Received: 17 October 2022 | Revised: 7 April 2023 | Accepted: 18 April 2023

DOI: 10.1002/ecs2.4641

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE
Agroecosystems

Suppression of weed communities by granivores over time in an agroecosystem

Jonathan G. Lundgren[1] | **Randy L. Anderson**[2]

[1]Ecdysis Foundation, Estelline, South Dakota, USA

[2]North Central Agricultural Research Laboratory, USDA-ARS, Brookings, South Dakota, USA

Correspondence
Jonathan G. Lundgren
Email: jonathan.lundgren@ecdysis.bio

Handling Editor: Heidi Liere

Abstract

Invertebrate granivore communities can consume numerous weed seeds in cropland, but how this granivory influences weed recruitment over time in continuous no-till systems is unknown. Weed and surface-active granivore communities were determined in soybeans (*Glycine max*) over 3 years in eastern South Dakota. We examined seed removal rates of sentinel redroot pigweed, green foxtail, and lambsquarters (*Chenopodium album*) seeds and applied gut content analysis of granivores to determine which species consume immuno-marked seeds of green foxtail (*Setaria viridis*). Weed stands with low diversity and high biomass production were associated with granivore community complexity. In turn, granivore community complexity was associated with weed communities with low diversity and high biomass in the subsequent growing season. Fall seed consumption, as measured by seed removal rates and gut content analysis of foxtail seed markers, was positively correlated with weed recruitment in the subsequent growing season. Seed specialists behaved differently toward focal weed species than the granivore community at large. *Gryllus pennsylvanicus* abundance was correlated with higher green foxtail consumption and removal rates. None of the other dominant green foxtail consumers revealed a similar set of responses. We propose a feedback mechanism whereby granivore community complexity in cropland leads to larger but fewer weeds over multiple years. Weed communities with these characteristics then lead to more complex granivore communities. If these relationships persist over time with minimal disturbance in continuous no-till cropping systems without pesticides, this feedback loop could reduce weed cover.

KEYWORDS
Carabidae, cricket, granivory, gut content analysis, seed bank, *Setaria viridis*, soybean, weed recruitment

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
Published 2023. This article is a U.S. Government work and is in the public domain in the USA. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

INTRODUCTION

Thousands of weed seeds from dozens of plant species can be found per square meter in cropland (Andreasen et al., 2018; Forcella et al., 1996), and this abundant resource represents a compact source of nutrients and energy that often rivals or exceeds the nutrient value of other foods for granivores (Davis & Raghu, 2010; Lundgren, 2009). Among the macroinvertebrates, earthworms, millipedes, isopods, crickets, carabid beetles, and ants are noted granivores of weed seeds within agroecosystems. Each species specializes on seeds with particular characteristics (Foffová et al., 2020; Honěk et al., 2007; Lundgren & Rosentrater, 2007), and suppressing weed recruitment necessitates the maintenance of a community of granivores. Granivory can be a major source of mortality for seed banks within integrated weed management programs (Blubaugh & Kaplan, 2016; Bohan et al., 2011; Bredeson et al., 2020; Carbonne et al., 2020; Daouti et al., 2022; Lundgren et al., 2013; White et al., 2007), but the impact of granivores on weed recruitment is affected by many factors (Davis et al., 2011). The influence of invertebrate community structure on the suppression of a focal pest is a growing emphasis in applied ecology (Finke & Snyder, 2010; Greenop et al., 2018; Lundgren & Fausti, 2015; Ostandie et al., 2021), but arguably has not been sufficiently prioritized within seed–granivore interaction studies.

Granivory has historically been assessed using removal rates of sentinel seeds, and recently developed molecular gut content analysis may provide additional insights into this ecosystem service. Microscopic gut content analysis was first used to establish granivore–seed interactions in the late 1800s (Forbes, 1881), but then this approach was largely overlooked until 2008 (Lundgren & Harwood, 2012). Molecular gut content analysis is well correlated with biological control of other organisms (Albertini et al., 2018; Choate & Lundgren, 2015; Lundgren & Fergen, 2014; Peterson et al., 2018), but there are few examples of this technique used to establish granivore–seed interactions in the field (Blubaugh et al., 2016; Frei et al., 2019; Lundgren et al., 2013). The technique substantiates our understanding of dominant granivorous taxa within agroecosystems and reveals new key granivorous groups that had not been previously suspected. Despite their widespread use, the question of whether granivory proxies (i.e., predation on seed cards and gut content analysis of seed consumption) are correlated with reduced seedling recruitment remains elusive.

The characteristics of a weed community within an agroecosystem could affect the population levels and foraging behavior of its granivorous consumers. Vegetation cover often increases arthropod diversity (LaCanne & Lundgren, 2018; Lundgren & Fergen, 2010) and ecosystem services provided by granivores (Barbercheck & Wallace, 2021; Blubaugh et al., 2016; Carbonne et al., 2022; Davis & Liebman, 2003; Heggenstaller et al., 2006; Meiss et al., 2010). For example, granivory is favored by cover crops and crop residue that is used in part to suppress weeds. Natural enemies are attracted to their prey resources (Holling, 1959; Vinson, 1976), and carabid beetles are numerically associated with seed rain from weeds (Bohan et al., 2011; Carbonne et al., 2022), but the presence of annual plants may represent a special circumstance. Granivores that specialize or prefer seeds of a particular weed may not accrue in a habitat with a historical legacy of this weed because annual weed communities may vary substantially from year to year in a crop field, and their seeds are an ephemeral resource. A more proximate cue for granivores that might suggest an impending resource would be the adult plants. A central question that warrants attention is whether granivores of a weed species are influenced by weed community structure.

As a farm system transitions from frequent tillage and herbicide use to continuous no-till with diverse rotations, weed pressure shifts and declines (Anderson, 2015, 2016; Daouti et al., 2022; Storkey & Neve, 2018). Here, we examined whether granivore–weed community interactions may be an important contributor to these changes in weed recruitment. To accomplish this, we measured weed communities and granivore communities, and used gut content analysis and removal rates of sentinel weed seeds as proxies for granivory in a series of fields undergoing transition to continuous no-till without agrichemical treatments. Soybeans in the Northern Great Plains were selected as the focal agroecosystem due to its large geographic footprint (34 million ha were planted with soybeans in 2020) (NASS, 2020), and an ongoing change in weed management practices prompted by glyphosate-resistant weeds motivates a search for developing integrated weed management schemes (Mortensen et al., 2012; Moss, 2019). We asked the questions: (1) Does weed community structure affect granivore communities and granivory rates? (2) Do granivore communities and granivory affect weed recruitment and weed community structure in the subsequent growing season? (3) Does dietary specialization on a weed species affect a granivore's ability to regulate a weed species' population growth? If granivory is affected by weed community characteristics and vice versa, then the resulting changes in weed communities of soybeans may thus result in regional shifts in this ecosystem service.

METHODS

This experiment was conducted over three years in the autumns of 2011, 2012, and 2013 near Brookings,

South Dakota, USA (44.3535 and −96.8059), in soybean fields that had a corn–soybean–spring wheat rotation in no-till prior to the study. In 2010, a winter rye cover crop preceded all of these rotations. Soybeans (Pioneer 91B56 RR, Pioneer Hibred International, Johnston, IA, USA) were drilled at 395,000 seeds per hectare, using 0.5 m row spacing. Planting dates were 11 May 2011, 17 May 2012, and 26 May 2013. No fertilizers, herbicides, insecticides, or fungicides were used after the study was established. Field dimensions were 7 × 10 m and occasionally abutted one another. Twenty-four fields within this matrix were examined in this study each year. Only 14 of the 24 fields were sampled in each year for all three years of study; the other 10 fields per year varied among years. Fields were embedded in a larger soybean field. Occasionally two fields would be adjacent to one another.

