

ORIGINAL ARTICLE

Soil Fertility and Crop Nutrition

Microarthropods improve oat nutritional quality and mediate fertilizer effects on soil biological activity

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Abstract

Soil biological processes are important drivers of crop productivity in agroecosystems. Soil microarthropods play key roles in nutrient cycling and plant nutrient acquisition, though little is known about how these effects manifest in crop production under different organic fertilizer amendments. We explored the interactive effects of microarthropods and fertilizers on crop productivity in two greenhouse experiments: experiment one involved a single Collembola species, and experiment two involved diverse microarthropod communities. Oats were grown as a model crop in both experiments under one of three initial fauna abundance levels (none, low, and high). In both experiments, four organic fertilization treatments were compared: alfalfa green manure, Kreher's Poultry Litter Compost, Chilean nitrate, and a nonamended control. Oat growth and development were evaluated weekly. During each experiment, 48 pots were selected randomly for destructive harvest at two separate times to mimic forage and grain harvest stages. At each harvest, multiple soil metrics (microarthropods, microbial biomass, microbial enzymes, and soil carbon and nitrogen) and plant metrics (biomass, reproduction, and tissue carbon and nitrogen content) were evaluated. Our findings indicated that microarthropods, both single species and diverse communities, stimulated nitrogen cycling and enhanced crop nutrient status. As microarthropod abundance and diversity increased, microarthropods exerted more effects on soil microbial activity. The effects of the microarthropods enhance the breakdown of fertilizers, ultimately making fertilizer choice less important for soil processes and plant nutrient availability. Our findings suggest that microarthropods drove oat production yields primarily through their effects on soil biological processes.

Abbreviations: BG, β -glucosidase; CN, Chilean nitrate; GM, alfalfa green manure; HC, high Collembola/community; LAP, leucine amino peptidase; LC, low Collembola/community; NAG, *N*-acetyl- β -D-glucosaminidase; NC, no Collembola/community; NF, no fertilizer control; PC, Kreher's Poultry Litter Compost; PER, peroxidase; PHOS, acid phosphatase; PHENOX, phenol oxidase.

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1 | INTRODUCTION

Organic farming practices are becoming more prevalent in US agriculture (USDA NASS, 2020). Certified organic cropland acres increased by 73%, to 1.4 million ha, between 2011 and 2019 (USDA ERS, 2020). Many other farms utilize organic management practices beyond those that seek official certification (USDA NOP, 2023). Organic farming systems are more reliant on internal ecosystem services, like nutrient cycling, for maximizing crop productivity than conventional farming systems. This reliance on ecosystem services translates to management differences between organic and conventional farming systems for both pest and nutrient management (Gomiero et al., 2011; Seufert et al., 2012).

Nutrient management in organic systems differs from conventional systems in that organic nutrient management often relies on the long-term accumulation and release of nutrients over multiple growing seasons from complex organic matter sources (Wortman et al., 2021). Organic fertilizer options vary from mineral (Chilean nitrate [CN]) to complex organic (cover crop green manures) nutrient sources (Huntley et al., 1997). As fertilizer sources become more complex, they are more dependent on soil biological processes to liberate nutrients and make them available to plants.

Given the variability in soil nutrient management in organic systems, it is important to understand the role of soil biota in soil nutrient cycling and plant nutrient availability. Soil microbes are central to many belowground processes that affect plant growth, and there is growing evidence that soil microarthropods moderate these processes by feeding on the microbes directly or by altering the composition of microbial food sources (Jernigan et al., 2022). Soil microarthropods, which include collembolans and mites, play a major role in soil organic matter decomposition and nutrient cycling (Grandy et al., 2016; Seastedt, 1984; Soong & Nielsen, 2016; Zhang et al., 2021). Research has revealed that microarthropod activities induce the liberation of carbon (C) and nutrients during the fragmentation of plant residues and predation on soil microbes and larger soil organisms, which can decrease microbial breakdown of organic matter (Carrillo et al., 2011; Filser et al., 2016). Through these mechanisms, microarthropods affect overall soil fertility.

Microarthropod effects on nutrient cycling are dependent on their density and diversity (Seastedt, 1984; Sjursen et al., 2005; Verhoef & Brussaard, 1990) and can manifest in crop growth and nutrient acquisition (Bardgett & Chan, 1999). For example, increasing microarthropod densities were found to increase N availability, which resulted in a decrease in shoot biomass of perennial ryegrass (*Lolium perenne* L.), possibly due to effects on plant-microbe competition (Cole et al., 2004). This study additionally showed that increasing species richness in microarthropod communities led to greater shoot biomass production in a greenhouse setting. Further

Core Ideas

- Microarthropods improved the nutritional quality of oats by stimulating nitrogen uptake.
- Following initial fertilizer additions, the effects of microarthropods on microbial communities diminished over time.
- Microarthropod effects on soil microbial activity modulate oat responses to different fertilizers.

research highlights that increasing microarthropod community abundance and diversity generally increases crop biomass production and nutrient acquisition (Eisenhauer et al., 2018; Forey et al., 2015; Thakur & Eisenhauer, 2015).

The processes described above are not direct cause-and-effect, as previous work suggests the importance of microarthropods for soil nitrogen (N) cycling and plant nutrient acquisition can vary based on nutrient input type (Cole & Bardgett, 2002). Researchers found that the role of fauna on nitrogen dynamics was more important for labile litters including clover (*Trifolium* spp.) and false indigo bush (*Amorpha fruticosa*) compared to more recalcitrant litters including wheat straw (*Triticum aestivum*) and pine (*Pinaceae* spp.) (Carrillo et al., 2011).

Despite awareness of the linkages between soil biology and belowground nutrient cycling, further research is needed to clarify the relationships between soil microarthropods, nutrient cycling, and crop yield (Jernigan et al., 2022). To that end, this research aimed to clarify the role of microarthropod communities in nitrogen cycling and plant nutrient acquisition under different fertilizer treatments.

2 | METHODS

2.1 | Experimental design

A pair of complementary greenhouse experiments was conducted at Cornell AgriTech in Geneva, NY (42.8774, -77.0071) between June and November 2019. The greenhouse was maintained at 24°C during the day and 21°C at night, with no supplemental lighting. Both experiments followed a randomized complete-factorial design and included microarthropod and fertilizer treatments (Figure A1). The first experiment's microarthropod treatment consisted of a single Collembola species (*Isotomiella minor*; NCBI, 2015) applied at three different abundance levels (no Collembola/community [NC], low Collembola/community [LC], and high Collembola/community [HC]). The second experiment's fauna treatment consisted of native microarthropod communities also applied at three different abundance levels (NC,

LC, and HC). The low and high abundance levels were set at 100 individuals per pot and 200 individuals per pot, respectively, based on reported agricultural microarthropod abundances (Coleman et al., 2018) and data were collected on microarthropod abundances in agricultural fields across New York State (A. Jernigan, unpublished data).

Both the single-species and diverse community experiments incorporated identical fertilizer treatments. Three organic fertilizers were chosen as treatments in addition to the no fertilizer control (NF) treatment: (1) Alfalfa green manure (GM), (2) Kreher's Poultry Litter Compost 5-4-3 (Organic Materials Review Institute) (PC), and (3) CN. These fertilizer sources were chosen to create a gradient of fertilizer plant availability based on C:N ratios, a known predictor of short-term N availability (Gutser et al., 2005). The C:N ratios of each fertilizer were 7.0, 5.2, and 0.015, respectively. Each fertilizer was air-dried, then ground using a ball mill to control for any physical differences among fertilizer types and to ensure uniform distribution of each fertilizer within their respective soil. The fertilizer treatments were applied at a rate of 56 kg N ha⁻¹, which converted to 0.057 g N pot⁻¹ (Clark, 2007). The amount of fertilizer added to each pot was standardized to the rate of 0.057 g N (GM = 0.915 g [6.15% N], PC = 0.896 g [6.38% N], and CN = 0.381 g [13.65% N]).

Soil (Arkport Series—coarse-loamy, mixed, active, mesic Lamellic Hapludalfs) was collected from Bluegrass Lane Turf and Landscape Research Center in Ithaca, NY (42.4596, -76.4606) in May 2019. The soil was defaunated by heating and drying at 60°C for 48 h, freezing at -20°C for 24 h, heating again for 72 h, and freezing again for 24 h (Helmberger et al., 2018). Potting mix was defaunated using the same protocol. We chose this method to remove animal life from the soil because it effectively eliminates soil fauna, while its effects on soil physical and chemical properties as well as microbial function are reduced compared with other defaunation methods (Huhta et al., 1989).

Defaunated potting mix was then mixed with the defaunated Arkport soil at a 1:1 ratio in four fiberglass containers by hand until the soil was homogeneous. The mixed soil was remoistened with deionized water to approximately one-third of its water holding capacity and allowed to incubate at room temperature for 14 days.

Soil was placed into 96 pots (11.43-cm diameter, 10.16-cm tall; surface area of pot = 102.6 cm²) for each experiment. Each pot was filled almost completely, leaving about 2.5 cm of space at the top. The average weight of dry soil in each pot was 210.6 g. Each pot was placed in an individual clear polyvinyl chloride tube that was capped with thrips netting (no-thrips insect screen, hole opening size: 192 μm, BioQuip Products, Inc.) on the top and bottom to prevent cross contamination of fauna treatments (Figure A1).

After the treatments were established, the pots were separated into four replicates in the corners of the greenhouse. Pots

were then randomized within each replicate. All pots were then watered to water holding capacity.

2.2 | Experiment 1 (single species)

The defaunated soil was transferred into the pots and the fertilizer treatments were then applied to pots at the standardized N rate. The fertilizers were mixed into the top 2 cm of soil in each pot. Oat (*Avena sativa* L.) seeds were planted at the approximate higher end of the recommended rate of 135–202 kg ha⁻¹, or 0.5 g of oat seed per pot (~20 seeds), to a depth of approximately 1 cm.

