included the random effect of Treatment nested within each Year-Site combination. We simplified models by removing non-significant interactions based on likelihood-ratio tests and AIC-based model comparisons until further simplification could not be supported in this baseline model. Inferences regarding statistical significance were based on a critical  $\alpha$  of 0.05. Two additional predictors, earthworm midden density and the order of seed removal (see below), were subsequently added to this baseline model in an attempt to explain more variability in removal differences. Where multiple models were compared, we used  $\Delta$ AIC (the difference between AIC values for competing models) to determine which model fit the data better. A  $\Delta$ AIC value of at least 2 indicates that the model with a lower AIC is preferable (Burnham & Anderson, 2002).

We also conducted analyses on a categorical variable we refer to as the 'first-take' metric, which expresses whether seeds in a given

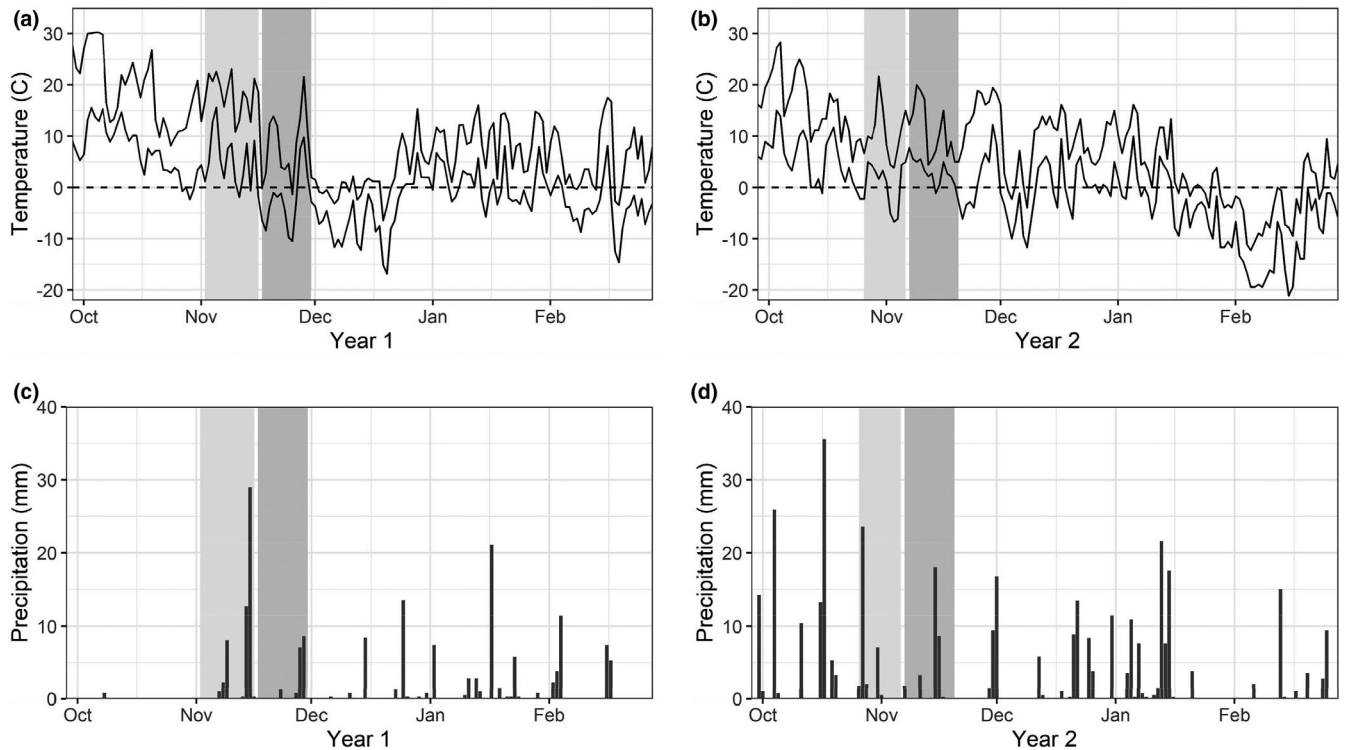
batch were first removed by mice, first removed by earthworms or whether mice and earthworms first removed seeds on the same day. Because the first-take variable is categorical with multiple levels, we used multinomial regression and the R package `MLOGIT` (Elff, 2020) to assess which factors influenced the probability of earthworms taking seeds first or a tie occurring, relative to mice being first. Model simplification followed the same procedures as above.