Weed community characteristics

Weed communities were sampled once per field annually and were assessed 7 weeks after emergence (6 July 2011, 18 July 2012, and 24 July 2013). Weed communities were sampled from quadrats at three random locations (0.33 m^2 each) per field in 2011, two random locations (0.5 m^2 each) per field in 2012, and four random locations (0.33 m^2 each) in 2013. Within each quadrat, all weeds were identified to species level and were enumerated. The weeds were then cut at the soil surface and were dried and weighed to determine weed biomass per unit area. Based on these measurements, the abundance, species richness, species diversity (Shannon *H*), and species evenness (Pielou's Index, *J*) were determined for each field. All measurements were standardized as per square meter for analyses. The weed community was comprised exclusively of annual species.

Deployment of marked seeds

Green foxtail (*Setaria viridis*) was selected as a focal weed species because of its consistent dominance within cropping systems of the region and its wide palatability to a range of granivores. To identify specific seed predators, seeds of green foxtail were marked and dispersed into each plot during the autumns of 2012 and 2013. Green foxtail seeds were locally collected in 2012 and were stored at 4°C until their use in the following experiments. Seeds were cleaned and dried, and placed into a glass flask. A solution of Rabbit IgG (Product I8140, Sigma Aldrich Inc, St Louis, MO, USA) was made in 1× phosphate-buffered saline (PBS); 1 g of seeds was marked with 12.5 μL of IgG in a 1.25 mL PBS solution. The seeds were stirred by hand in this solution for 2 min. The antibody solution was then vacuumed from the seeds through a Buchner funnel, and seeds were air-dried for 24 h. Within 24 h of marking, the seeds were deployed into the field. A centralized area (1.5 × 3 m) of each plot was flagged, and 4 g of marked seeds was disseminated evenly throughout this area by hand. This resulted in a seed density of 1700 (2012) and 1050 (2013) per m^2, which is reflective of green foxtail seed densities in other agroecosystems (Forcella et al., 1996). The entire process was repeated in August, September, and October of the final two study years, directly before the sentinel seed dishes were deployed and the granivore communities were assessed.

Granivore community survey

In each study year, granivores were sampled using barrier-linked pitfall traps to amplify capture rates (Lundgren et al., 2013; Lundgren & Harwood, 2012). In the middle of each field, a sheet metal barrier (1 m long, 30 cm tall) was placed perpendicular to the soybean rows. A pitfall trap (10-cm diameter, covered with a 0.33 × 0.33 m board) was placed on either end of the barrier to capture any foraging seed predators encountering the barrier and walking right or left. A 1-cm^2 piece of Dichlorvos-impregnated vinyl (Hot shot No-pest Strip, United Industries Corporation, St Louis, MO, USA) was placed into the collecting jar of each pitfall to kill specimens. Seed predators were collected 12 and 24 h after the marked seeds were deployed; these specimens were frozen at −20°C for gut content analysis. Research has found that the protein marker in positive samples degrades quickly after this duration (Blubaugh et al., 2016; Lundgren et al., 2013). In all study years, traps were deployed monthly in August, September, and October. In 2011, specimens were harvested from the pitfall traps after 3 days. In 2012–2013, the pitfalls were allowed to continue to operate for 72 h after the marked seeds were deployed (except for the September and October samples in 2012, which were collected after 48 h due to rain), and all specimens collected (at 0–12, 12–24, and 24–72 h from when the seeds were deployed) were identified to species level (or as low a taxonomic unit as possible under a microscope; operational taxonomic unit [OTU]) and eventually pooled for community assessments. The sex of crickets was also recorded. This trap duration balances collecting sufficient numbers to reflect the community structure without trapping out the insects from a focal field. The result is a monthly assessment of the granivore community collected per plot per day.

Gut analysis to identify key granivores

In 2012 and 2013, granivores collected within 24 h (a subset of the full community) of the Rabbit-IgG marked seeds being deployed were subjected to ELISA-based gut content analysis. Each specimen was washed in 70% ethanol for 10 s to remove surface contaminants. Samples greater than 1 cm in length had their guts dissected with sterile instruments under the microscope. The guts or entire specimens (for smaller seed predators) were then macerated in PBS and frozen until they could be analyzed.

Each specimen was analyzed for the seed marker using Double Antibody Sandwich ELISA. First, 100 μL of primary antibody (1:500 in water; Anti-Rabbit IgG made in goat, Product R-2004, Sigma Aldrich) was incubated in each well for approximately 16 h at 4°C. The primary antibody was ejected, and 360 μL of blocking agent (1 g dry milk in 100 mL water) was added for 30 min. The blocking agent was ejected and wells were triple rinsed with PBST (a 0.05% solution of Tween-20 [Product P1379, Sigma Aldrich] in PBS). Next, 100 μL of the sample was incubated in the well at approximately 28°C for 1 h. The sample was ejected, wells were rinsed in PBST, and 100 μL of secondary antibody (anti-Rabbit IgG made in goat conjugated with horseradish peroxidase, 1:1000 in 1% milk solution; Product A6154, Sigma Aldrich) was incubated in the wells for 1 h at 28°C. The secondary antibody was ejected and the plate was triple rinsed with PBST. Wells were then incubated for 30 min with 50 μL of tetramethylbenzidine (BioFX, SurModics, Eden Prairie, MN, USA). Absorbance (optical density) was then read at 650 nm using a spectrophotometer (μQuant, Bio-Tek Industries, Winooski, VT, USA). On each plate, positive (1:500 solution of Rabbit IgG) and negative (water) control series were used to verify the efficacy of the reaction. A conservative two-tier approach was used to reduce false positives. If the samples on this first assay had absorbances that exceeded the mean of the negative control series by 2.5× the SD of the negative control series, then they were advanced for a second screening. In this second ELISA, each sample was run twice on a single plate using identical reaction conditions and steps, except that one of the wells replaced the primary antibody with PBS. Samples were considered positive if they exceeded this sample-specific negative control by 2.5× the SD of the blank negative control series (no sample). Thus, every positive sample was verified using two sets of stringent controls.

Seed removal rates

Sentinel seed dishes (Lundgren et al., 2013; Lundgren & Harwood, 2012) were deployed once per month; these dishes were concurrent with the seed marking trial and granivore community assessment. Sentinel seeds were affixed in plastic Petri dishes (10-cm diameter; with a 0.5-cm-tall rim) (Fargin Icewhole, Becton Dickinson, Lincoln Park, NJ, USA). In each dish, three 3-cm-long pieces of double-sided tape were used to affix 25 seeds each of common lambsquarters (*Chenopodium album*), redroot pigweed (*Amaranthus retroflexus*), and green foxtail to the tape. Fine quartz sand was then used to cover the exposed tape. Five of these dishes were embedded in each plot in a fixed, centralized "×" pattern. Seeds were exposed to granivory for 3 days, after which the dishes were collected and the mean number of each seed species removed per dish per day was recorded. The lip of the Petri dish may have affected foraging patterns, but the detritus on the soil surface occurred widely and produced similar barriers as the lips of our Petri dishes.

Data analysis

All statistics were conducted on Systat 13.1 (Systat Software, San Jose, CA, USA), and outputs of all statistical analyses that are not presented in this text are displayed in Appendix S1: Table S1. All data can be accessed at https://osf.io/sz9rh. All species encountered here were primarily univoltine, to the best of our knowledge. Centipedes, mites, spiders, Diptera, Hemiptera, and phalangiids were not included in these analyses. *Gryllus pennsylvanicus* and millipedes were not collected in 2011 but were collected in the later two years of the study. Species were defined as granivores if members of their family are known granivores or if their diets are poorly defined. The number of individuals and species was summed across months to generate an annual value. These annual sums were used to generate the species diversity (Shannon *H*) and evenness (Pielou's *J*) metrics for comparison.