Live Collembola (*I. minor*) were then transferred from maintained lab colonies into pots (Jernigan, 2023). The Collembola used to start the lab colonies were collected in August 2015 from leaf litter retrieved from the Cornell Loomis farm in Geneva, NY (42.887264, -77.009832). Control treatments received no Collembola [NC], low abundance [LC] treatments received approximately 100 Collembola, and high abundance [HC] treatments received approximately 200 Collembola, with an error range of ±10 Collembola. Collembola were counted out using a microscope into individual specimen cups for each pot using deionized water and transfer pipettes. Specimen cups were placed upside down on soil surface of the pot for approximately 1 h to ensure all collembolans moved from the specimen cups into the soil. The soil moisture was kept the same for all treatments by adding additional water to the control pots.

2.3 | Experiment 2 (diverse community)

A preliminary fauna extraction was completed on soil cores collected from a research field in Geneva, NY (42.8872, -77.0098) under a grass cover crop to calculate fauna abundances. Soil cores were collected to a depth of approximately 13 cm using turfgrass cup cutters (10.8-cm diameter). Over the course of the 3-day extraction, each sample was placed on Berlese funnels and the temperature was gradually increased from 30°C to 50°C. After the soil samples were removed from the Berlese funnels, soil dry mass was determined by weighing the soil from each funnel. Invertebrates were extracted into 70% ethanol, then topped off with 95% ethanol and stored until the samples were processed. In this study, soil fauna included mites, Collembola, and other taxa within the Arthropoda. Extracted fauna were identified to family using published taxonomic keys (Borror & DeLong, 1964; Dindal, 1990; Krantz et al., 2009). All arthropod abundances are reported as the number of individuals per kilogram dry soil. The fauna data were used to determine the amount of soil needed to extract sufficient animal numbers for the experiment.

On September 10, 2019, 60 soil cores were collected from the same field used for preliminary fauna analysis. Soil cores were placed individually on Berlese funnels (20-cm mesh diameter) and fauna were extracted into a deli cup containing a few centimeters of soil from each bulk soil treatment container. After the extraction was completed, the soil and fauna were then gently mixed back into the original bulk soil containers for their respective microarthropod abundance treatments. The bulk soil was layered between each deli cup of live microarthropods, then mixed by hand. This process was repeated until all the soil was homogeneously mixed. This approach was used to reduce the amount of physical mixing required and subsequently minimize damage to fauna. Each bulk soil container was then allowed to sit for 2 h to allow the fauna to further distribute throughout the soil. The soil with the incorporated microarthropod treatments was then transferred into the pots.

Six additional pots were filled to the same volume with soil from each bulk soil container for each abundance treatment. The soil in each of these pots was then placed onto individual Berlese funnels to extract the soil fauna and determine the approximate initial microarthropod communities applied to the pots for each treatment using the extraction method described previously (No. of individual per pot: control = 0 ± 0 , low = 42.7 ± 3 , high = 130.9 ± 5). The fertilizer treatments and oat seeds were then applied as described previously and were gently mixed into the soil to prevent disturbance of the soil fauna communities.

2.4 | Maintenance and weekly measurements

Pots were watered approximately every alternate day to maintain soil moisture content. Approximately 2 weeks after the experiments were set up, the oats were thinned to 15 plants per pot. Any weeds present were also removed during the thinning process.

Weekly checks were conducted to measure (1) the number of oat plants germinated, (2) the height of the tallest and shortest oat plant, and (3) the average oat growth stage for each pot. The height of oat plants was chosen as a nondestructive proxy for plant biomass during the weekly checks, and Zadoks growth scale was used to determine oat growth stages (Zadoks et al., 1974). Signs of nutrient deficiencies or disease were also recorded.

2.5 | Harvest metrics

During each experiment, two destructive harvests were conducted, where half of the pots ($n = 48$) were randomly selected to be harvested. The first harvest was conducted after approximately 4–5 weeks when the majority of the oats were at

boot stage which corresponds with the timing of forage harvest. The second harvest was completed after approximately 8 weeks when the majority of the oats were at the soft dough stage corresponding with the typical timing of grain harvest.

2.5.1 | Oat biomass measurements

Each pot was destructively harvested by first clipping all aboveground oat biomass and separating the shoot biomass from the seed biomass. Weed biomass was clipped and placed into a separate bag. The pot was then inverted, and the soil was separated from the pot, which was stabilized by the roots. The soil and root mass were cut in half using a saw, then the soil was split into two bags: one designated for microarthropod extraction and the other for all other soil analyses. The bulk analyses soil was then processed by first removing the root biomass by hand. Once most of the root biomass was removed, the soil was divided in half again and placed into separate bags: one refrigerated (4°C) and the other frozen (-2°C) until further processing. The oat biomass (shoots, roots, and seeds) and weed biomass were dried at 60°C for 4 days. The oat seeds were also counted, and all biomass was weighed after drying.

2.5.2 | Microarthropod measurements

The soil designated for microarthropod extraction was placed onto Berlese funnels to extract fauna immediately after destructively harvesting the pots using the protocol described previously. All arthropod abundances are reported as the number of individuals kg^{-1} dry soil.

2.5.3 | Microbial biomass measurements

The fresh refrigerated soil was passed gently through a 2-mm sieve and 5 g of soil was weighed to determine gravimetric soil moisture content. Two additional 5 g subsamples were collected from each soil sample and used for a modified chloroform fumigation/extraction to quantify microbial biomass (Jenkinson & Powlson, 1976). Half of all samples were fumigated by adding 3 mL of chloroform to cotton balls placed in the top of the centrifuge tube and resealing the tube for 24 h. After 24 h, the tubes were vented to remove all residual chloroform gas from the soil samples. All samples (fumigated and non-fumigated) were then extracted in 25 mL of 0.5 M K_2SO_4 . Samples were shaken on a benchtop rotary shaker for 60 min at 170 rpm. After settling, extracts were filtered through 2.5- μm filter paper (Whatman grade 5). Extracts were frozen at -20°C and later analyzed for total organic C and N on a Shimadzu TOC-TN analyzer (Shimadzu Scientific Instruments, Inc.). Microbial biomass C was determined by subtracting non-fumigated from fumigated C values and

by applying a k_{EC} value of 0.45 (Joergensen, 1996). Microbial biomass N was derived using the same calculations and applying a k_{EC} value of 0.54. Biomass C and N is presented as $\mu\text{g g}^{-1}$ dry soil.

2.5.4 | Microbial extracellular enzyme activity

Potential soil microbial extracellular enzyme activity was assessed using protocols outlined in previous studies (Grandy et al., 2008; Saiya-Cork et al., 2002; Wickings & Grandy, 2011). The activities of four hydrolytic enzymes: *N*-acetyl- β -D-glucosaminidase (NAG), β -glucosidase (BG), acid phosphatase (PHOS), and leucine amino peptidase (LAP), and two oxidative enzymes: phenol oxidase (PHENOX) and peroxidase (PER), were measured.

Soil slurries were created from a 1 g soil subsample from sieved frozen soil and 120 mL sodium acetate buffer (pH 6.5). Hydrolytic enzyme activities were measured on black 96-well plates receiving one of the different substrates containing the fluorescent compound methylumbelliferone, except for LAP which used the fluorescent compound methylcoumarin. Oxidative enzymes were measured using clear 96 well plates, receiving L-3,4-dihydroxyphenylalanine (L-DOPA) alone for PHENOX or L-DOPA plus hydrogen peroxide (0.3%) for PER. Hydrolytic enzyme plates were incubated for 3–4 h and oxidative enzyme plates were incubated for 22–24 h. Hydrolytic enzyme plates were then evaluated at 360 nm excitation and 460 nm emission wavelengths and oxidative enzyme plates at 450 nm absorbance wavelength using a microplate reader (Synergy, BioTek Instruments). Potential enzyme activity for each substrate was calculated as nmol of substrate $\text{h}^{-1} \text{g}^{-1}$ dry soil.

2.5.5 | Carbon and nitrogen content in soil and oat tissues

The dried soil and oat tissues were pulverized using a ball mill grinder (8000D Mixer/Mill, SPEX SamplePrep), weighed into tin capsules, and combusted to determine C and N concentration. Soil C and N was measured by elemental analysis (Costech EA 4010 CHNS-O Analyzer, Costech Analytical Technologies) using acetanilide, organic rye flour, and certified soil reference material (Elemental Microanalysis, Ltd.) as standards and quality controls.

2.6 | Statistical analysis

All data analyses were performed in R version 3.4.2 (R Core Team, 2017). For univariate analyses, we used analysis of

variance (ANOVA) to test for differences in each response variable and harvests using the *lmer* function in the “lme4” package. Microarthropod treatment, fertilizer treatments, and their interaction were included as fixed effects, and a random replicate effect was included to account for potential variability in greenhouse conditions. Data were transformed as $\ln(x + 1)$ or square root transformed as necessary to meet the assumptions of normality and homoscedasticity for the ANOVAs. Pairwise mean comparisons were made by using Fisher’s least significant difference method, with Tukey adjustment and significance was declared for $p \leq 0.05$.

A redundancy analysis was performed to model the effect of the soil environment on oat growth for the corresponding soil and plant variable datasets collected at each harvest in both experiments. The redundancy analysis was performed using the *rda* function in the “vegan” package (Oksanen et al., 2010). All variables were standardized using the *decostand* function in the vegan package. Multicollinearity of the predictor variables was checked for each model using the *vif.cca* function in the vegan package. A permutation-based multivariate ANOVA (Anderson, 2001) was then run using the *anova.CCA* function of the vegan package. The soil variable constraints on the plant variables were compared “by terms.” Results were plotted using the vegan package.

3 | RESULTS

3.1 | Experiment 1 (single species)

3.1.1 | Weekly plant growth metrics

Seedling emergence was lower in pots receiving GM compared to the other fertilizer treatments at weeks 1 and 2, with an average of 13.4 plants per pot compared to 15 plants per pot in the other treatments after thinning (Table A1).