### 3 | RESULTS

#### 3.1 | Abiotic conditions and their effect on earthworm and mouse activity

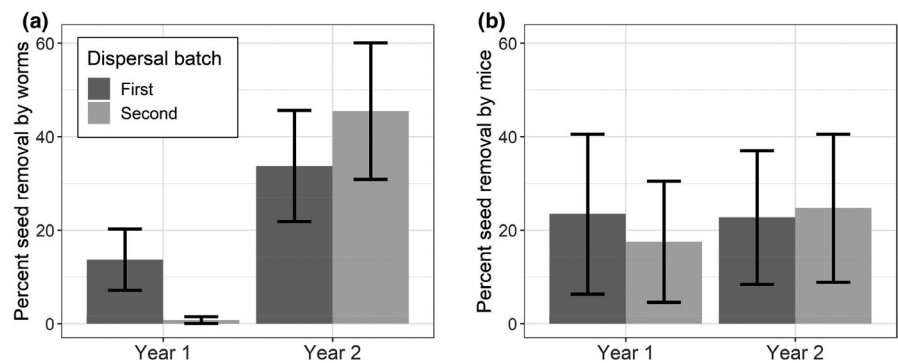
In year 1, the study area received 0.8 mm of precipitation during the 4 weeks before the first seed dispersal compared to 116 mm over the same time period in year 2 (Figure 1). Total rainfall during the 4-week period following initial seed dispersal was similar between years, with 72 mm received in year 1 and 67 mm in year 2. Although the average of daily air temperatures over the 4-week period following initial seed dispersal was similar between years, temperatures in year 1 declined steadily following initial seed dispersal, with minimum temperatures remaining mostly below 0°C beginning 15 days after the first seed dispersal and coinciding with the second dispersal. In contrast, temperatures in year 2 fluctuated without a clear downward trend, with minimum temperatures remaining mostly above 0°C during the 2 weeks following each seed dispersal batch.

Earthworm foraging varied substantially over time and appeared to be driven by temperature and precipitation. Within the first 4–6 days after seed dispersal, earthworms removed a lower percentage of seeds in year 1 than in year 2 (means  $\pm$  SE of  $7 \pm 2\%$  in year 1 and  $40 \pm 5\%$  in year 2; Year effect:  $p = 0.004$ ), presumably reflecting drier and colder conditions in year 1. Earthworm sensitivity to air temperatures likely also influenced their activity within years, leading to different responses to dispersal date between years (Figure 2a; Year  $\times$  Dispersal Batch interaction  $p < 0.001$ ). In year 1, earthworm activity differed strongly between dispersal batches (Tukey  $p = 0.007$ ), with  $14 \pm 3\%$  of the first batch and only  $0.8 \pm 0.4\%$  of the second batch removed in the first 4–6 days post-dispersal. Average minimum air temperatures during those intervals were 8.6 and  $-4.9^\circ\text{C}$ , for the first and second dispersal batch respectively. In contrast, earthworm activity increased from the first to the second dispersal batch in year 2 (Tukey  $p = 0.002$ ), with  $34 \pm 6\%$  of the first dispersal batch and  $46 \pm 7\%$  of the second dispersal batch removed in the first 4–6 days after dispersal, when minimum air temperatures averaged 2.6 and  $4.9^\circ\text{C}$  respectively. Unlike earthworms, mice took a similar percentage of seeds from each dispersal batch and year (Figure 2b; year 1:  $24 \pm 9\%$  from batch 1 and  $18 \pm 7\%$  from batch 2; year 2:  $23 \pm 7\%$  from batch 1 and  $25 \pm 8\%$  from batch 2;  $p > 0.2$  for the effects of Year, Dispersal Batch and their interaction). Mice also remained active over winter, whereas earthworms were mostly inactive. In year 1, between the first week of December and early March, mice removed an average of  $50 \pm 7\%$  of the remaining intact seeds, whereas earthworms removed only  $0.3 \pm 0.3\%$ . In