The effects of sample year on individual weed community and granivore community characteristics were compared using ANOVAs, and significant differences among sample years were revealed using Fisher's least significant difference means comparisons.

To examine the influence of weed community on granivore community structure within a single growing season, linear mixed models (with year as a random factor, weed community parameter was the predictor variable, and granivore community parameter was the response variable) were used to compare annual granivore and weed community characteristics (abundance, richness, Shannon *H*, and Pielou's *J*). It is important to note that pitfall traps selectively measure the active invertebrate community, and rather than

the actual relative abundance of each taxon, pitfall traps measure the "activity-density" of this community (Kaspari et al., 2022).

To examine the influence of granivore community structure and granivory on weed recruitment and community complexity, general linear mixed model (with site as a random effect, granivore community parameter was the predictor variable, and weed community parameter was the response variable) was used to compare granivore community characteristics in the preceding year with weed community characteristics in the same field during the following season. The same relationships were examined between granivory rates (percentage of granivores positive for the foxtail-associated protein marker; and seed removal rates for each seed species) and weed community characteristics. Granivore communities and seed removal rates from 16 fields in 2011 were compared with weed communities in the same fields in 2012, and granivores from 15 fields in 2012 were compared with weed communities in 2013. Results from the gut content analysis from 2012 were compared with weed community characteristics in 15 fields in 2013.

To determine which species could be considered important green foxtail consumers, we evaluated which species were in the top 10% of abundance within the complete community (which was pooled across months and years). Then we ranked the community based on the proportion of each population that was positive for green foxtail seed marker protein and selected the top five most frequent consumers. Species on both lists were considered important green foxtail seed consumers. Linear mixed models were used to explore relationships between the abundance of the dominant three green foxtail consumers (*G. pennsylvanicus*, millipedes, and *Notiobia terminata*) and weed community characteristics and green foxtail abundance within a given study year. Green foxtail consumption rates and green foxtail seed removal rates were also related using a linear mixed model using field as a random variable. The same procedures were then applied to compare specialist granivore abundance and granivory rates to foxtail recruitment in the subsequent season.

RESULTS

Weed community

A total of 18 weed species were collected in soybean fields (Table 1; Appendix S1: Table S2). Common lambsquarters, redroot pigweed, and green foxtail were the dominant species in 2011, accounting for 65% of weeds in 2011. In 2012, rank order of the most abundant weeds was horseweed, green foxtail, common lambsquarters, and yellow oxeye. Common lambsquarters and green foxtail made up 37% of all weeds in 2012. Redroot pigweed was <1% of total weed abundance in 2012. In 2013, green foxtail was by far the dominant weed found, constituting 78% of all weeds found in the system. Redroot pigweed and common lambsquarters represented only 2% and 4% of the weeds in 2013. Weed biomass increased significantly ($F_{2,61} = 0.96$, $p < 0.001$), and richness ($F_{2,61} = 18.38$, $p < 0.001$), abundance ($F_{2,60} = 19.59$, $p = 0.001$), and diversity ($F_{2,60} = 10.19$, $p < 0.001$) decreased significantly over the 3-year study (Table 1). Weed evenness ($F_{2,60} = 0.34$, $p = 0.34$) did not vary significantly across sample years.

Granivore community

We identified 82 OTUs (e.g., morphospecies; 5707 invertebrate specimens; Table 1) as potential granivores (Appendix S1: Table S3) from a total of 8080 specimens. This community is represented by four classes, nine orders, and 20 families. The inventory is an underestimate of species because some of the taxa were grouped (e.g., Staphylinidae). More than half of the community (45 taxa) were species of Carabidae. In each field, we captured 79.26 ± 10.98 granivore specimens (mean ± SE), and there were 14.35 ± 0.63 granivore species, which produced a Shannon H of 1.97 ± 0.06. General trends in these data were an increasing abundance and species richness accumulating annually, and significantly fewer species and lower diversity in October versus early in the year (Table 2; Appendix S1: Table S4). Granivore abundance (i.e., activity-density) ($F_{2,67} = 37.78$, $p < 0.001$),

TABLE 1 Weed community characteristics in soybean fields per square meter.

Year	Biomass (g)	Abundance (no. weeds)	Richness (no. weed species)	Species diversity (H)	Community evenness (J)
2011	404.31 ± 63.74 A	40.06 ± 4.75 B	7.25 ± 0.36 A	1.61 ± 0.08 A	0.82 ± 0.04
2012	1034.04 ± 157.60 B	78.13 ± 10.07 A	5.75 ± 0.37 B	1.33 ± 0.07 B	0.78 ± 0.02
2013	1386.00 ± 113.73 C	16.14 ± 4.19 C	4.04 ± 0.34 C	1.01 ± 0.10 C	0.77 ± 0.05

Note: Data (mean ± SE) are reported from 16 fields in 2011 and 24 fields each in 2012 and 2013. Values within a column followed by different letters are significantly different from one another ($\alpha = 0.05$).

species richness ($F_{2,69} = 108.85$, $p < 0.001$), species diversity (H) ($F_{2,69} = 35.37$, $p < 0.001$), and community evenness (J) ($F_{2,69} = 5.66$, $p = 0.01$) increased significantly between the first and second years of the experiment (Table 2).

Gut content analyses

Thirty-eight of these granivore taxa were collected within the first 24 h of trap deployment and were analyzed for marked green foxtail seeds (Appendix S1: Table S3); 24 OTUs tested positive for the marker. Millipedes (Julidae), isopods, and crickets (*G. pennsylvanicus* and *Allonemobius* sp.) were the most frequently positive and abundant green foxtail consumers in the system. Female *G. pennsylvanicus* were much more likely to consume green foxtail than males (60% of specimens vs. 17%). Foxtail-consuming carabid adults included *Amara carinata*, *Amara musculis*, *Anisodactylus ovularis*, *Anisodactylus rusticus*, *Bembidion rapidum*, *Elaphropus*, *Harpalus caliginosus*, *Harpalus pensylvanicus*, *N. terminata*, and *Pterostichus permundus*; at least 5% of individuals in each of these populations consumed green foxtail (the most frequent consumers were *N. terminata* and *P. permundus*) (Appendix S1: Table S3). The single centipede tested was positive for the green foxtail marker.

Seed removal rates

On average, across all years, 20.52 ± 1.46%, 17.65 ± 1.60%, and 57.16 ± 2.11% of common lambsquarters, redroot pigweed, and green foxtail seeds, respectively, were removed per field over the 72-h observation period (Table 3; Appendix S1: Table S5). Total seed removal rates were 31.78 ± 1.45%, pooled across seed species. Granivores removed greater numbers of green foxtail seeds relative to redroot pigweed and common lambsquarters in 97% of the fields. The fewest seeds were always removed in October relative to the other months; otherwise there were few consistent trends in monthly seed removal rates across years.

Does weed community structure affect granivore communities?