Within the NC treatment, oats developed faster in pots receiving PC and GM than when receiving other fertilizers (week 2 growth stages = 11.4 vs. 11.0; week 3 growth stages = 12.5 vs. 12.0) (Table A1). After week 3, there were no longer any significant differences in plant growth and development between the treatments (Table A1).

3.1.2 | Harvest metrics

Collembola abundances

At harvest 1, *Collembola* abundances had decreased relative to the start of the experiment in both the LC and HC treatments, though these treatments were no longer significantly different from each other (Figure 1). At harvest 2, there were very low abundances in all three treatments (<10 individuals per pot on average) (Figure 1).

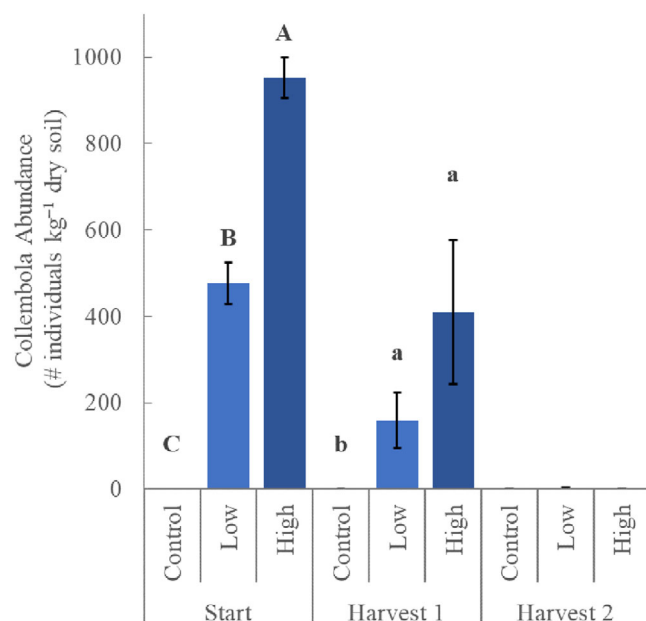


FIGURE 1 Collembola treatment effects on collembolan abundances (No. of individuals kg⁻¹ dry soil) in the single-species experiment. Separate mean comparisons were conducted for each time point. Bars with the same letters are not significantly different (Fisher's least significant difference [LSD], $p > 0.05$).

Oat biomass

Oats produced more seeds in the absence of Collembola than in their presence at low densities ($p = 0.0125$, means: NC = 33.2a, LC = 20.7b, HC = 27.1ab). Oat root, shoot, and seed biomass was not significantly ($p > 0.05$) affected by Collembola treatments or fertilizer type.

Oat tissue carbon and nitrogen

At harvest 1, Collembola and fertilizer had an interactive effect on oat root and shoot tissue C and N, as well as the C:N ratio, excluding the percent of C in oat shoots (Table 1). Generally, the presence of the Collembola increased the magnitude of the effect of fertilizers on N content of the roots and had mixed effects on root C content. The presence of the Collembola increased the effect of the fertilizers on N content of the shoots.

By harvest 2, the N content of the roots increased as the fertilizer plant availability increased (Table 1). The N content of the shoots was greater when Collembola were present and increased as the fertilizer source was more plant available. The N content of the seeds tended to increase as the fertilizer source was more plant available (NF < GM < PC < CN); moreover, the presence of the Collembola exacerbated this effect.

Microbial biomass carbon and nitrogen

At harvest 1, there was greater microbial biomass C in the NC compared to HC abundances, and NF pots had greater

microbial biomass C than the pots that received GM and CN (Table 2). The GM and CN pots had greater microbial biomass N than the NF and PC pots (Table 2). Within the NC treatment, the microbial biomass C:N ratio was higher in the absence of fertilizer than the other fertilizer treatments, and the pots with PC had a higher microbial biomass C:N ratio than the pots with CN (Table 2).

At harvest 2, microbial biomass C and N, and their ratio were all impacted by both the Collembola and fertilizer treatments (Table 2). The microbial biomass C was up to 22% greater when there were NC and LC abundances present (Table 2). The microbial biomass C differed significantly between each fertilizer treatment (CN < GM < PC < NF). The microbial biomass N was up to 21% greater when Collembola were present and was greater in the presence of all three fertilizer treatments compared to nonamended soil (Table 2). The microbial biomass C:N ratio was greater in the absence of Collembola and increased significantly between each fertilizer treatment (CN < GM < PC < NF) (Table 2).

Microbial extracellular enzyme activities

At harvest 1, the microbial extracellular enzyme activities each had varying responses to the treatments (Table 2). NAG activity was 30% greater in the HC abundances compared to the NC. The pots that received PC with HC abundances had greater PER activity than the pots that received PC with LC abundances. In the NC, the GM pots had greater LAP activity than the other fertilizer treatments, and the PC pots had greater PHOS activity than the NF. The NF had the greatest PHENOX activity compared to the soils with fertilizers added (Table 2).

At harvest 2, there was greater LAP activity in the NF and GM pots compared to the CN pots. There was 39% greater PER activity when there was NF compared to the pots that received GM and CN (Table 2).

Soil carbon and nitrogen

At harvest 1, in the HC treatment, soils receiving NF or PC had greater soil C than those receiving CN (Table 1). At harvest 2, in the NC treatment, the NF soil had greater soil C than the soil that received PC and CN. However, in the LC treatment, the NF soil had greater soil C than the GM and CN, and the PC had greater soil C than the GM (Table 1).

3.1.3 | Redundancy analysis and metric correlations

The redundancy analysis PerMANOVA model was significant at both harvests ($p = 0.001$ and $p = 0.042$, respectively), indicating that the soil variables were significantly correlated to the plant metrics (Table A2). At harvest 1, microbial biomass

TABLE 1 The effect of Collembola abundance and fertilizer treatments on the nutrient composition of soils and plant tissues for the single-species experiment.

Harvest 1	p-value	Collembola	Fertilizer	Collembola × fertilizer	Soil		Roots		Shoots		Seeds		
					%N	%C	C:N	%N	%C	C:N	%N	%C	C:N
		Control			0.3723	0.0372	0.0071	0.1413	0.4260	0.0447	0.2351	0.2420	0.3435
		Low density			0.3972	0.0433	0.0317	<0.0001	0.0007	<0.0001	<0.0001	<0.0001	<0.0001
		High density			0.4311	0.0411	0.0563	0.0086	0.0001	0.0502	0.0092	0.1092	0.0011
		No fertilizer											
		Green manure											
		Compost											
		Chilean nitrate											
		Control											
		Low density											
		High density											
		No fertilizer											
		Green manure											
		Compost											
		Chilean nitrate											
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TABLE 1 (Continued)

		Soil %N	Soil %C	Soil C:N	Roots %N	Roots %C	Roots C:N	Shoots %N	Shoots %C	Shoots C:N	Seeds %N	Seeds %C	Seeds C:N
Fertilizer	High density			25.9	1.3			1.7a	42.6a	28.6b			
	No fertilizer			27.3a	1.1c			0.8d	42.7a	55.9a			
	Green manure			24.5b	1.2bc			1.7bc	42.7a	26.3bc			
	Compost			25.0b	1.3ab			1.4c	42.4ab	32.3b			
	Chilean nitrate			24.2b	1.4a			2.5a	42.0b	17.5d			
Interaction effects													
No Collembola	No fertilizer	5.5a					36.3a				2.8cd	43.3ab	15.8ab
	Green manure	5.1ab					29.1ab				2.9cd	44.2a	15.1ab
	Compost	4.8ab					27.1ab				2.8cd	43.8ab	15.9ab
Low Collembola	Chilean nitrate	4.5b					28.5ab				3.4bc	43.4ab	13.4bcd
	No fertilizer	5.5a					37.3a				2.6d	43.1b	17.1ab
	Green manure	4.5b					22.4b				3.3bc	43.6ab	14.0bc
High Collembola	Compost	5.2ab					27.8ab				3.1cd	43.7ab	14.4bc
	Chilean nitrate	4.8ab					23.4b				4.2a	42.1c	10.1cd
	No fertilizer	5.5ab					27.7ab				2.8cd	43.2ab	15.6ab
Compost	Green manure	5.0ab					27.8ab				3.7ab	43.5ab	11.8cd
	Chilean nitrate	4.9ab					29.1ab				3.1bcd	44.0ab	14.5bc
	No fertilizer	5.2ab					21.0b				3.6ab	43.7ab	12.3d

Note: Significance levels from the analysis of variances (ANOVAs) performed the metrics with means ($p < 0.05$, in bold). Means with the same letters are not significantly different (Fisher's least significant difference [LSD], $p > 0.05$).

TABLE 2 The effect of Collembola abundance and fertilizer treatments on the microbial metrics for the single-species experiment.