**FIGURE 1** Weather data in the period before and immediately after experimental seed dispersal events in year 1 (a, c) and year 2 (b, d) of the study. Temperature plots (a, b) depict daily minimum and maximum temperatures. Precipitation plots (c, d) depict daily precipitation. The two shaded regions in each panel indicate the 2 weeks immediately following giant ragweed seed dispersal events

**FIGURE 2** Seed removal by earthworms (a) and mice (b) within the first 4–6 days following dispersal. Error bars show 95% confidence intervals



year 2, mice removed an average of  $23 \pm 6\%$  of remaining intact seeds, whereas earthworms removed only  $6 \pm 2\%$ .

### 3.2 | Treatment effects on seed removal by mice and earthworms

The relative proportion of seeds removed by mice versus earthworms between the time of dispersal and the end of winter depended on site-level Cover (high or low vegetative cover) and Treatment (vegetated or control plot, paired within site), but these effects also varied by year (significant Treatment  $\times$  Cover  $\times$  Year and Treatment  $\times$  Year interactions; Table 1, baseline model; Figure 3a). In both years, mice removed relatively more seeds than did earthworms in the high cover plots (Figure 3a). In the low cover plots and in the control plots,

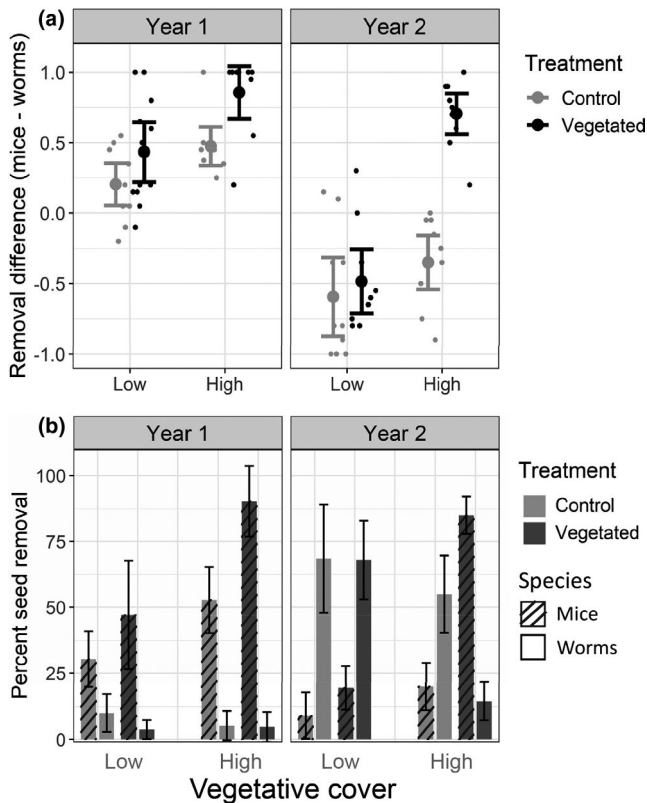
relative seed removal varied by year due to differences in earthworm activity (Figure 3b). In year 1, when earthworm activity was low, earthworms removed fewer seeds compared to mice, but in year 2 when earthworm activity was high, they removed more seeds than mice (Figure 3a). Overall, our study conditions in this baseline model explained nearly 70% of the variation in proportion of giant ragweed seeds removed by mice versus earthworms ( $R^2 = 0.68$ ).

### 3.3 | Additional factors influencing mouse versus earthworm seed removal

Earthworm population density estimates in control plots were more than twice than those in vegetated plots in both years: In year 1, there were  $22 \pm 1$  middens/m<sup>2</sup> in control versus  $10 \pm 2$  in vegetated