The granivore community structure (response variable) was adapted to weed community characteristics (predictor variable), but within a growing season, granivore communities responded differently to weed communities than they did over the three years of research. When examined across study years (i.e., when data from all study years were pooled), weed communities with high biomass and low complexity supported a more complex granivore community (as measured with pitfall traps) within this agroecosystem. The number of granivore species ($F_{1,30} = 13.15$, $p = 0.001$) (Figure 1A), granivore abundance ($F_{1,30} = 9.28$, $p = 0.005$), and granivore diversity (H) ($F_{1,30} = 4.24$, $p = 0.048$) were positively correlated with weed biomass (Appendix S1: Figure S1); evenness of the granivore community was uncorrelated with weed biomass ($p > 0.05$). In contrast, there was a negative correlation between weed species richness and diversity and some granivore community characteristics. Specifically, weed species richness was negatively correlated with granivore abundance ($F_{1,30} = 4.93$, $p = 0.03$)

TABLE 2 Granivore community characteristics per soybean field over three years.

Year	Abundance (no. granivores)	Species richness (no. granivore species)	Species diversity (H)	Community evenness (J)
2011	30.88 ± 4.30 A	7.83 ± 0.58 A	1.41 ± 0.09 A	0.64 ± 0.05
2012	81.67 ± 5.67 B	17.50 ± 0.64 B	2.27 ± 0.05 B	0.80 ± 0.01
2013	87.73 ± 5.26 B	17.71 ± 0.35 B	2.23 ± 0.10 B	0.78 ± 0.03

Note: Values are given as mean ± SE and those values within a column followed by different letters are significantly different from one another ($\alpha = 0.05$).

TABLE 3 Seed removal rates of three weed species over time.

Year	Common lambsquarters	Redroot pigweed	Green foxtail	Total seeds consumed
2011	21.34 ± 1.55	26.65 ± 1.78	52.13 ± 2.09	100.12 ± 3.97
2012	10.94 ± 1.47	7.47 ± 1.17	30.46 ± 2.09	48.87 ± 3.59
2013	14.40 ± 1.16	6.05 ± 0.66	46.34 ± 1.71	66.78 ± 2.56

Note: Seed dishes (25 seeds per species) were deployed in soybean fields and removal rates were assessed after 3 days. Each value represents the seeds removed or damaged (mean ± SE) from each of the 24 soybean fields.

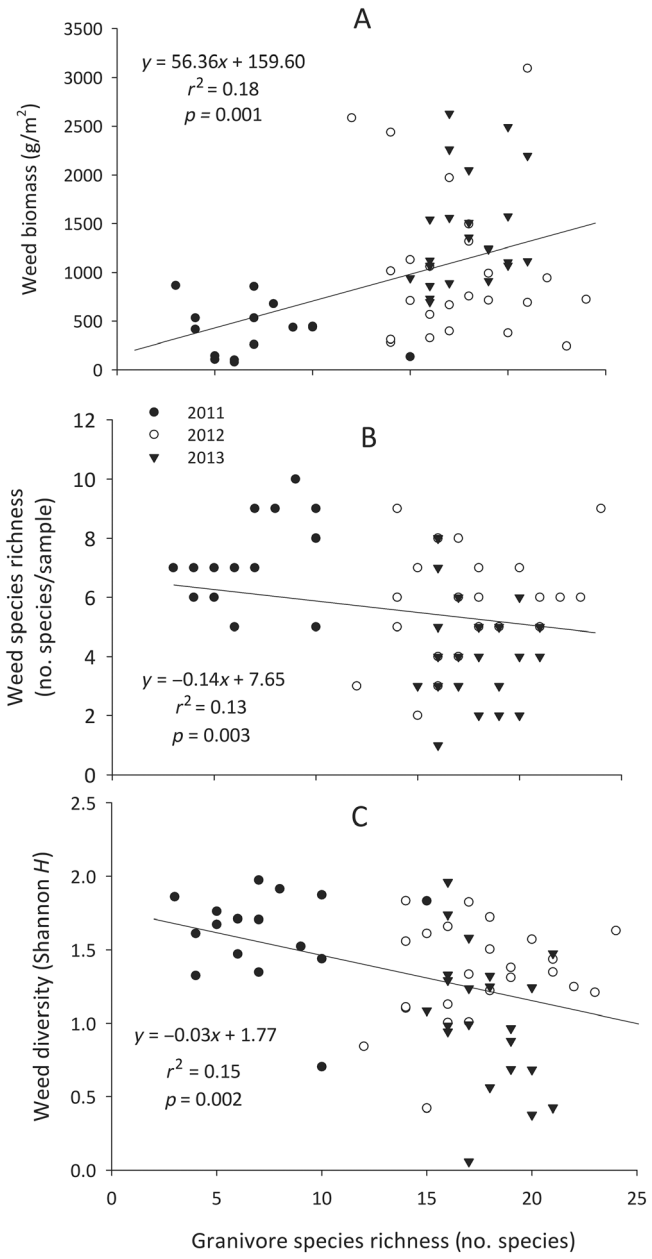


FIGURE 1 Weed community structure, (A) weed biomass, (B) weed species richness, and (C) weed diversity, is correlated with granivore species richness in soybeans over three sample years. All data points represent the correlations between these communities during a designated sample year, and the three sample years are designated by different symbols. Within individual sample years, there were no correlations between weed community structure and granivore species richness, but when all site years were examined, significant correlations were found in all three contrasts ($\alpha = 0.01$).

and granivore species richness ($F_{1,30} = 8.97$, $p = 0.005$) (Figure 1B; Appendix S1: Figure S1). Weed diversity was negatively correlated with granivore species richness ($F_{1,30} = 9.72$, $p = 0.004$) (Figure 1C) and granivore species diversity ($F_{1,30} = 5.86$, $p = 0.03$) (Appendix S1: Figure S1). Weed abundance and weed community evenness were uncorrelated with granivore community characteristics ($p > 0.05$). Figures of these contrasts not presented here are included in Appendix S1: Figures S1 and S2.

Does weed community structure affect granivory rates?

Weed community characteristics (predictor variable) were poorly related to granivory (response variable). Weed biomass, weed abundance, weed richness, weed diversity, and weed evenness in a field were uncorrelated with the proportion of granivores positive for foxtail protein in their guts ($p > 0.05$) (Appendix S1: Figure S1). Of the weed community characteristics tested, only weed species richness was positively correlated with total seed removal rates from the sentinel seed dishes ($F_{1,30} = 4.41$, $p = 0.04$) (Appendix S1: Figure S1). Weed biomass, abundance, diversity, and community evenness were uncorrelated with total seed removal rates ($p > 0.05$) (Appendix S1: Figure S3). When examining the removal rates of individual weed seed species, lambsquarters and foxtail removal rates were entirely unrelated to any of the weed community characteristics (an exception was that foxtail removal rates were correlated with weed abundance; $F_{1,29} = 12.27$, $p = 0.002$). Pigweed removal rates drove the relationship between total seeds removed and weed community characteristics. Specifically, more pigweed seeds were removed at higher weed diversity levels ($F_{1,30} = 13.68$, $p = 0.001$) and in fields with higher weed species richness ($F_{1,30} = 18.03$, $p < 0.001$) (Appendix S1: Figure S3); weed biomass had a negative effect on the number of pigweed seeds removed ($F_{1,30} = 9.88$, $p = 0.004$) (Appendix S1: Figure S3).

Does granivore community structure affect subsequent weed problems?