Harvest 1	<i>p</i> -value	Microbial C	Microbial N	Microbial C:N	NAG	LAP	PHOS	PHENOX	Peroxidase
		Collembola	0.9005	0.8882	0.0367	0.0273	0.2904	0.0221	0.1046
		Fertilizer	<0.0001	<0.0001	0.0642	<0.0001	0.1216	0.0251	0.6373
		Collembola × fertilizer	0.3373	0.2866	0.1150	0.0030	0.0011	0.5414	0.0114
Main effects									
Collembola		Control	131a	14.2	21.5b			1.52a	
		Low density	123ab	14.2	26.7ab			1.25ab	
		High density	118b	13.6	30.4a			0.82b	
Fertilizer		No fertilizer	147a	8.8b	15.9			2.00a	
		Green manure	120b	16.9a	34.3			1.07b	
		Compost	135ab	11.3b	23.5			1.15b	
		Chilean nitrate	93c	22.8a	31.2			0.56b	
Interaction effects									
No Collembola		No fertilizer		18.6a		70.3b	346b		0.39ab
		Green manure		7.9b		520.6a	113b		0.51ab
		Compost		9.0b		59.7b	575a		0.38ab
		Chilean nitrate		4.5b		48.6b	223b		0.57ab
Low Collembola		No fertilizer		16.9a		83.8b	453b		0.54ab
		Green manure		5.7b		141.8b	114b		0.79ab
		Compost		14.4a		70.7b	140b		0.39b
		Chilean nitrate		4.0b		62.3b	205b		0.48ab
High Collembola		No fertilizer		15.1a		63.0b	647a		0.46ab
		Green manure		8.9b		78.8b	229b		0.57ab
		Compost		13.4a		77.8b	121b		1.04a
		Chilean nitrate		4.0b		41.0b	199b		0.52ab
Harvest 2	<i>p</i> -value	Microbial C	Microbial N	Microbial C:N	NAG	LAP	PHOS	PHENOX	Peroxidase
		Collembola	0.0005	0.0104	0.7870	0.8138	0.3567	0.3896	0.2190
		Fertilizer	<0.0001	<0.0001	0.1003	0.0145	0.1023	0.0024	0.0182
		Collembola × fertilizer	0.5856	0.0509	0.7070	0.7418	0.6413	0.3077	0.5134
Main effects									
Collembola		Control	207a	10.1b	20.0a	99.1		0.74	0.59
		Low density	197a	12.8a	14.9b	94.5		0.64	0.45
		High density	163b	12.1ab	12.7b	94.1		0.62	0.52

(Continues)

TABLE 2 (Continued)

Fertilizer	Microbial C	Microbial N	Microbial C:N	NAG	LAP	PHOS	PHENOX	Peroxidase
No fertilizer	271a	2.7b	101.0a		102.5a		0.96a	0.72a
Green manure	166c	20.6a	7.9c		105.0a		0.59b	0.44b
Compost	209b	17.0a	12.1b		101.8ab		0.60b	0.49ab
Chilean nitrate	109d	19.4a	5.4d		77.1b		0.55b	0.45b

Note: Significance levels from the analysis of variances (ANOVAs) performed the metrics with means ($p < 0.05$, in bold), in bold). Means with the same letters are not significantly different (Fisher's least significant difference [LSD]); $p > 0.05$.

Abbreviations: LAP, leucine amino peptidase; NAG, *N*-acetyl- β -D-glucosaminidase; PHOS, acid phosphatase; PHENOX, phenol oxidase.

N and C and the microbial enzymes LAP and BG were significantly correlated to the plant metrics (Figure 2; Table A2). At harvest 2, microbial biomass N and C and the microbial enzyme BG were significantly correlated to the plant metrics (Figure 2; Table A2).

3.2 | Experiment 2 (diverse community)

3.2.1 | Fauna treatment starting confirmation

The fauna treatment check at the initiation of the experiment confirmed there were three distinct increasing abundance levels as desired ($p < 0.0001$; No. of individual per pot: control = 0 ± 0 , low = 42.7 ± 3 , high = 130.9 ± 5).

3.2.2 | Weekly plant growth metrics

Seedling emergence was lower at weeks 1 and 2 in pots receiving GM compared to the other fertilizer treatments, with an average of 12.6 plants per pot compared to 15 plants per pot in the other treatments after thinning (Table A3). Generally, oats that received GM were developmentally behind the other fertilizer treatments (Table A3).

3.2.3 | Harvest metrics

Microarthropod abundances

At harvest 1, within the LC treatment, the GM pots averaged over six times as many microarthropods than the other fertilizer treatments, and within the HC treatment the GM pots had more microarthropods than the CN (Figure 3). At harvest 2, NC controls had fewer microarthropods than the LC and HC treatments, and the GM averaged more than twice as many microarthropods than the three other fertilizer treatments (Figure 3). The composition of the initial microarthropod communities added to the pots ($p = 0.99$) and the microarthropod communities at both harvests did not differ between the fauna or fertilizer treatments.

Oat biomass

At both harvests, there were no significant effects of microarthropods on oat biomass production ($p > 0.05$). At harvest 1, the oats that received CN and PC produced more shoot biomass than those that received NF and GM, and the oats that received GM produced less root biomass than those that received the other three fertilizer treatments (Figure 4). However, when the lower germination in the GM pots is accounted for, the shoot biomass differences were not

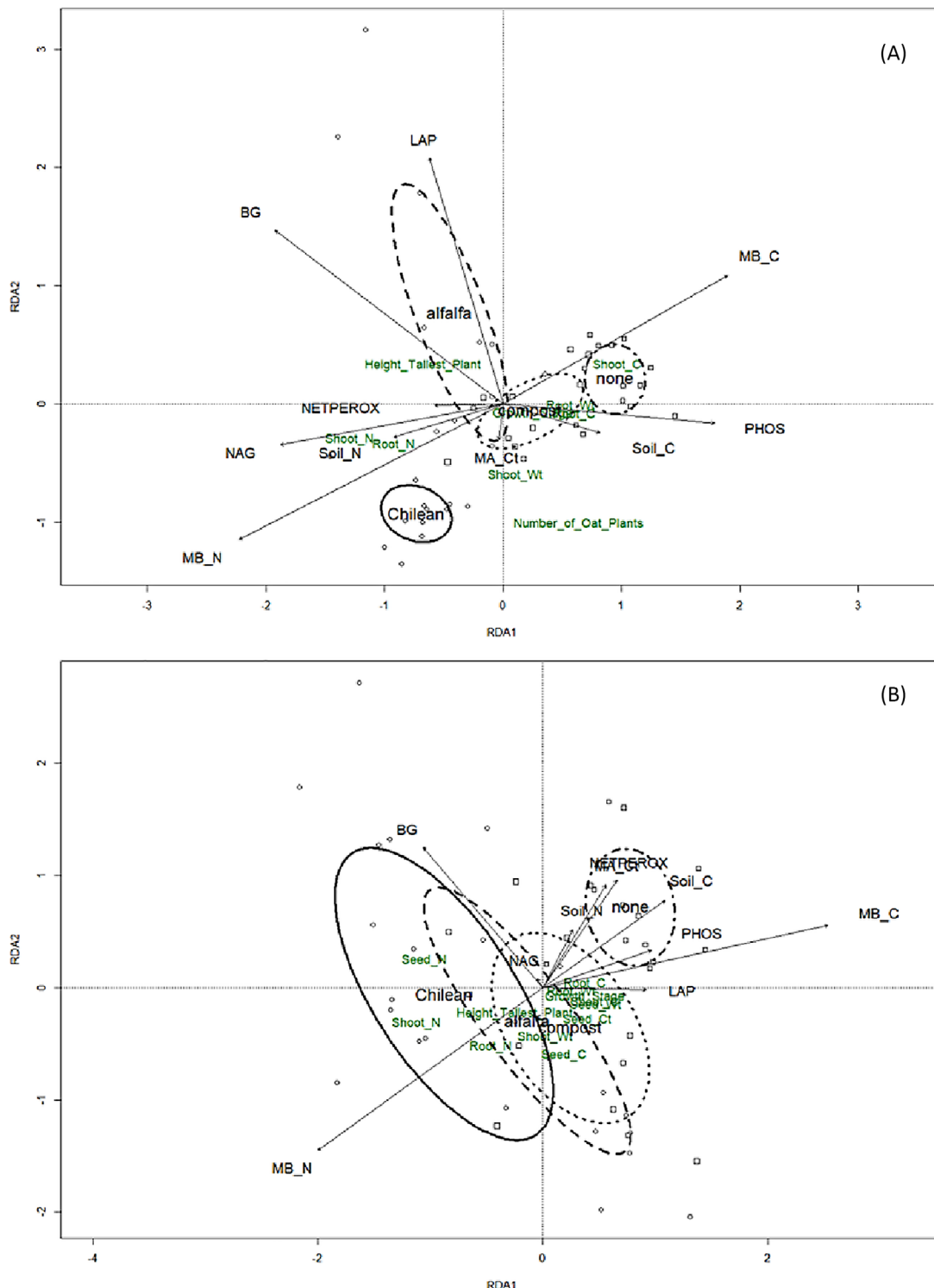


FIGURE 2 Ordinations of the redundancy analysis indicating the relationships between the soil and plant metrics at harvest 1 (A) and harvest 2 (B) in the single-species experiment to evaluate the effect of the soil metrics on plant growth. Arrows represent soil metrics, and green text indicates plant metrics. Ellipse lines indicate fertilizer treatment: none = dashes and dots, alfalfa = all dashes, compost = all dots, and Chilean nitrate = solid line. BG, β -glucosidase; LAP, leucine amino peptidase; NAG, *N*-acetyl- β -D-glucosaminidase; PHOS, acid phosphatase; RDA, redundancy analysis; NETPEROX, net peroxidase; MB, microbial biomass; MA_Ct, microarthropod count.