**TABLE 1** Parameter estimates (with standard errors, SE) and test statistics for statistical models incorporating various predictor variables explaining variation in post-winter seed removal difference values. Removal difference is the proportion of giant ragweed seeds removed by mice minus the proportion removed by earthworms. Significant model terms ( $p < 0.05$ ) are indicated with bold font. Positive parameter estimates for the Treatment and Cover effects indicate proportionally more seeds removed by mice than by earthworms in the vegetated relative to control plots and in low relative to high cover sites respectively. Positive parameter estimates for the effects of Year and Dispersal Batch indicate proportionally more seeds removed by mice than by earthworms in the later year and dispersal batch. The first-take metric is a categorical indicator of earthworms (W) removing seeds first or a tie occurring (Tie), relative to mice (M) removing seeds first

	Baseline model ( $R^2 = 0.683$ ; AIC = 45.8)			Baseline + middens model ( $R^2 = 0.756$ ; AIC = 32.3)			Baseline + middens + first-take model ( $R^2 = 0.793$ ; AIC = 19.2)		
	Estimate (SE)	$\chi^2$	p	Estimate (SE)	$\chi^2$	p	Estimate (SE)	$\chi^2$	p
Intercept	0.365 (0.13)	8.51	0.004	0.85 (0.16)	26.88	<0.001	0.935 (0.15)	37.75	<0.001
First-take (W vs. M)	–	–	–	–	–	–	-0.294 (0.07)	16.41	<0.001
First-take (Tie vs. M)	–	–	–	–	–	–	-0.177 (0.09)	–	–
Midden density	–	–	–	-0.667 (0.17)	14.74	<0.001	-0.541 (0.16)	11.03	0.001
Treatment (Trt)	0.301 (0.18)	2.91	0.088	0.037 (0.17)	0.05	0.830	0.04 (0.16)	0.06	0.799
Cover	-0.114 (0.15)	0.60	0.437	-0.081 (0.14)	0.36	0.550	-0.073 (0.12)	0.34	0.559
Year	<b>-0.733 (0.19)</b>	<b>15.21</b>	<b>&lt;0.001</b>	<b>-0.862 (0.16)</b>	<b>27.70</b>	<b>&lt;0.001</b>	<b>-0.709 (0.15)</b>	<b>21.03</b>	<b>&lt;0.001</b>
Dispersal Batch	0.037 (0.04)	0.67	0.413	0.028 (0.04)	0.39	0.530	-0.039 (0.04)	0.77	0.379
Trt x Cover	0.004 (0.2)	0.00	0.985	-0.027 (0.19)	0.02	0.888	-0.065 (0.17)	0.14	0.705
Trt x Year	<b>0.754 (0.27)</b>	<b>8.07</b>	<b>0.005</b>	<b>0.722 (0.23)</b>	<b>10.02</b>	<b>0.002</b>	<b>0.663 (0.22)</b>	<b>9.43</b>	<b>0.002</b>
Cover x Year	-0.131 (0.25)	0.28	0.595	-0.097 (0.21)	0.21	0.650	-0.129 (0.2)	0.43	0.513
Trt x Cover x Year	<b>-0.949 (0.35)</b>	<b>7.45</b>	<b>0.006</b>	<b>-0.871 (0.3)</b>	<b>8.28</b>	<b>0.004</b>	<b>-0.771 (0.28)</b>	<b>7.54</b>	<b>0.006</b>