More diverse and abundant granivore communities (predictor variables) in the preceding year were associated with fewer weeds (response variables) (Figure 2). Granivore community structure in the preceding year was negatively associated with weed abundance (abundance: $F_{1,12} = 30.45$, $p < 0.001$; richness: $F_{1,12} = 47.95$, $p < 0.001$; H: $F_{1,12} = 30.01$, $p < 0.001$) (Figure 2A; Appendix S1: Figure S1). Weed richness was similarly affected by granivore community structure in the preceding year (abundance: $F_{1,13} = 10.74$, $p = 0.01$; richness: $F_{1,13} = 13.66$, $p = 0.003$; H: $F_{1,13} = 8.25$, $p = 0.01$)

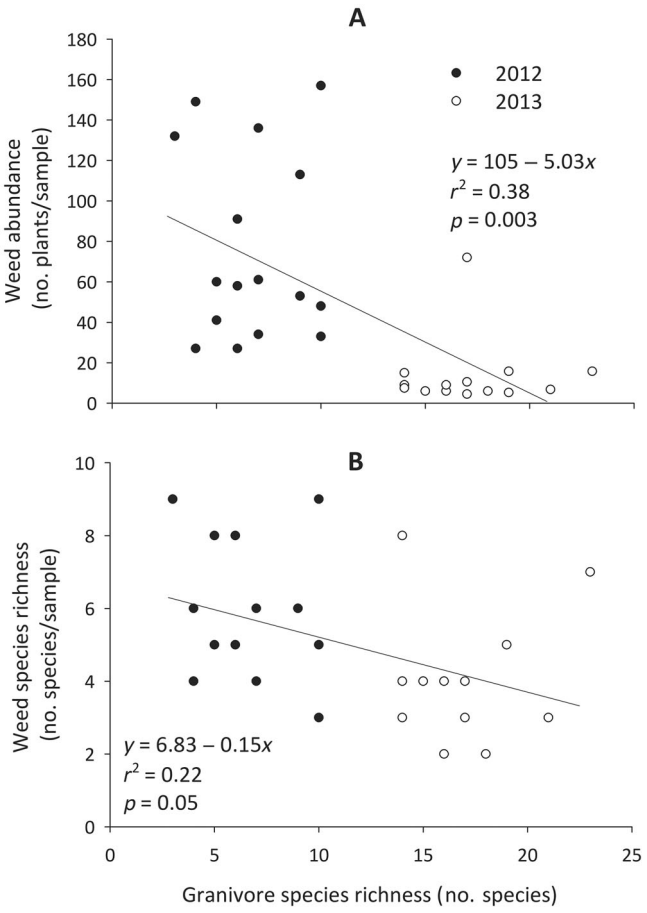


FIGURE 2 Granivore species richness affects weed recruitment, (A) weed abundance and (B) weed richness, in the subsequent field season in soybeans. All data points represent the correlations between granivore communities during the previous year (i.e., 2011 and 2012) and the weed community in the designated, subsequent year in the same field, and the three sample years are designated by different symbols. Within individual sample year contrasts (i.e., 2011 granivores with 2012 weeds), there were no correlations between weed recruitment and granivore species richness, but when all site years were examined, significant correlations were found in all three contrasts ($\alpha = 0.01$).

(Figure 2; Appendix S1: Figures S4 and S5). More abundant and species-rich granivore communities were associated with less weed diversity (H) in the subsequent year (abundance: $F_{1,13} = 7.96$, $p = 0.01$; richness: $F_{1,13} = 6.19$, $p = 0.03$) (Appendix S1: Figure S4); granivore diversity (H) in the preceding year was not associated with weed species diversity (H) ($F_{1,13} = 2.24$, $p = 0.16$) (Appendix S1: Figure S5). Granivore community diversity (H) in the preceding season was positively correlated with the amount of weed biomass ($F_{1,13} = 6.34$, $p = 0.03$), as was granivore species richness ($F_{1,13} = 4.78$, $p = 0.048$); granivore abundance was not correlated with weed biomass ($p > 0.05$) (Appendix S1: Figure S4).

Does granivory affect subsequent weed communities?

Greater granivory rates (predictor variables) in the previous year were associated with altered weed community structure (response variable). The more seeds that were removed in the previous year were strongly correlated with greater weed abundance ($F_{1,12} = 23.73$, $p < 0.001$) and species richness ($F_{1,13} = 7.01$, $p = 0.02$), and lower weed biomass ($F_{1,13} = 5.11$, $p = 0.39$) (Appendix S1: Figure S6). Seed removal rates in the preceding year were not associated with weed diversity ($F_{1,13} = 0.97$, $p = 0.34$) (Appendix S1: Figure S6). Gut content analysis detecting consumption of green foxtail was not associated with weed community structure (abundance: $F_{1,11} = 0.91$, $p = 0.36$; richness: $F_{1,13} = 2.57$, $p = 0.13$; biomass: $F_{1,13} = 0.48$, $p = 0.50$; H: $F_{1,13} = 1.36$, $p = 0.27$) (Appendix S1: Figure S6). Higher foxtail consumption (measured in frequency of consumption based on gut analysis) in the preceding season was associated with higher foxtail abundance ($F_{1,11} = 5.48$, $p = 0.04$).

Does dietary specialization on a weed species affect its ability to regulate a weed species population growth?

The gut content analysis identified specific foxtail seed consumers. Only three species were ranked as being both abundant and frequent green foxtail seed consumers (based on gut content analysis): millipedes, *G. pennsylvanicus*, and *N. terminata*. While all of these species were important consumers of green foxtail, various aspects of their responses to green foxtail suggest different degrees of specialization by granivores on this seed species.

During the current season, these abundant green foxtail consumers responded differently to weed community characteristics. None of the granivore abundance were correlated with foxtail abundance (millipedes: $F_{1,13} = 0.03$, $p = 0.87$; *G. pennsylvanicus*: $F_{1,13} = 0.28$, $p = 0.61$; *N. terminata*: $F_{1,13} = 0.98$, $p = 0.34$). Although they were all regarded as dominant consumers, trophic connections of these granivores were different during the focal growing season. Millipede ($F_{1,14} = 14.04$, $p = 0.002$) and *G. pennsylvanicus* ($F_{1,14} = 5.32$, $p = 0.04$) (Figure 3) abundance was both positively correlated with green foxtail removal rates. Foxtail abundance was not correlated with the proportion of *G. pennsylvanicus* ($F_{1,9} = 0.10$, $p = 0.76$), millipedes ($F_{1,7} = 0.002$, $p = 0.97$), or *N. terminata* ($F_{1,10} = 0.69$, $p = 0.43$) that were positive for the foxtail marker protein. *N. terminata* abundance was negatively correlated with green foxtail removal rates

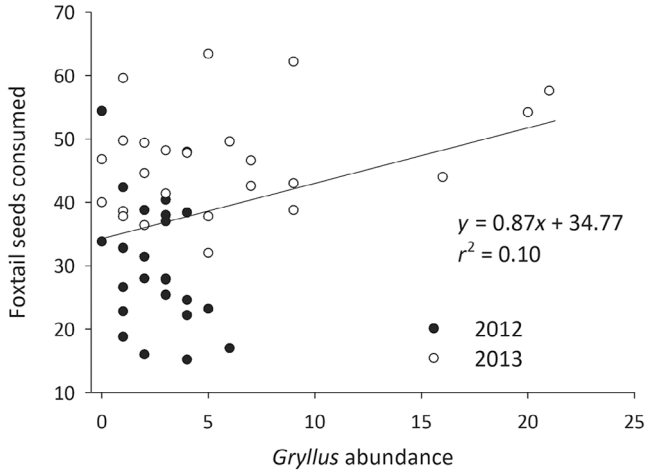


FIGURE 3 The abundance of *Gryllus pennsylvanicus* is positively associated with green foxtail (*Setaria viridis*) seed removal rates in soybeans.

($F_{1,14} = 5.96$, $p = 0.03$). In relation to the other seed species, millipede abundance was positively correlated with common lambsquarters seed removal rates ($F_{1,14} = 4.76$, $p = 0.047$), but *G. pennsylvanicus* and *N. terminata* were not ($p > 0.05$). None of these green foxtail consumers were numerically associated with pigweed removal rates during the current season.