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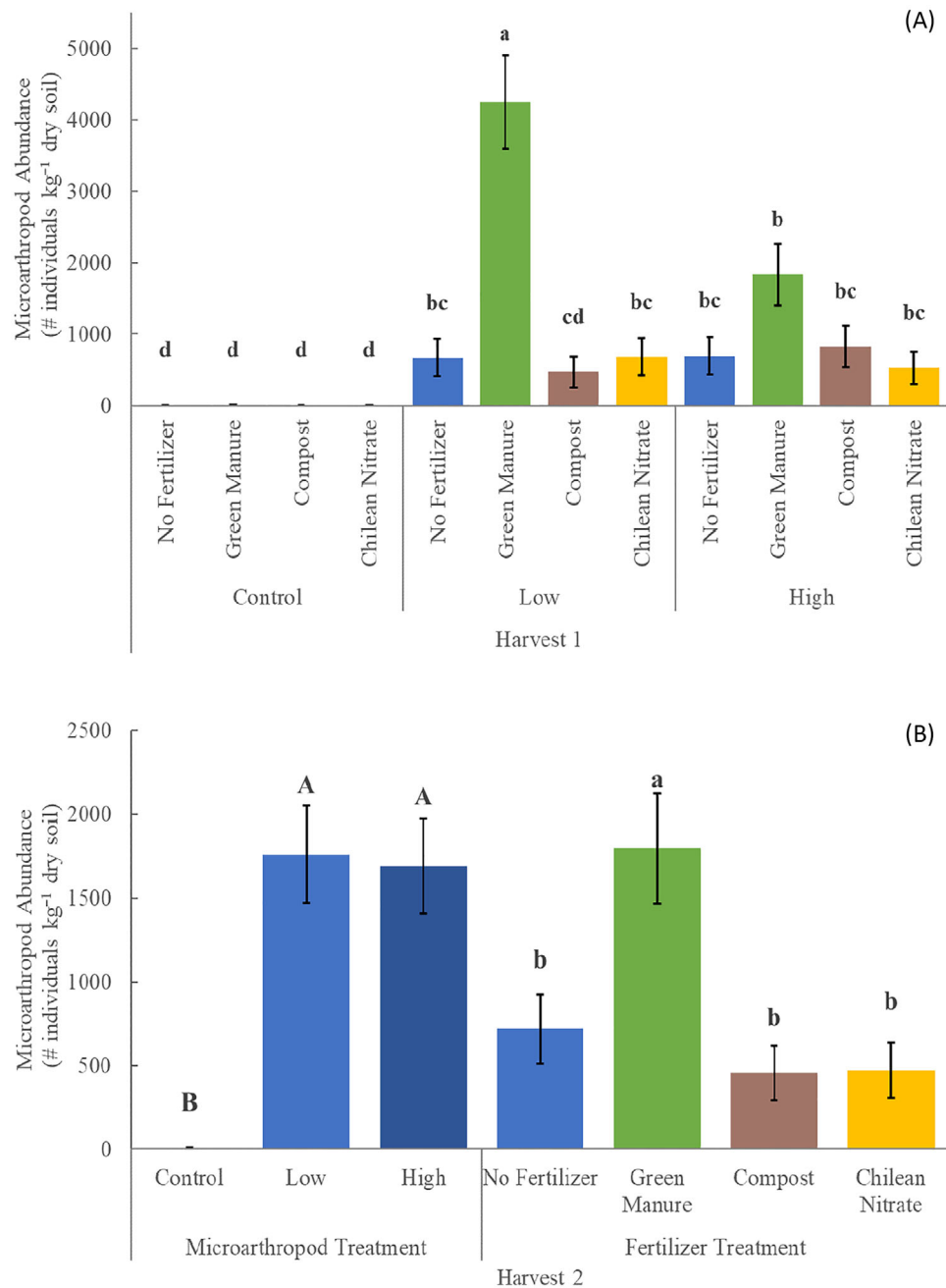


FIGURE 3 Fauna abundance and fertilizer effects on microarthropod abundances (No. of individuals kg⁻¹ dry soil) in the diverse community experiment at harvest 1 (A) and harvest 2 (B). Separate mean comparisons were conducted for each treatment's main effect at harvest 2. Bars with the same letters are not significantly different (Fisher's least significant difference [LSD], $p > 0.05$).

significantly different between the three fertilizers ($p > 0.05$). At harvest 2, the oats that received CN produced more shoot biomass than all other treatments, with an average of 41% more shoot biomass compared to the NF soil (Figure 4). In contrast, the absence of fertilizer increased oat root biomass by up to 41%. Also at harvest 2, oat seed numbers and biomass were approximately twice as high in pots receiving CN and PC than those receiving NF and GM (Figures 4 and 5), but the oats grown in GM were developmentally delayed by up to 10 growth stages (Table A3).

Oat tissue carbon and nitrogen

At harvest 1, microarthropods generally decreased oat root C and the C:N ratio, and as the fertilizer source was more plant available, root N increased and root C:N ratio decreased (Table 3). The presence of microarthropods also tended to increase oat shoot N and C, and as the fertilizer source was more plant available, the shoot N increased.

By harvest 2, we observed similar effects on the oat root and shoot C and N content as at harvest 1. At harvest 2, the seeds also showed very similar effects of the fertilizer

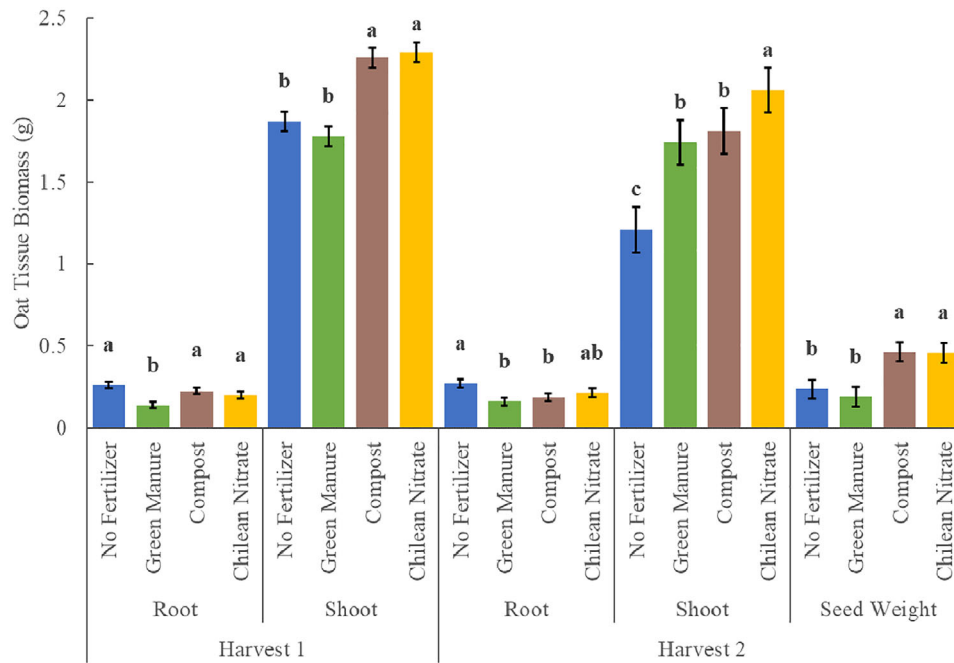


FIGURE 4 Fertilizer effect on oat tissue biomass in the diverse community experiment to evaluate oat growth. Separate mean comparisons were conducted for each oat tissue type within each harvest time point. Bars with the same letters are not significantly different (Fisher's least significant difference [LSD], $p > 0.05$).

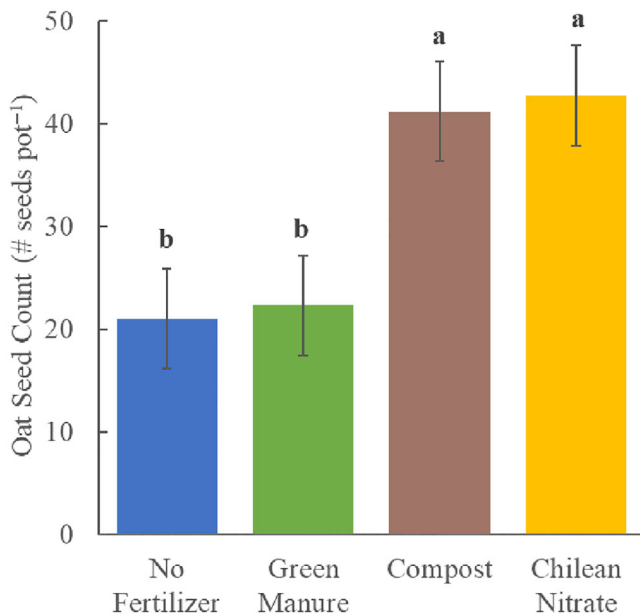


FIGURE 5 Fertilizer treatment effects on oat seed count at harvest 2 in the diverse community experiment to evaluate grain production. Bars with the same letters are not significantly different (Fisher's [LSD], $p > 0.05$).

treatment, with the N and C content generally increasing as the fertilizer source was more plant available, however there were no effects of the microarthropods on the C and N content of the seeds (Table 3). Oat seed C and N content were significantly affected by the application of GM since the oats in that

treatment matured slower than the other treatments and were less developed (Table 3; Table A3).

Microbial biomass carbon and nitrogen

At harvest 1, within the HC treatment, soil that received the CN had up to 72% less microbial C than the soil that received the other fertilizer treatments (Table 4). The pots with no fauna had 19% less microbial biomass N than the pots with LC and HC abundances, and the NF soils had up to 33% less microbial biomass N than the soils that received the other three fertilizer treatments. The pots with HC abundances had lower microbial biomass C:N ratio than those with NC, and the soils that received CN had a lower ratio than the soils with NF and PC (Table 4).

At harvest 2, the soils that received PC had 29% greater microbial biomass C than the soils that received CN (Table 4). The pots with HC abundances had 14% greater microbial biomass N than those with NC, and the soils that received PC had greater microbial biomass N than the soils that received NF and CN. The soils that received CN had less microbial biomass N than those that received all the other fertilizer treatments (Table 4).

Microbial extracellular enzyme activities

At harvest 1, all five microbial extracellular enzyme activities were significantly impacted by the fauna and fertilizer treatment interactions (Table 4). NAG and LAP were uniquely affected by the fertilizer treatments within each fauna

TABLE 3 The effect of fauna abundance and fertilizer treatments on the nutrient composition of soils and plant tissues for the diverse community experiment.