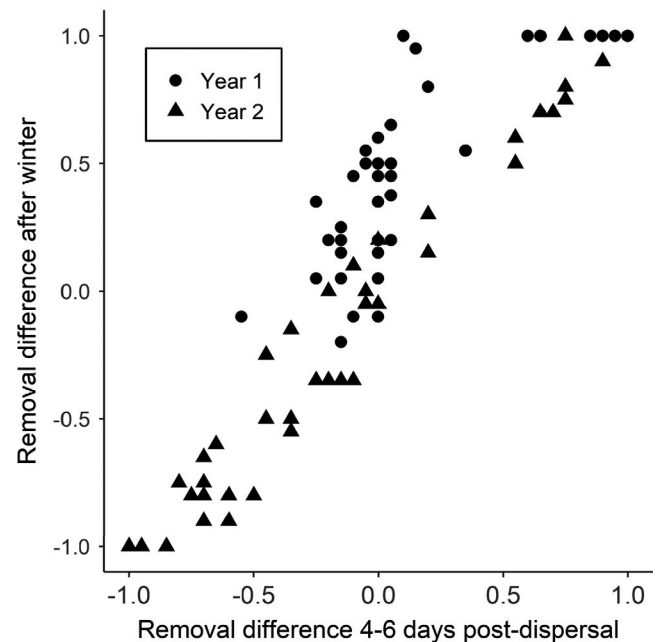


**FIGURE 3** Removal difference (a) and per cent of giant ragweed seeds removed by mice and earthworms (b) at the first census following winter in each experiment year. Removal difference is the proportion of seed removed by mice minus the proportion removed by earthworms, so positive values indicate that most seeds were removed by mice, and negative values indicate most were removed by earthworms. Error bars represent 95% confidence intervals

plots ( $p < 0.002$ ), and in year 2, there were  $37 \pm 5$  middens per transect in control versus  $14 \pm 3$  in vegetated plots ( $p < 0.002$ ). These differences likely reflect the history of lower soil disturbance and greater availability of organic residues in the frequently mowed grass roadways where the control plots were established (Edwards & Bohlen, 1996). There were no differences in earthworm populations between low and high cover sites (each year: Cover effect  $p > 0.50$ ) and no interactions between Cover and Treatment ( $p > 0.75$ ).

Accounting for standardized midden density variation by adding this term to our baseline model did not change any of the significant effects but highlighted an additional significant negative effect of midden density on removal differences (Table 1, baseline + middens model), indicating that more seeds were removed by earthworms in plots that had a higher density of earthworm middens. Accounting for midden densities in this way led to a better fitting model ( $\Delta\text{AIC} = 13.5$ ) that explained over 75% of the variation in removal differences (Table 1).

The estimates of proportional seed removal by mice versus earthworms from early spring were highly correlated with proportional seed removal within the first 4–6 days of seed dispersal ( $r = 0.90$ ,  $t_{80} = 18.6$ ,  $p < 0.001$ ; Figure 4). Based on a subset of plots



**FIGURE 4** Correlation between removal difference values assessed at 4–6 days post-dispersal and at the first census after winter

from two of our four dispersal batches for which we had quantified seed removal within the first 24 hr following dispersal (batch 1 in year 1 and batch 2 in year 2), these patterns were largely determined within just a single day after dispersal ( $r = 0.83$ ,  $t_{38} = 9.3$ ,  $p < 0.001$ ).

The inclusion of a first-take categorical variable indicating whether seeds were first removed by earthworms or if a tie occurred (earthworms and mice first removing seeds the same day), relative to mice being first, yielded a final model in which all significant effects from the previous models were unchanged and the first-take variable was also significant (Table 1, baseline + middens + first-take model). Where mice removed seeds first, proportionally more seeds were removed by mice (higher removal difference values), and where earthworms removed seeds first, proportionally more seeds were removed by earthworms. In cases where a tie occurred, proportional seed removal did not differ from those when either earthworms or mice accessed seeds first (Tukey  $p > 0.115$ ). This final model fit our data much better than either of the two previous models ( $\Delta\text{AIC} = 13.1$  and 26.6, for the baseline model and baseline + middens model respectively), explaining nearly 80% of the variation in removal differences (Table 1).

### 3.4 | Factors influencing whether rodents or earthworms removed seeds first

The likelihood of earthworms removing seeds before mice was higher in year 2 than in year 1 and higher in the first than in the second dispersal batch (Table 2), both consistent with our previous observations that earthworm activity was influenced by abiotic

conditions. The probability of earthworms removing seeds first was also increased by 91% in the control plots compared to the vegetated plots, consistent with higher earthworm population densities in the control plots. The likelihood of a tie (relative to first removal by mice) was also higher in year 2 than in year 1 and in the first dispersal batch relative to the second (Table 2). Whether a site was considered low versus high cover did not influence whether earthworms or mice were more likely to remove seeds first ( $p > 0.2$ ; Table 2).