The abundance of *G. pennsylvanicus* in the preceding season was positively correlated with the number of foxtail plants in the subsequent year ($F_{1,13} = 9.56$, $p = 0.01$). There was no correlation between the abundance of *N. terminata* or millipedes in the previous year and foxtail abundance ($p < 0.05$). *G. pennsylvanicus* proportion positive from the gut content analysis in the previous year was positively correlated with foxtail abundance in the focal year ($F_{1,9} = 8.15$, $p = 0.02$), but *N. terminata* and millipede proportion positive was unrelated to the abundance of foxtail ($p > 0.05$).

DISCUSSION

Complex interactions govern how weed and granivore communities interact in cropland. Weed communities in these soybean fields were often depauperate in species (usually less than 8 species per field) and an even narrower suite of species dominated the community. Over the 3-year experiment, weed communities were increasingly comprised of fewer species, but larger individuals (as represented by biomass) (Table 1, Figure 1). Weed communities with large individuals of a few species were associated with greater granivore diversity, and this granivore community in turn was associated with simpler weed communities with a few large individuals. Although granivore community structure was negatively associated with weed recruitment, granivory (as measured by seed removal and gut analysis) was positively related to weed recruitment; additional work should focus on how these granivory proxies reflect relative seed abundance. Finally, this work seems to describe a unique community of agrobionts, species that have adapted to living in cropland. Specialization of granivores on particular seed species, as well as niche partitioning of the granivore community, supports the idea of harboring complex granivore communities that are resilient to relative resource fluxes within a habitat and can respond quickly to pest outbreaks.

Why did simpler weed communities with larger individuals support more complex granivore communities over multiple years? Reductions in weed diversity have been widely observed in agroecosystems over the past 75 years (Storkey & Neve, 2018). An important question to keep in mind when interpreting our results is whether more diverse weed communities with lower biomass may be a desirable characteristic of agroecosystems (Gaba et al., 2020). Larger, mature weeds may produce more seeds than many small plants (Aarssen & Taylor, 1992; Geddes & Gulden, 2018; Klinkhamer & De Jong, 1987), and many of these small plants may not even be reproductive. Measuring seed rain would have helped to resolve whether these fields varied in seed resources relative to parent plant abundance and size. In addition to producing additional seed resources, larger weeds might also provide different microclimates (Hinsinger et al., 2009; Horton et al., 1984) for invertebrates on the soil surface, or affect the movement of granivores leading to higher pitfall trap captures in dense plant communities (Adis, 1979; Koivula et al., 2003). Thus, more resources or a better microclimate might have attracted and supported a more diverse and abundant granivore community.

Why was greater granivore community complexity associated with fewer, larger weeds over time? A more diverse granivore community might have reduced competition of emerging seedlings (Blubaugh & Kaplan, 2016; White et al., 2007). Microclimate on the soil, including temperature and moisture availability, affects seed germination rates (Boddy et al., 2012; Travlos et al., 2018), and often safe germination sites are scarce relative to seed availability (Davis, 2006). By reducing the seed reservoir and subsequent seedling emergence, a smaller number of weeds may have germinated, but these seedlings that remained were more successful. Over time, granivory may also have selected for a weed community that was adapted to granivore pressure, as the number of weed species per square meter after three seasons was only 56% of the number of weed species found at the onset of

the study (Table 1). Natural selection of the weed community may have occurred through a range of different defensive mechanisms, including seed defensive chemistry, mechanical components of the seed, or seed nutritional quality (Lundgren, 2009). The remaining weed community in the following year was less diverse with fewer, larger plants. This is the exact scenario that supports improved granivore community structure. Thus, a feedback loop seems to be supported that should lead to reduced weed cover over time.

Was there specialization of the granivore community on particular weed species? This work adds to our knowledge regarding which insects are the most important granivores in an agroecosystem. Of the 82 OTUs collected, only 38 taxa were abundant enough to justify gut analysis; this gut analysis revealed that 24 of these taxa were granivorous on green foxtail seeds. Ants, carabids, and crickets are often regarded as the most important granivores in agroecosystems (Lundgren, 2009), but gut analysis (which definitively establishes trophic interactions between insects and seeds) provided a different perception. Isopods, millipedes, and especially crickets (especially female *G. pennsylvanicus*) were likely the most important granivores of at least green foxtail in soybeans of this region. While it is not exclusively granivorous, *G. pennsylvanicus* could be considered a small grass seed specialist (Brust, 1994; Lundgren & Harwood, 2012; Lundgren & Rosentrater, 2007). Its abundance was positively associated with the consumption rates, removal rates, and green foxtail abundance within a field. There were no numerical responses by *G. pennsylvanicus* to the other seed species. A closer look at the data revealed that *G. pennsylvanicus* females had a stronger preference for green foxtail seeds than males (also observed by Carmona et al., 1999), which may be related to their gut bacterial communities or sex-specific nutritional requirements (Schmid et al., 2014). Furthermore, green foxtail seed removal rates in *G. pennsylvanicus* were supported by the gut content analysis. However, *G. pennsylvanicus* abundance and green foxtail consumption in the previous season were correlated with greater green foxtail abundance in the following season. This suggests that this seed specialization may have dampened recruitment of green foxtail seedlings, but not sufficiently to reduce green foxtail recruitment. It is noteworthy that the spatial arrangement in our study may have increased the ambient granivore abundance over surrounding cropland. The fact that seed predators responded to weed community characteristics on a relatively small spatial scale suggests that they are finely tuned to local resource availability. It appears that these patterns behave similarly under local- and landscape-level scales (Carbonne et al., 2022).

Unexpectedly, both methods for measuring granivory showed that more granivory in the preceding year was associated with greater weed abundance and diversity in a focal growing season. Both of these metrics are indices of biological control of weed communities, but very little work has focused on whether these metrics of predation scale with weed seedling recruitment, the ultimate goal of biological control. Gut content analysis provides a direct trophic linkage between consumers and a focal food item, but directly equating gut analysis to reductions in pest abundance is challenging (Lundgren & Fergen, 2014; Naranjo & Hagler, 2001; Weber & Lundgren, 2009). Recent criticism has been levied against using seed removal as a proxy for seed predation (Moore & Swihart, 2008; Vander Wall et al., 2005), but this is yet to be demonstrated for invertebrate granivore communities. Nevertheless, several recent studies show that granivores (based on exclusion studies and trap captures) are associated with seedbank and seedling reductions in agronomic weeds (Blubaugh & Kaplan, 2016; Bohan et al., 2011; Carbonne et al., 2020; White et al., 2007). Granivory proxies measure seed consumption rates, but seed consumption rates are affected by availability of resources; greater seed consumption may be a reflection of more seeds available in a habitat, thus potentially leading to more weeds.

Cropland is defined by monotypic plant communities with high biomass, and animal species have adapted to live in these depauperated plant communities. In other habitats, increasing plant diversity usually increases insect diversity and pollination and predation, but we did not observe this same pattern in the current system. We hypothesize that the invertebrate community that we measured was comprised in large part of agrobionts (sensu Luczak, 1975): species that are better adapted to ephemeral, low-diversity plant communities (Samu & Szinetár, 2002). Cropland was associated with similar shifts in the communities of pollinators (Mogren et al., 2016), carabid beetles (Saska et al., 2007), and spiders (Samu & Szinetár, 2002). Our data suggest that land management plans focused on entire insect communities may attract potentially important organisms that contribute key ecosystem services that may be missed if we manage only for a token few beneficial species.

AUTHOR CONTRIBUTIONS

Jonathan G. Lundgren and Randy L. Anderson conceived the manuscript, and collected and entered data for the manuscript. Jonathan G. Lundgren analyzed the data and wrote the manuscript.