Harvest 1	p-value	Fauna	Fertilizer	Fauna × fertilizer	Soil %N	Soil %C	Soil C:N	Roots %N	Roots %C	Roots C:N	Shoots %N	Shoots %C	Shoots C:N	Seeds %N	Seeds %C	Seeds C:N	
		Fauna	Fertilizer	Fauna × fertilizer	<0.0001	<0.0001	<0.0001	0.1363	0.0351	0.0087	< 0.0001	0.0245	<0.0001				
		Fertilizer			0.0017	0.8454	0.1649	< 0.0001	0.0500	< 0.0001	< 0.0001	0.0004	<0.0001				
		Fauna × fertilizer			0.0164	0.0007	0.0008	0.1250	0.3773	0.0541	0.4093	0.5559	0.0002				
Main effects																	
		Control						1.1	35.1ab	33.3a	2.4b	41.6b					
		Low density						1.2	35.6a	31.0ab	2.5b	41.9ab					
		High density						1.2	33.9b	30.0b	2.8a	42.3a					
		No fertilizer						0.8b	34.6ab	43.6a	1.4c	41.6bc					
		Green manure						1.4ab	33.8b	24.7c	3.7a	41.4c					
		Compost						1.1b	36.0a	33.0b	2.2b	42.5a					
		Chilean nitrate						1.5a	35.0ab	24.5c	3.7a	42.2ab					
Interaction effects																	
		No fauna						0.177ab	6.9a	39.4a				31.5a			
		Green manure						0.176abc	5.4b	31.2c				11.9e			
		Compost						0.186a	6.7ab	36.2ab				22.3bc			
		Chilean nitrate						0.172bc	5.8b	33.9bc				12.1e			
		No fertilizer						0.167c	5.2b	31.1c				33.0a			
		Green manure						0.181a	5.8b	32.2bc				11.6e			
		Compost						0.176ab	5.4b	30.9c				20.3cd			
		Chilean nitrate						0.172bc	5.8b	33.5bc				11.7e			
		No fertilizer						0.165c	4.9b	29.5c				25.8b			
		Green manure						0.176a	5.4b	30.6c				11.1e			
		Compost						0.165c	5.1b	31.1c				17.6d			
		Chilean nitrate						0.165c	5.3b	31.9bc				10.9e			
		High fauna															
		Low fauna															
		High															
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TABLE 3 (Continued)

		Soil %N	Soil %C	Soil C:N	Roots %N	Roots %C	Roots C:N	Shoots %N	Shoots %C	Shoots C:N	Seeds %N	Seeds %C	Seeds C:N
Main effects													
Fauna	Control	0.195a			0.86b	37.2ab	45.2a	1.2b		38.6a	1.8	28.0	18.4
	Low density	0.182b			0.89ab	37.9a	44.1ab	1.3b		36.0b	1.9	36.0	20.3
	High density	0.190ab			0.96a	36.0b	39.1c	1.5a		32.4c	1.9	36.1	20.4
Fertilizer	No fertilizer	0.167b			0.67c	35.5b	53.9a	0.8d		54.4a	1.4b	32.8ab	25.6a
	Green manure	0.192a			0.99b	37.1ab	39.0bc	1.7b		25.3c	1.4b	17.0b	15.3c
	Compost	0.196a			0.89b	37.4a	42.6b	1.0c		42.3b	2.3a	46.4a	20.5b
	Chilean nitrate	0.200a			1.09a	38.1a	35.8c	2.1a		20.8d	2.7a	46.3a	17.4bc
Interaction effects													
No fauna	No fertilizer			40.2a									
	Green manure		7.0a										
	Compost		5.7bc										
Low fauna	Chilean nitrate		6.5ab										
	No fertilizer		7.1a										
	Green manure		5.5c										
High fauna	Chilean nitrate		5.8bc										
	No fertilizer		5.6bc										
	Green manure		5.0c										
High fauna	Green manure		5.1c										
	Compost		5.4c										
	Chilean nitrate		5.7b										

Note: Significance levels from the analysis of variance (ANOVAs) performed the metrics with means ($p < 0.05$, in bold). Means with the same letters are not significantly different (Fisher's [LSD], $p > 0.05$).

TABLE 4 The effect of fauna abundance and fertilizer treatments on the microbial metrics for the diverse community experiment.

Harvest 1	<i>p</i> -value	Microbial C	Microbial N	Microbial C:N	NAG	BG	LAP	PHOS	PHENOX	Peroxidase
Fauna		0.1247	0.0006	0.0021	0.1505	0.9104	0.0088	0.6092	0.4339	0.2162
Fertilizer		0.0022	< 0.0001	< 0.0001	0.0001	0.3051	0.0000	0.7697	0.7988	0.6501
Fauna × fertilizer		0.0321	0.1729	0.0538	0.0005	0.0057	< 0.0001	0.0141	0.0007	0.4397
Main effects										
Fauna			20.8b	9.2a						
Low density			25.6a	7.3ab						
High density			25.4a	6.3b						
No fertilizer			18.5b	10.4a						
Green manure			27.5a	6.1bc						
Compost			23.7a	8.3ab						
Chilean nitrate			26.0a	5.6c						
Interaction effects										
No fauna		174.8a			16.7a	16.8a	10.0b	51.8a	0.13ab	
Green manure		167.7a			10.8b	13.0ab	5.1d	36.4a	0.22ab	
Compost		194.9a			13.1ab	15.2ab	17.6ab	40.2a	0.63a	
Chilean nitrate		188.6a			8.4b	10.1b	4.3d	41.2a	0.30ab	
No fertilizer		192.9a			12.1a	14.7ab	7.9c	43.7a	0.20ab	
Green manure		176.5a			13.6a	12.5ab	6.3cd	46.0a	0.25ab	
Compost		195.4a			12.1a	14.2ab	7.8c	44.9a	0.27ab	
Chilean nitrate		137.3a			8.6b	13.1ab	4.1d	39.0a	0.21ab	
No fertilizer		206.9a			9.5b	12.6ab	19.2a	32.6b	0.67a	
Green manure		148.4a			13.3a	13.6ab	10.3bc	48.1a	0.29ab	
Compost		190.3a			10.7b	11.5ab	6.7cd	41.6a	0.02b	
Chilean nitrate		58.4b			9.9b	15.9ab	4.9d	40.9a	0.49ab	
<i>p</i> -value		0.7117	0.0396	0.6590	0.0033	0.2401	0.0760	0.3015	0.0351	0.0913
Fertilizer		< 0.0001	0.7016	<0.0001	0.2326	< 0.0001	<0.0001	0.0649	0.0001	0.0907
Fauna × fertilizer		0.1283	0.1692	0.8841	< 0.0001	0.0605	0.1536	0.0002	0.5985	
Main effects										
Fauna		140	10.8b				6.57		0.31b	0.36
Low density		152	11.4ab				8.1		0.44a	0.34
High density		148	12.5a				7.74		0.43ab	0.40

(Continues)

TABLE 4 (Continued)

	Microbial C	Microbial N	Microbial C:N	NAG	BG	LAP	PHOS	PHENOX	Peroxidase
Fertilizer	151ab	11.2b				9.07ab		0.32	0.46ab
Green manure	154ab	12.1ab				6.80b		0.43	0.23c
Compost	164a	13.9a				10.02a		0.36	0.34bc
Chilean nitrate	117b	9.1c				4.89c		0.47	0.50a
Interaction effects									
No fauna				15.1a			55.3a		
Green manure				8.3b			31.3b		
Compost				8.4b			37.5b		
Chilean nitrate				6.0c			30.4b		
Low fauna				7.7bc			35.4b		
Green manure				9.1b			35.0b		
Compost				9.6b			46.8a		
Chilean nitrate				5.9c			26.7b		
High fauna				8.2bc			33.2b		
No fertilizer				7.5c			38.4b		
Green manure				10.7b			43.2a		
Compost				5.8c			26.9b		
Chilean nitrate									

Note: Significance levels from the analysis of variances (ANOVAs) performed the metrics with means ($p < 0.05$, in bold). Means with the same letters are not significantly different (Fisher's least significant difference [LSD], $p > 0.05$).

Abbreviations: BG, β -glucosidase; LAP, leucine amino peptidase; NAG, *N*-acetyl- β -D-glucosaminidase; PHOS, phosphatase; PHENOX, phenol oxidase.

treatment. Within the NC treatment, 40% more BG was produced in the soils that received NF compared to the soils that received CN. The lowest PHOS activity was in the HC treatment when there was NF added. The PC fertilizer affected PHENOX activity variability the most, with the greatest activity in the absence of fauna and the least activity when HC abundances were present.

At harvest 2, NAG and PHOS were also impacted by the fauna and fertilizer interactions (Table 4). There was greater LAP activity in the pots that received PC compared to those that received GM and CN, and in the NF and GM pots compared to the CN pots (Table 4). There was greater net PER activity in the soils that received CN compared to those that received the PC and GM, and greater activity in the NF soil compared to the soil that received GM (Table 4). Fauna presence increased PHENOX activity by up to 30% (Table 4).

Soil carbon and nitrogen

At harvest 1, in the presence of fauna, the soils that received GM had the greatest N content; however, when fauna were not present, the soils that received PC had the greatest N content (Table 3). At harvest 2, the soil N content was slightly greater in the NC and HC treatments, and in the absence of fertilizer, soil N was reduced by up to 16% (Table 3). At both harvests, the soil C tended to decrease as microarthropod abundance increased, with soil C increasing as the fertilizer source was more plant available; however, this effect was more pronounced when there were no microarthropods present.

3.2.4 | Redundancy analysis and metric correlations

The redundancy analysis PerMANOVA model was significant at both harvests ($p = 0.001$ and $p = 0.0001$, respectively), indicating that the soil variables were significantly correlated to the plant metrics (Table A2). At harvest 1, microarthropod abundance, microbial biomass N, and the microbial enzymes NAG and LAP were significantly correlated to the plant metrics (Figure 6; Table A2). At harvest 2, the microbial enzymes NAG and BG and soil C and N content were all significantly correlated to the plant metrics (Figure 6; Table A2).

4 | DISCUSSION

4.1 | Drivers of oat production outcomes

4.1.1 | Microarthropods

The addition of microarthropods, as a single species or diverse communities, improved the nutritional quality of the

oats by stimulating N uptake. Given the important role that microarthropods play in N availability in soils (Filser, 2002; Verhoef & Brussaard, 1990), this positive effect on N uptake was expected. The presence of Collembola has been found to increase the uptake of N in annual bluegrass (*Poa annua* L.), perennial ryegrass (*Lolium perenne* L.), and white clover (*Trifolium repens* L.) (Forey et al., 2015; Scheu et al., 1999; Winck et al., 2020). Interestingly, in our study, the magnitude of the effect of microarthropods on oat tissue N content varied between the forage and grain harvest dates. The magnitude of these effects may have been greater at the forage harvest, especially in the single-species experiment, due to the timing of the fertilizer additions. The microarthropods likely enhanced the initial fertilizer breakdown and increased plant available N earlier in the experiment, however this impact would diminish over time as the soil microbial community continued to make N plant available. To our knowledge, this is the first study illustrating that the impacts of diverse microarthropod communities on crop nutrient composition vary over time at different plant growth stages.