## 4 | DISCUSSION

Results from our study were consistent with the expectation that the net effect of competing predators on a common seed pool should reflect species-specific responses to environmental conditions. Much of the variation in relative seed removal by *L. terrestris* was attributable to its greater sensitivity to variation in precipitation and temperature compared to mice. The lower proportion of seeds removed by earthworms in year 1 (7%) compared to year 2 (40%) corresponded to a lack of precipitation preceding the first seed dispersal and freezing temperatures following the second seed dispersal. Others have reported decreased foraging by *L. terrestris* with declining soil moisture and as temperatures approach freezing (Edwards & Bohlen, 1996; Perreault & Whalen, 2006). It is common for *L. terrestris* to migrate deeper into the soil and enter an inactive period (aestivation) in response to unfavourable conditions at the soil surface (Edwards & Bohlen, 1996; Potvin & Lilleskov, 2017). The sequential stresses of dry soil followed by freezing temperatures in year 1 may explain the particularly low foraging rates by earthworms observed following the second seed dispersal of that year. Low seed removal over winter in both years of our study is consistent with studies by others reporting reduced *L. terrestris* activity in midwinter (Potvin & Lilleskov, 2017).

In contrast to earthworms, foraging by mice was similar over years and dispersal batches, suggesting little sensitivity to variation in rainfall and temperature. Although seed removal by mice can be enhanced by rainfall, which may increase the ability of mice to detect seeds via olfaction (Vander Wall, 1998), mice also detect food through visual cues (Greenwood, 1985). The roles of olfaction and visualization in detection of giant ragweed by mice remain unclear, but the large size of giant ragweed seeds may facilitate visual detection. Although cold temperatures can reduce foraging by mice (Guiden & Orrock, 2020; Manson & Stiles, 1998), decreasing temperatures and declining day length in autumn can stimulate seed predation and caching (Barry, 1976; Davis & Raghu, 2010). This may explain the lack of response by mice to seed dispersal date in our study. Mice can also maintain activity during cold temperatures via behavioural and physiological adjustments, such as shifting to diurnal foraging and entering into daily torpor (Guiden & Orrock, 2020; Lynch et al., 1978), which could account for the continued removal of seeds by mice we observed over winter.

Our results agree with previous findings that foraging by mice increases with plant cover (Cromar et al., 1999; Hulme, 1997; Manson

& Stiles, 1998). In sites with high cover, mice removed more giant ragweed seeds than earthworms regardless of abiotic conditions, but in low cover sites and the controls, seed removal by mice decreased, particularly in year 2 when earthworms were more active. In contrast, cover level had little direct impact on earthworm foraging; however, earthworms foraged more in the control plots than in the vegetated plots. This probably reflected long-term population responses to the favourable conditions in the control plots, which were established on permanent grass roadways. The control plots harboured greater earthworm population densities than the vegetated plots, which likely contributed to the greater seed share taken by earthworms in the controls. Higher earthworm populations in our control plots were consistent with other research showing greater *L. terrestris* abundance in grassy field margins than in adjacent crop fields (Holden et al., 2019).

We found that a species' ultimate share of the seed pool was largely predicted by its activity during the first week after seed dispersal, providing additional evidence that species-specific responses to abiotic conditions at the time seeds were dispersed played an important role in the competitive outcome. Locating seeds first may confer an initial advantage to a given seed predator that compounds over time. Rodents must weigh the advantage of nutritional gain against the metabolic cost and predation risk of foraging (Lichti et al., 2017). In the case of competing seed predators, there would be diminishing returns as a given seed pool dwindles, thus possibly conferring an asymmetric competitive advantage to the first species to locate and remove seeds.

The time required for predators to detect seeds depends, in part, on seed predator population densities (Den Ouden et al., 2005). In the Midwestern United States, *L. terrestris* population densities in crop fields can range from 1 to 40 earthworms/m<sup>2</sup> (Gibson et al., 2013; Simonsen et al., 2010) compared to mouse populations of 11–19 mice/ha (Berl et al., 2017; Clark & Young, 1986; Getz & Brighty, 1986). With a foraging range of up to 30 cm from their burrow openings (Nuutinen & Butt, 2005), an earthworm population of only 4 earthworms/m<sup>2</sup> could theoretically forage the entire soil surface nightly. Although a mouse can forage over a much larger area than an earthworm, it must do so while managing predation risk that varies with vegetative cover. Such microhabitat characteristics strongly influence rates of rodent seed removal (Den Ouden et al., 2005). Based on these considerations, we hypothesized that *L. terrestris* would remove seeds before mice in all plots. Indeed, in control plots, earthworms were more likely to remove seeds before mice, presumably reflecting both higher earthworm population densities and the tendency for mice to avoid open habitats. However, mice were more likely to remove seeds before earthworms in vegetated plots, suggesting that potential advantages conferred by an established *L. terrestris* population can be overcome where conditions are highly suitable for mouse foraging.