ACKNOWLEDGMENTS

We thank Janet Fergen, Ryan Bell, Nicole Berg, Mike Bredeson, Beth Choate, Megan Fischer, Chloe Kruse,

Claire LaCanne, Marissa Layman, Jacob Pecenka, Ryan Schmid, Cally Strobel, Mallory Thompson, and Ashton Walters for field assistance. Mark Longfellow helped analyze the green foxtail seeds for protein markers. We have no funding sources to declare.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Lundgren, 2023) are available from Open Science Framework: https://doi.org/10.17605/OSF.IO/SZ9RH.

ORCID

Jonathan G. Lundgren https://orcid.org/0000-0002-9860-3613

REFERENCES

Aarssen, L. W., and D. R. Taylor. 1992. "Fecundity Allocation in Herbaceous Plants." *Oikos* 65: 225–232.

Adis, J. 1979. "Problems of Interpreting Arthropod Sampling with Pitfall Traps." *Zoologischer Anzeiger Jena* 202: 177–184.

Albertini, A., S. Marchi, C. Ratti, G. Burgio, R. Petacchi, and S. Magagnoli. 2018. "*Bactrocera oleae* Pupae Predation by *Ocypus olens* Detected by Molecular Gut Content Analysis." *BioControl* 63: 227–239.

Anderson, R. L. 2015. "Integrating a Complex Rotation with No-Till Improves Weed Management in Organic Farming. A Review." *Agronomy and Sustainable Development* 35: 967–974.

Anderson, R. L. 2016. "Converting Perennial Legumes to Organic Cropland without Tillage." *Renewable Agriculture and Food Systems* 31: 166–171.

Andreasen, C., H. A. Jensen, and S. M. Jensen. 2018. "Decreasing Diversity in the Soil Seed Bank after 50 Years in Danish Arable Fields." *Agriculture, Ecosystems and Environment* 259: 61–71.

Barbercheck, M. E., and J. Wallace. 2021. "Weed-Insect Interactions in Annual Cropping Systems." *Annals of the Entomological Society of America* 114: 276–291.

Blubaugh, C. K., J. R. Hagler, S. A. Machtley, and I. Kaplan. 2016. "Cover Crops Increase Foraging Activity of Omnivorous Predators in Seed Patches and Facilitate Weed Biological Control." *Agriculture, Ecosystems and Environment* 231: 264–270.

Blubaugh, C. K., and I. Kaplan. 2016. "Invertebrate Seed Predators Reduce Weed Emergence Following Seed Rain." *Weed Science* 64: 80–86.

Boddy, L. G., K. J. Bradford, and A. J. Fischer. 2012. "Population-Based Threshold Models Describe Weed Germination and Emergence Patterns across Varying Temperature, Moisture and Oxygen Conditions." *Journal of Applied Ecology* 49: 1225–36.

Bohan, D. A., A. Boursault, D. R. Brooks, and S. Petit. 2011. "National-Scale Regulation of the Weed Seedbank by Carabid Predators." *Journal of Applied Ecology* 48: 888–898.

Bredeson, M. M., D. Beck, and J. G. Lundgren. 2020. "Arthropod Granivory of Lime-Coated Cover Crop Seeds." *Environmental Entomology* 49: 848–853.

Brust, G. E. 1994. "Seed-Predators Reduce Broadleaf Weed Growth and Competitive Ability." *Agriculture, Ecosystems and Environment* 48: 27–34.

Carbonne, B., D. A. Bohan, H. Foffová, E. Daouti, B. Frei, V. Neidel, P. Saska, J. Skuhrovec, and S. Petit. 2022. "Direct and Indirect Effects of Landscape and Field Management Intensity on Carabids through Trophic Resources and Weeds." *Journal of Applied Ecology* 59: 176–187.

Carbonne, B., S. Petit, V. Neidel, H. Foffová, E. Daouti, B. Frei, J. Skuhrovec, et al. 2020. "The Resilience of Weed Seedbank Regulation by Carabid Beetles, at Continental Scales, to Alternative Prey." *Scientific Reports* 10: 19315.

Carmona, D. M., F. D. Menalled, and D. A. Landis. 1999. "*Gryllus pennsylvanicus* (Orthoptera: Gryllidae): Laboratory Weed Seed Predation and within Field Activity-Density." *Journal of Economic Entomology* 92: 825–29.

Choate, B. A., and J. G. Lundgren. 2015. "Invertebrate Communities in Spring Wheat and the Identification of Cereal Aphid Predators through Molecular Gut Content Analysis." *Crop Protection* 77: 110–18.

Daouti, E., B. Feit, and M. Jonsson. 2022. "Agricultural Management Intensity Determines the Strength of Seed Predation." *Agriculture, Ecosystems and Environment* 339: 108132.

Davis, A. S. 2006. "When Does It Make Sense to Target the Weed Seed Bank?" *Weed Science* 54: 558–565.

Davis, A. S., D. Daedlow, B. J. Schutte, and P. R. Westerman. 2011. "Temporal Scaling of Episodic Point Estimates of Seed Predation to Long-Term Predation Rates." *Methods in Ecology and Evolution* 2: 682–690.

Davis, A. S., and M. Liebman. 2003. "Cropping System Effects on Giant Foxtail (*Setaria faberi*) Demography: I. Green Manure and Tillage Timing." *Weed Science* 51: 919–929.

Davis, A. S., and S. Raghu. 2010. "Weighing Abiotic and Biotic Influences on Weed Seed Predation." *Weed Research* 50: 402–412.

Finke, D. L., and W. E. Snyder. 2010. "Conserving the Benefits of Predator Biodiversity." *Biological Conservation* 143: 2260–69.

Foffová, H., Z. S. Cavar, A. Honek, Z. Martinková, P. Tarkowski, and P. Saska. 2020. "Which Seed Properties Determine the Preferences of Carabid Beetle Seed Predators?" *Insects* 11: 757.

Forbes, S. A. 1881. "Notes on Insectivorous Coleoptera." *Bulletin of the Illinois State Laboratory of Natural History* 1: 153–160.

Forcella, F., D. H. Peterson, and J. C. Barbour. 1996. "Timing and Measurement of Weed Seed Shed in Corn (*Zea mays*)." *Weed Technology* 10: 535–543.

Frei, B., Y. Gueney, D. A. Bohan, M. Traugott, and C. Wallinger. 2019. "Molecular Analysis Indicates High Levels of Carabid Weed Seed Consumption in Cereal Fields across Central Europe." *Journal of Pest Science* 92: 935–942.

Gaba, S., N. Cheviron, T. Perrot, S. Piutti, J.-L. Gautier, and V. Bretagnolle. 2020. "Weeds Enhance Multifunctionality in Arable Lands in South-West of France." *Frontiers in Sustainable Food Systems* 4: 71.

Geddes, C. M., and R. H. Gulden. 2018. "Candidate Tools for Integrated Weed Management in Soybean at the Northern Frontier of Production." *Weed Science* 66: 662–672.

Greenop, A., B. A. Woodcock, A. Wilby, S. M. Cook, and R. F. Pywell. 2018. "Functional Diversity Positively Affects Prey

Suppression by Invertebrate Predators: A Meta-Analysis." *Ecology* 99: 1771–82.

Heggenstaller, A., F. D. Menalled, M. Liebman, and P. R. Westerman. 2006. "Seasonal Patterns in Post-Dispersal Seed Predation of *Abutilon theophrasti* and *Setaria faberi* in Three Cropping Systems." *Journal of Applied Ecology* 43: 999–1010.