Our diverse microarthropod communities had few notable effects on plant growth (i.e., biomass, height, and reproduction [seeds]), despite many other studies finding microarthropods to affect the growth of annual grass species (Chauvat & Forey, 2021; Eisenhauer et al., 2018; Forey et al., 2015; Kuřáková et al., 2018). Other studies using diverse microarthropod assemblages found positive effects of microarthropods on plant reproductive measurements (Eisenhauer et al., 2018; Forey et al., 2015; Kaneda et al., 2012). Our diverse community experiment may not have had the same positive effects on reproductive measurements observed in the existing literature due to greater diversity and the occurrence of more multitrophic interactions in comparison to those studies. These results contrasted with our finding that *I. minor*, regardless of abundance level, decreased oat seed production while increasing seed N content. Similar to our single-species experiment findings, Schutz et al. (2008) found that the collembolan *Protaphorura fimata* Gisin negatively impacted wheat ear production (*Triticum aestivum* L.) (Schütz et al., 2008).

Interestingly, in the diverse community experiment, despite the limited direct effects of the microarthropod treatments on plant growth metrics, microarthropod abundance was significantly correlated to the oat growth metrics at the first harvest. This relationship appeared to be governed by the response of microarthropods to our fertilizer treatments. Specifically, there was an increase in microarthropod abundance in pots that received green manure, with up to four times as many individuals compared to the other fertilizer treatments. These findings indicate that microarthropod responses to and degradation of fertilizers, in this case their stimulation of microbial enzyme activity in the pots that received green manure, can lead to important effects on plant growth outcomes.

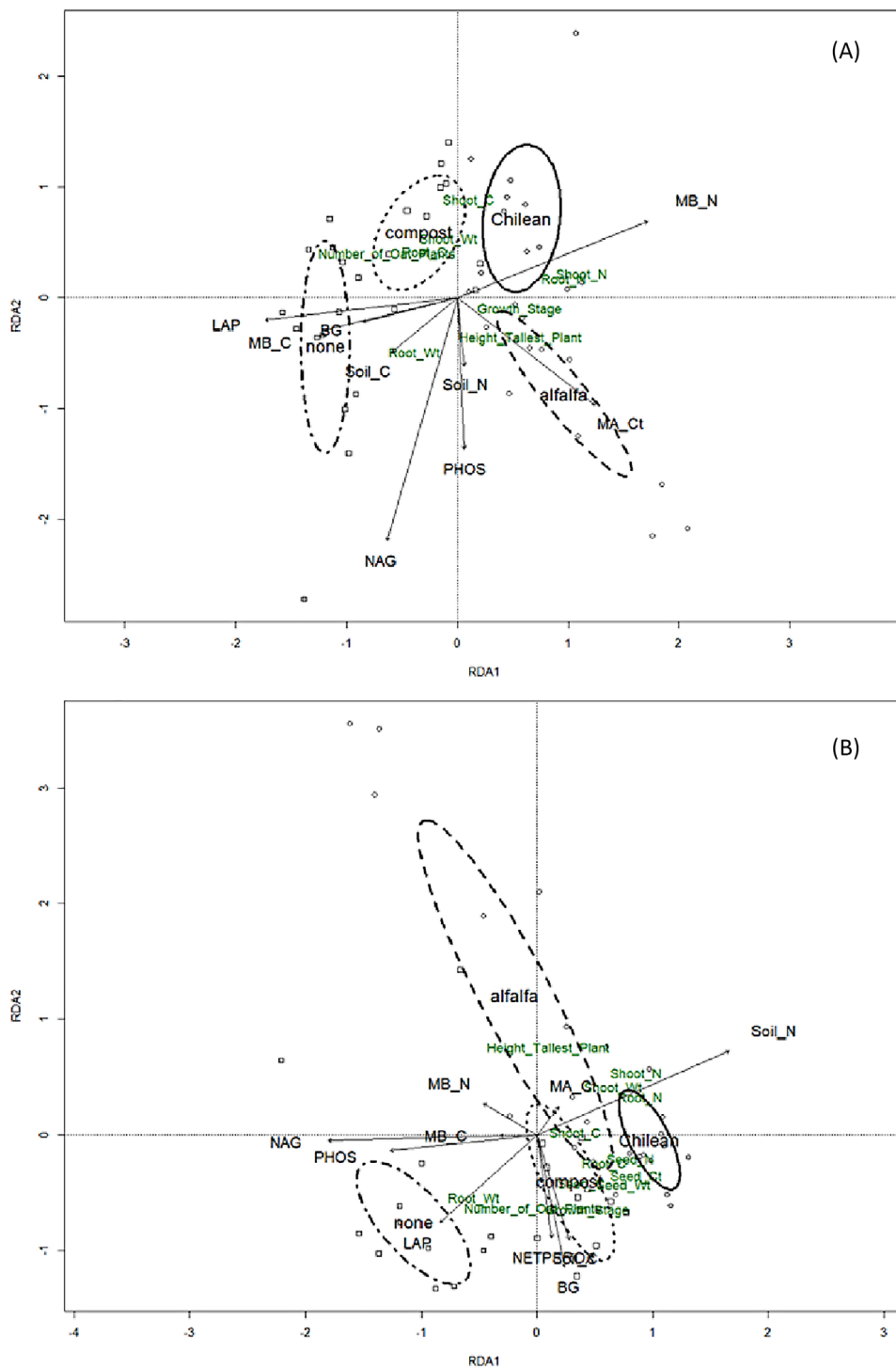


FIGURE 6 Ordinations of the redundancy analysis indicating the relationships between the soil and plant metrics at harvest 1 (A) and harvest 2 (B) in the diverse community experiment to evaluate the effect of the soil metrics on plant growth. Arrows with corresponding text represent soil metrics, and green text indicates plant metrics. Ellipse lines indicate fertilizer treatment: none = dashes and dots, alfalfa = all dashes, compost = all dots, Chilean nitrate = solid line. BG, β -glucosidase; LAP, leucine amino peptidase; NAG, *N*-acetyl- β -D-glucosaminidase; PHOS, acid phosphatase; RDA, redundancy analysis; NETPEROX, net peroxidase; MB, microbial biomass; MA_Ct, microarthropod count.

The time since fertilizer addition was an important determinant in the relationships between the soil and plant metrics in the diverse community experiment. From the forage harvest to the grain harvest, the redundancy analysis showed the metrics that were correlated to oat growth transitioned from biotic community and activity metrics (microarthropod abundance, microbial biomass N, NAG, and LAP) to soil nutrient content and microbial enzyme activity (soil N, soil C, NAG, and BG). This shift in the soil metrics relationships with the plant growth metrics suggests that the stage of fertilizer breakdown drives the soil processes that impact plant growth. This shift may have been observed in the diverse community experiment since soil mesofauna community complexity and abundance can influence chemical trajectories of organic matter inputs (Ball et al., 2022).

4.1.2 | Fertilizer composition

Fertilizer composition can be an important driver of plant growth outcomes. In both experiments, we observed that regardless of the presence of soil fauna, increasing fertilizer plant availability stimulated the initial growth of oats, generally shifted biomass production from roots to shoots, and improved N uptake in the oat tissues. Fertilizers that are more plant available are known to stimulate initial plant growth, shift biomass production from plant roots to shoots, and increase plant N uptake (Jones, 2012), as observed in our study.

While the plant availability gradient of the fertilizers, based on C:N ratios, predicted oat growth outcomes well overall, the GM had unique effects on oat growth. The GM was the least plant available based on initial C:N ratio, though the C:N ratio of the green manure was similar to that of the compost (Velthof et al., 1998). This suggests the effects of the green manure may have more to do with the unique tissue chemistry of this material. Green manure has more labile plant compounds compared to compost, which has already undergone a degree of microbial decay (Charest & Beauchamp, 2002; Swift et al., 1979; Thambirajah et al., 1995).

The primary and secondary metabolites in the GM may be driving specific oat growth and development outcomes. In both experiments, oat germination was negatively impacted by the application of GM. Despite their many benefits, there is evidence that some green manures contain allelochemicals that inhibit the germination of monocotyledonous plant species (Rugare et al., 2021; Singh et al., 2010). In addition to suppressing germination, in the diverse community experiment, the green manure delayed oat maturation and development while improving oat growth and nutritional quality over the course of the experiment. The green manure also increased the abundance of microarthropods, which may have altered the soil environment through their activity in a manner

that shifted oat growth toward increased biomass production instead of maturation.

These findings suggest that incorporating green manures may be beneficial when growing oats for forage; however, the delayed maturation caused by the green manure could be less ideal for grain production when considering crop rotation management.

4.2 | Drivers of soil biological activity

4.2.1 | Microbial biomass

The chemistry of fertilizer amendments is known to be a strong regulator of microbial biomass C (Kallenbach & Grandy, 2011), which serves as a proxy for microbial community size. The findings from both experiments provide additional support for this phenomenon: as nutrient inputs to soil became increasingly more plant available, those soils supported lower microbial biomass C. This may be due to the N in these fertilizers, like the Chilean nitrate, being less fauna available, thus increasing dependence on fungal grazing by the fauna, which can lead to a decrease in microbial biomass.