Although mice are not recognized as predators of earthworms (Edwards & Bohlen, 1996), they do consume earthworms occasionally, thus it is possible that mice affect earthworm foraging. *Lumbricus terrestris* withdraws rapidly and anchors itself within its burrow upon



**TABLE 2** Parameter estimates (with standard errors, *SE*), transformed probabilities and test statistics from multinomial logistic models explaining variation in the first-take metric, a categorical indicator of earthworms removing seeds first or a tie occurring (Tie), relative to mice removing seeds first. Significant model terms ( $p < 0.05$ ) are indicated in bold font. Positive parameter estimates for Treatment and Cover effects indicate that earthworms removed seeds first or a tie was more likely than mice removing seeds first in the vegetated relative to control plots and in low relative to high cover sites respectively. Positive parameter estimates for the effects of Year and Dispersal Batch indicate that earthworms collecting seeds first or a tie was more likely than mice collecting seeds first in the later year and dispersal batch

	Earthworms versus mice				Tie versus mice			
	Estimate ( <i>SE</i> )	Probability	Z	<i>p</i> -value	Estimate ( <i>SE</i> )	Probability	Z	<i>p</i> -value
Intercept	1.06 (0.87)	0.74	1.22	0.222	-0.34 (1.21)	0.41	-0.28	0.777
Treatment	<b>-2.37 (0.82)</b>	0.09	<b>-2.9</b>	<b>0.004</b>	-0.67 (0.91)	0.34	-0.73	0.465
Cover	1.08 (0.86)	0.75	1.25	0.211	-0.75 (1.18)	0.32	-0.63	0.527
Year	<b>3.86 (1.12)</b>	0.98	<b>3.45</b>	<b>0.001</b>	<b>4.94 (1.42)</b>	0.99	<b>3.48</b>	<b>&lt;0.001</b>
Dispersal batch	<b>-2.57 (0.85)</b>	0.07	<b>-3.02</b>	<b>0.003</b>	<b>-2.22 (0.96)</b>	0.1	<b>-2.32</b>	<b>0.02</b>

being physically contacted (Edwards & Bohlen, 1996), which interrupts its foraging for food. However, because mice do not consume earthworms during fall months (Whitaker Jr., 1966), it is unlikely that mice would impact earthworm foraging for giant ragweed seeds.

Overall, our results support the view that the distribution of a common seed pool among competing predators is driven by multiple environmental factors that vary over time and space, potentially culminating in a continuum of different seed fate outcomes. The potential for different seed fate outcomes across environments may also influence whether a seed predator acts as a mutualist or antagonist for a given plant species (Siepielski & Benkman, 2008; Theimer, 2005). Mice and *L. terrestris* both behave as giant ragweed antagonists when mice consume seeds and earthworms bury some seeds below their emergence depth limits (Regnier et al., 2008). However, earthworms may also behave as mutualists when competing with mice for seeds, given that the reduction in seedling recruitment they exert through deep seed burial (<40%; Regnier et al., 2008) is substantially lower than losses due to rodent consumption of cached seeds (>90%; Abbott & Quink, 1970; Den Ouden et al., 2005; Howard & Evans, 1961). Furthermore, seed mortality estimates based on reductions in seedling recruitment from earthworm-buried seeds likely underestimate seed survival, since giant ragweed seeds buried below emergence depth limits can remain dormant 5 years or longer (Harrison et al., 2007).