Hinsinger, P., A. G. Bengough, D. Vetterlein, and I. M. Young. 2009. "Rhizosphere: Biophysics, Biogeochemistry and Ecological Relevance." *Plant and Soil* 321: 117–152.

Holling, C. S. 1959. "Some Characteristics of Simple Types of Predation and Parasitism." *The Canadian Entomologist* 91: 385–398.

Honěk, A., Z. Martinkova, P. Saska, and S. Pekar. 2007. "Size and Taxonomic Constraints Determine the Seed Preferences of Carabidae (Coleoptera)." *Basic and Applied Ecology* 8: 343–353.

Horton, R., O. Aguirre-Luna, and P. J. Wierenga. 1984. "Soil Temperature in a Row Crop with Incomplete Surface Cover." *Soil Science Society of America Journal* 48: 1225–32.

Kaspari, M., M. D. Weiser, K. E. Marshall, M. Miller, C. Siler, and K. de Beurs. 2022. "Activity Density at a Continental Scale: What Drives Invertebrate Biomass Moving across the Soil Surface?" *Ecology* 103: e03542.

Klinkhamer, P. G., and T. J. De Jong. 1987. "Plant Size and Seed Production in the Monocarpic Perennial *Cynoglossum officinale* L." *New Phytologist* 106: 773–783.

Koivula, M., D. J. Kotze, L. Hiisivuori, and H. Rita. 2003. "Pitfall Trap Efficiency: Do Trap Size, Collecting Fluid and Vegetation Structure Matter?" *Entomologica Fennica* 14: 1–14.

LaCanne, C. E., and J. G. Lundgren. 2018. "Regenerative Agriculture: Merging Food Production and Natural Resource Conservation in a Profitable Business Model." *PeerJ* 6: e4428.

Luczak, J. 1975. "Spider Communities of the Crop Fields." *Polish Ecological Studies* 1: 93–110.

Lundgren, J. 2023. "Granivory in Soybeans." Dataset. OSF. https://doi.org/10.17605/OSF.IO/SZ9RH.

Lundgren, J. G. 2009. *Relationships of Natural Enemies and Non-Prey Foods*. Dordrecht: Springer International.

Lundgren, J. G., and S. W. Fausti. 2015. "Trading Biodiversity for Pest Problems." *Science Advances* 1: e1500558.

Lundgren, J. G., and J. K. Fergen. 2010. "The Effects of a Winter Cover Crop on *Diabrotica virgifera* (Coleoptera: Chrysomelidae) Populations and Beneficial Arthropod Communities in No-Till Maize." *Environmental Entomology* 39: 1816–28.

Lundgren, J. G., and J. K. Fergen. 2014. "Predator Community Structure and Trophic Linkage Strength to a Focal Prey: The Influence of the Prey's Anti-Predator Defense." *Molecular Ecology* 23: 3790–98.

Lundgren, J. G., and J. D. Harwood. 2012. "Functional Responses to Food Diversity: The Effect of Seed Availability on the Feeding Behavior of Facultative Granivores." *Journal of Entomological Science* 47: 160–176.

Lundgren, J. G., and K. A. Rosentrater. 2007. "The Strength of Seeds and Their Destruction by Granivorous Insects." *Arthropod-Plant Interactions* 1: 93–99.

Lundgren, J. G., P. Saska, and A. Honěk. 2013. "Molecular Approach to Describing a Seed-Based Food Web: The Post-Dispersal Granivore Community of an Invasive Plant." *Ecology and Evolution* 3: 1642–52.

Meiss, H., L. Le Lagadec, N. Munier-Jolain, R. Waldhardt, and S. Petit. 2010. "Weed Seed Predation Increases with Vegetation Cover in Perennial Forage Crops." *Agriculture, Ecosystems and Environment* 138: 10–16.

Mogren, C. L., T. A. Rand, S. W. Fausti, and J. G. Lundgren. 2016. "The Effects of Crop Intensification on the Diversity of Native Pollinator Communities." *Environmental Entomology* 45: 865–872.

Moore, J. E., and R. K. Swihart. 2008. "Factors Affecting the Relationship between Seed Removal and Seed Mortality." *Canadian Journal of Zoology* 86: 378–385.

Mortensen, D. A., J. F. Egan, B. D. Maxwell, M. R. Ryan, and R. G. Smith. 2012. "Navigating a Critical Juncture for Sustainable Weed Management." *BioScience* 62: 75–84.

Moss, S. 2019. "Integrated Weed Management (IWM): Why Are Farmers Reluctant to Adopt Non-Chemical Alternatives to Herbicides?" *Pest Management Science* 75: 1205–11.

Naranjo, S. E., and J. R. Hagler. 2001. "Toward the Quantification of Predation with Predator Gut Immunoassays: A New Approach Integrating Functional Response Behavior." *Biological Control* 20: 175–189.

NASS. 2020. "National Agriculture Statistics Service: USDA." www.nass.usda.gov.

Ostandie, N., L. Muneret, B. Giffard, D. Thiéry, and A. Rusch. 2021. "The Shape of the Predator Biomass Distribution Affects Biological Pest Control Services in Agricultural Landscapes." *Functional Ecology* 35: 193–204.

Peterson, J. A., E. C. Burkness, J. D. Harwood, and W. D. Hutchison. 2018. "Molecular Gut-Content Analysis Reveals High Frequency of *Helicoverpa zea* (Lepidoptera: Noctuidae) Consumption by *Orius insidiosus* (Hemiptera: Anthocoridae) in Sweet Corn." *Biological Control* 4: 1–7.

Samu, F., and C. Szinetár. 2002. "On the Nature of Agrobiont Spiders." *Journal of Arachnology* 30: 389–402.

Saska, P., M. Vodde, T. Heijerman, P. Westerman, and W. von der Werf. 2007. "The Significance of a Grassy Field Boundary for the Spatial Distribution of Carabids within Two Cereal Fields." *Agriculture, Ecosystems and Environment* 122: 427–434.

Schmid, R. B., R. M. Lehman, and J. G. Lundgren. 2014. "Sex-Specific Interactions of Microbial Symbioses on Cricket Dietary Selection." *Environmental Entomology* 43: 896–902.

Storkey, J., and P. Neve. 2018. "What Good Is Weed Diversity?" *Weed Research* 58: 239–243.

Travlos, I., I. Gazoulis, P. Kanatas, A. Tsekoura, S. Zannopoulos, and P. Papastylianou. 2018. "Key Factors Affecting Weed Seeds' Germination, Weed Emergence, and Their Possible Role for the Efficacy of False Seedbed Technique as Weed Management Practice." *Frontiers in Agronomy* 2: 1.

Vander Wall, S. B., K. M. Kuhn, and M. J. Beck. 2005. "Seed Removal, Seed Predation, and Secondary Dispersal." *Ecology* 86: 801–6.

Vinson, S. B. 1976. "Host Selection by Insect Parasitoids." *Annual Review of Entomology* 21: 109–133.

Weber, D. C., and J. G. Lundgren. 2009. "Assessing the Trophic Ecology of the Coccinellidae: Their Roles as Predators and Prey." *Biological Control* 51: 199–214.

White, S. S., K. A. Renner, F. D. Menalled, and D. A. Landis. 2007. "Feeding Preferences of Weed Seed Predators and Effect on Weed Emergence." *Weed Science* 55: 606–612.

SUPPORTING INFORMATION

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

How to cite this article: Lundgren, Jonathan G., and Randy L. Anderson. 2023. "Suppression of Weed Communities by Granivores over Time in an Agroecosystem." *Ecosphere* 14(8): e4641. https://doi.org/10.1002/ecs2.4641