We observed shifts in microbial biomass C:N ratios in both experiments that may indicate differences in community composition. Microbial communities with lower C:N ratios generally have more bacteria, whereas microbial communities with higher C:N ratios generally have more fungi (Jenkinson & Ladd, 1981; McGill et al., 1982). The effects of the microarthropods on the ratio of C:N in the microbial biomass were greater in the single-species experiment compared to the microarthropod community experiment. In both experiments, the overall trend was that as the microarthropod abundances increased, the microbial biomass C:N ratio decreased, likely because microarthropod preferentially feed on fungi over bacteria, which would select for a more bacteria dominated community (Lussenhop, 1992). This effect may have been diminished in the community experiment due to top-down pressure from the predators on the microbivores in the community.

4.2.2 | Microbial activity

In both experiments, the microarthropod treatments had mixed effects on microbial enzyme activity. In the single-species experiment, *I. minor* only affected microbial enzymes at the first harvest, which may be due to their diminished abundances at the second harvest. Increasing *I. minor* abundances stimulated the microbial breakdown of chitin. *I. minor* decreased the fertilizer effects on potential amino acid and phosphorus breakdown, while increased the magnitude of the fertilizer effects on potential lignin breakdown. In the diverse community experiment, at the first harvest, greater

microarthropod abundances reduced the magnitude of the fertilizer effects on most microbial enzymes and soil C and N content, which was still the case at the second harvest but to a lesser degree and on fewer enzymes. While the microarthropods generally decreased the fertilizer effects, at the first harvest, greater microarthropod abundance led to increased fertilizer effects on amino acid breakdown and microbial C, suggesting that the microarthropods may have been liberating more amino acids for microbes to break down, which aided in increasing the overall size of the microbial community (Moorhead & Sinsabaugh, 2006; Saqib & John Whitney, 2006). These results align with previous findings of microarthropod presence having mixed effects on microbial enzyme activity (Crowther et al., 2012; Wickings & Grandy, 2011).

Comparing the experiments, we observed that diverse microarthropod communities had a greater number of effects on microbial enzymes that persisted longer to the second harvest. This suggests that more diverse microarthropod communities have a greater impact on the biological activity of the microbial communities. The effects of the microarthropod communities on microbial community activity affected the breakdown of the fertilizers, generally making the fertilizer source less important in determining soil nutrient availability for crops.

Interestingly, in most harvests, the enzyme BG was significantly correlated to the plant growth metrics. Aside from the minor treatment effects observed at the second harvest in the diverse community experiment, BG was rarely affected by the microarthropod and fertilizer treatments imposed. This may suggest that BG, the enzyme that breaks down cellulose, may be a good predictor of plant growth outcomes. This enzyme may be a better predictor of plant growth outcomes because cellulose is an important building block for plant growth or it is not strongly affected by external factors such as other soil biota or fertilizer amendments in this study.

5 | CONCLUSIONS

Our study illustrated that microarthropods, both a single species and diverse communities, stimulated N cycling and enhanced crop nutrient status. Results indicated that microarthropods likely have few direct effects on crop growth and development, except in the case of specific species that, when in high enough abundances, may influence aspects of crop production like crop growth stage development and seed count as observed with *I. minor*. In both the single-species and diverse community experiments, the effects of the microarthropods diminished over time from the initial fertilizer additions, highlighting the importance of their initial interactions with new nutrients entering the soil environment. The indirect influence of microarthropods on crop production via their effects on microbial communities can be quite

significant. Our work suggests that, through their impacts on soil microbial activity, microarthropods may narrow the distinction among different fertilizers.

AUTHOR CONTRIBUTIONS

Ashley B. Jernigan: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing—original draft; writing—review and editing. **Jenny Kao-Kniffin:** Conceptualization; writing—review and editing. **Sarah Pethybridge:** Conceptualization; writing—review and editing. **Kyle Wickings:** Conceptualization; funding acquisition; methodology; resources; supervision; writing—original draft; writing—review and editing.


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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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APPENDIX

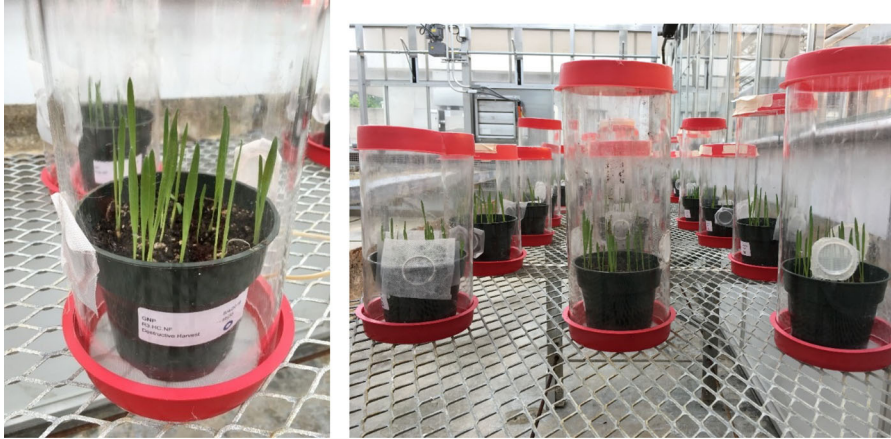


FIGURE A1 Experimental set up photos.

TABLE A.1 The effect of Collembola abundance and fertilizer treatments on oat growth from the single-species experiment weekly checks.

p-value	Week 1		Week 2		Week 3		Week 4		Week 5		Week 6		Week 7		Week 8	
	Height of tallest	Height of shortest	Number of plants	Growth stage	Height of tallest	Number of plants	Growth stage	Height of tallest	Height of tallest	Height of tallest	Height of shortest	Height of tallest	Height of tallest	Height of tallest	Height of tallest	Height of tallest
	0.7688	0.3666	0.0445	0.5371	0.6506	0.2432	0.0553	0.1125	0.0736	0.5749	0.0846	0.1672	0.0378	0.0921		
	0.0259	0.0005	< 0.0001	0.0649	0.0049	< 0.0001	0.0014	< 0.0001	0.0002	0.0079	0.0001	0.0004	0.0004	0.0010		
	0.9664	0.9592	0.9281	0.0082	0.9142	0.2301	0.0029	0.4433	0.4317	0.3278	0.1481	0.1356	0.0807	0.1897		
	fertilizer															
	Main effects															
	Control	14.6	2.1	18.5a	11.1	30.4	14.3	12.1	39.6	41.5	26.9	57.0	50.2	50.6a	50.1	
	Low density	14.8	2.6	20.0a	11.1	30.4	14.8	12.1	40.2	44.8	27.1	53.1	47.0	46.3b	46.6	
	High density	14.8	2.9	20.2a	11.0	29.8	14.7	12.0	38.3	41.6	28.0	53.4	46.6	45.8b	45.7	
	No fertilizer	14.2b	3.1a	21.2a	11.0	28.3b	15.6a	12.0	35.6c	37.3b	26.3ab	49.0c	43.1c	42.9c	43.0c	
	Green manure	14.4ab	1.3b	14.5b	11.1	31.2a	13.4b	12.2	43.0a	46.3a	25.2b	60.2a	53.7a	53.4a	53.1a	
	Compost	15.1ab	2.8a	21.8a	11.1	31.2a	15.6a	12.0	40.4ab	43.4a	28.4ab	52.5bc	45.6bc	45.1bc	45.2bc	
	Chilean nitrate	15.2a	3.5a	20.8a	11.0	30.0ab	15.0a	12.0	38.5b	43.5a	29.4a	56.2ab	49.4ab	48.8ab	48.6ab	
	Interaction effects															
	No Collembola				11.0b											
	Green manure				11.0b											
	Compost				11.4a											
	Chilean nitrate				11.0b											
	No fertilizer				11.0b											
	Collembola															
	Green manure				11.2ab											
	Compost				11.0b											
	Chilean nitrate				11.0b											
	No fertilizer				11.0b											
	Collembola															
	Green manure				11.1b											
	Compost				11.0b											
	Chilean nitrate				11.0b											

Note: Significance levels from the analysis of variances (ANOVAs) performed the metrics with means ($p < 0.05$, in bold). Means with the same letters are not significantly different (Fisher's least significant difference [LSD], $p > 0.05$).

TABLE A 2 Redundancy analysis (RDA) results data for both the single-species and diverse community experiments at both harvests.

PerMANOVA model	Single-species experiment			Diverse community experiment		
	Forage harvest			Forage harvest		
	10	10	10	9	9	10
Degrees of freedom						
<i>F</i> -value	2.79	1.43	1.43	1.97	1.97	2.41
<i>p</i> -value	0.001	0.042	0.042	0.003	0.003	0.001
Soil variable	Variance	<i>F</i> -value	<i>p</i> -value	Variance	<i>F</i> -value	<i>p</i> -value
Microarthropod abundance	0.1648	1.18	0.304	0.2578	1.10	0.288
Microbial biomass N	1.5422	11.12	0.002	1.0471	4.48	0.002
Microbial biomass C	0.3785	2.73	0.016	0.6484	2.77	0.016
NAG	0.1652	1.19	0.328	0.161	0.68	0.656
LAP	0.5903	4.25	0.002	0.1157	0.49	0.838
BG	0.4061	2.92	0.012	0.5701	2.44	0.048
PHOS	0.159	1.14	0.316	0.1395	0.59	0.634
NETPEROX	0.108	0.77	0.576	0.1977	0.84	0.522
Soil N	0.1692	1.22	0.274	0.1185	0.50	0.768
Soil C	0.1869	1.34	0.204	0.1007	0.43	0.892
				0.1738	1.07	0.36
				0.1883	0.88	0.456
				0.2706	1.27	0.244
				0.1166	0.54	0.764
				1.3403	6.30	0.004
				0.3383	1.59	0.164
				0.9791	4.60	0.004
				0.0615	0.28	0.96
				0.2637	1.24	0.274
				0.7753	3.64	0.006
				0.7993	3.75	0.01

Note: Significant *p*-values (<0.05) are in bold.

Abbreviations: BG, β -glucosidase; LAP, leucine amino peptidase; NAG, *N*-acetyl- β -D-glucosaminidase; PHOS, phosphatase; NETPEROX, net peroxidase.