The fact that *L. terrestris* cached giant ragweed seeds in all test environments suggests earthworms have the potential to act mutualistically with giant ragweed by burying seeds at depths that prevent predation by mice but are still conducive to seedling emergence. This outcome, when integrated over broad temporal and spatial scales that include arable fields and ruderal habitats, could facilitate giant ragweed seed survival and spread in agricultural landscapes. Giant ragweed abundance in ruderal habitats was identified recently as the single factor most strongly associated with its abundance in crop fields of the United States and Canada (Regnier et al., 2016). Thus, monitoring and control of giant ragweed in field borders is essential to prevent incursions into nearby crop fields. Cropping systems based heavily on soybean production are more likely to increase giant ragweed population

densities, and giant ragweed biotypes with multiple herbicide resistance and/or a prolonged emergence period further challenge efforts to manage giant ragweed (Liebman & Nichols, 2020; Page & Nurse, 2015; Regnier et al., 2016). Where *L. terrestris* is abundant, these challenges are likely to be exacerbated, thus making it particularly important to prevent seed return and diversify cropping systems to reduce opportunities for giant ragweed to establish and reproduce (Liebman & Nichols, 2020).

The assessment of the relative impact of earthworm seed burial on giant ragweed spread requires more detailed information on the distribution and abundance of *L. terrestris*. Recent surveys indicate *L. terrestris* is more common in the north-eastern than the western regions of the US Corn Belt (Regnier et al., 2016; Reynolds, 2011), therefore we expect greater impacts in this area. It seems likely that the increasing adoption of conservation tillage practices (Conservation Technology Information Center, 2021) that favour *L. terrestris* populations is also favouring giant ragweed establishment via the mutualism described in this paper. Research in no-tillage crop fields in the eastern US Corn Belt indicated that as much as 95% of the total giant ragweed seedling population emerged from earthworm burrows in areas where the two species co-occurred (Schutte et al., 2010), suggesting *L. terrestris* can exert considerable control over giant ragweed seed dispersal and seedling establishment when conditions are favourable for earthworm population growth and foraging.

## 5 | CONCLUSIONS

Our results reinforce the view that interactions among the environment and competing seed predators determine the fate of seed pools. In addition, they highlight the crucial importance of early seed acquisition in determining seed competition outcomes—particularly the importance of being the first seed predator to detect seeds. The interaction of *L. terrestris* and mice competing for giant ragweed seeds in this study was driven by their differential responses to abiotic and biotic environmental conditions, and their competitive outcomes suggest a greater likelihood for *L. terrestris* to behave

as a giant ragweed mutualist in environments where the probability of seed predation by rodents is high and when temperature and precipitation conditions are favourable for earthworm foraging. An understanding of these outcomes may be helpful in limiting giant ragweed populations in managed environments, interpreting historical changes in its populations over time and space and predicting its population dynamics where it is newly introduced. Since our current study was limited to evaluating giant ragweed seed losses only, further research is needed to clarify the population-level implications of *L. terrestris* activity, particularly where giant ragweed seed banks may buffer against short-term seed losses to predation. The ability of *L. terrestris* to compete with rodents for seeds in all test environments suggests *L. terrestris* may affect seed predation dynamics of other large-seeded species in other plant communities. This research adds to the growing body of literature illustrating the potential for an introduced seed disperser to exert effects on the seed predation dynamics of a native plant species, with potential consequences for its establishment and spread across the landscape.

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#### CONFLICT OF INTEREST

The authors declared that there is no conflict of interest.

#### AUTHORS' CONTRIBUTIONS

E.E.R. conceived the ideas and designed the methodology, with J.L. and S.K.H. contributing; J.L. and F.D. collected the data; S.M.H. led the data analysis, with all authors contributing; E.E.R. led the writing, with S.M.H., S.K.H. and J.L. contributing. All authors contributed critically to the drafts and gave final approval for publication.

#### DATA AVAILABILITY STATEMENT

Data and analysis scripts for this paper are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.v15dv41w9> (Hovick et al., 2021).

#### ORCID

Emilie E. Regnier  <https://orcid.org/0000-0002-6264-0236>  
 Stephen M. Hovick  <https://orcid.org/0000-0003-1774-9686>  
 Jianyang Liu  <https://orcid.org/0000-0002-4516-2949>  
 Steven Kent Harrison  <https://orcid.org/0000-0001-8937-1614>  
 Florian Diekmann  <https://orcid.org/0000-0002-7961-6769>

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#### SUPPORTING INFORMATION

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