ELUCIDATING THE ROLE OF SOIL MICROARTHROPODS IN CROPPING SYSTEM MANAGEMENT

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ELICIDATING THE ROLE OF SOIL MICROARTHROPODS IN CROPPING SYSTEM MANAGEMENT

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Soil microarthropods, a diverse group of fauna dominated by springtails (Collembola) and mites (Acari), mediate many soil biological processes. While our understanding of the effects of microarthropods on these processes has increased greatly, we still have a limited understanding of how these effects manifest in crop production. The goal of this work was to investigate how soil microarthropods affect major areas of crop management. A multi-year field experiment was conducted to model how soil microarthropods affect crop production under different cover cropping strategies. The relative importance of soil nutrient cycling, plant pathogens, and weed competition in crop production was investigated using multi-model piecewise structural equation modeling. Soil and microbial community carbon and nitrogen were important determinants in bean production. The microarthropods had more positive effects on bean production when there were more food resources available. A greenhouse experiment investigated the effects of microarthropod abundance and diversity on nitrogen cycling and how these effects manifest in crop production. Microarthropods, in both single species and diverse communities, stimulate nitrogen cycling and enhance crop nutrient status. Another greenhouse experiment examined how microarthropods could potentially affect weed community assemblage. Collembola reduced germination more for the broadleaf weeds than the grass weeds. The Collembola decreased broadleaf weed biomass (up to 45% reduction for certain species) more than the grass weed biomass. A follow-up lab experiment revealed that the Collembola

only affected the germination of yellow foxtail, indicating that the Collembola were more likely impacting the broadleaf weed growth by feeding on their roots than directly affecting germination. A series of lab experiment were then conducted to delve into the mechanisms and spatio-temporal dynamics of microarthropod-plant pathogen interactions. The dominant mechanism in the *Rhizoctonia solani* and Collembola interactions was consumption of the pathogen, however there was potential for pathogen dispersal. Increasing Collembola abundances decreased the growth rate of *R. solani*. Within a mineral substrate, our findings indicate that it is not the physical soil environment diminishing the collembolan control of pathogens, but that it is the presence of organic matter. These studies indicate that soil microarthropods can play a role in multiple aspects of crop management.

BIOGRAPHICAL SKETCH

Ashley Jernigan was born and raised in rural North Carolina. From a young age she was very curious and found solace exploring the natural world around her. Her desire to learn led her to the North Carolina School of Science and Mathematics for her last two years of high school, during which time she had her first research experience working with Dr. Daniel Richter in the Soils and Forest Ecology lab at Duke University.

Ashley attended Cornell University in Ithaca, New York, graduating with a Bachelor of Science in International Agriculture & Rural Development with minors in Soil Science and Human Nutrition in 2016. During her undergraduate studies she worked with Dr. Matthew Ryan in the Sustainable Cropping Systems Lab and completed an honors thesis.

Prior to starting graduate school, Ashley returned to work with Dr. Ryan and investigated the legacy effects of contrasting organic grain cropping systems on soil health indicators, soil invertebrates, weeds, and crop yield. This research project sparked her interest in the role of soil microarthropods in agricultural systems. She started her Ph.D. in the department of Entomology at Cornell University in 2018 under the guidance of Dr. Kyle Wickings. As a graduate student Ashley enjoyed working to serve farmers and her community.

To my dear husband, Matthew Boyd, whose encouraging presence I will forever cherish.

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INTRODUCTION

Soil microarthropods, a diverse group of soil fauna dominated by springtails (Collembola) and mites (Acari), are known to mediate many soil biological processes (Lavelle et al. 2006). While our understanding of the effects of microarthropods on these processes has increased greatly (Wagg et al. 2014; Filser et al. 2016; Beretta et al. 2022; Gergócs et al. 2022; Potapov 2022), we still have a limited understanding of how these effects manifest in plant growth and development.

The interactions of microarthropods within soil environments help connect smaller and larger scale activities due to their intermediate size. Microarthropods fall in the category of soil mesofauna (0.1-2 mm), the intermediate size category between microfauna (<0.1 mm) and macrofauna (>2 mm) (Briones 2018). Microarthropods can alter both the composition and function of soil microbial communities by feeding on microbes, while simultaneously being an important food source for larger fauna (Briones 2014).

Through their interactions within the soil environment and other biota, microarthropods affect plants both indirectly and directly. Microarthropods indirectly impact plants through their influence on soil organic matter decomposition, nutrient cycling, pathogen density, and plant-soil feedbacks, all of which converge to have nuanced impacts on plant health (Neher and Barbercheck 2019). Microarthropods may also impact plants directly through interacting with plant roots (Eerpina *et al*., 2017), though there is comparatively less evidence of these interactions in the literature.

In **Chapter 1**, I review the current understanding of direct microarthropod-plant interactions, how microarthropod-microbe interactions indirectly impact plant growth, and key areas for future study. Microarthropod impacts on plants are primarily routed through their

interactions with microbial communities, mediating organic matter decomposition, nutrient cycling and allocation, and plant-pathogen dynamics in soils. Overall, existing evidence indicates that the overall effects of microarthropods on plants is positive.

In **Chapter 2**, I explored how soil microarthropods affect crop production under different cover cropping strategies. Several soil, plant pathogen, weed, and crop metrics were measured in this multi-year field experiment. The relative importance of soil nutrient cycling, plant pathogens, and weed competition in crop production was investigated using multi-model piecewise structural equation modeling. Soil nutrient status was an important determinant of total bean weight. Microbial biomass nitrogen was an important soil metric, consistently having a negative effect on total bean weight. The microarthropods had more positive effects on bean production when there are more food resources available, as in the rolled cereal rye treatment.

In **Chapter 3**, I researched into how the effects of microarthropod abundance and diversity on nitrogen cycling manifest in crop production. Our findings indicate that microarthropods, both single species and diverse communities, stimulate nitrogen cycling and enhance crop nutrient status. As microarthropod abundance and diversity increased, microarthropods exerted a greater number of effects on soil microbial activity. These effects enhanced 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 outcomes primarily through their effects on soil biological processes.

In **Chapter 4**, I examined how microarthropods could potentially affect weed community assemblage. Collembola increased weed germination shortly after planting, though this effect diminished over time. By the end of the experiment the Collembola reduced germination more for the broadleaf weeds than the grass weeds. At harvest, the Collembola had decreased total

weed biomass production by up to 23%. The Collembola decreased broadleaf weed biomass (up to 45% reduction for certain species) more than the grass weed biomass. A follow-up lab experiment was conducted to understand the potential mechanisms driving the greenhouse experiment results. The lab experiment focused on the individual weed species interactions with Collembola to investigate why the collembolans had more of an effect on the broadleaf weeds compared to the grasses. The Collembola only affected the germination of the yellow foxtail in the lab experiment, indicating that the Collembola were more likely impacting the broadleaf weed growth by feeding on their roots than directly affecting germination in the greenhouse experiment. Our findings indicate that Collembola, and microarthropods in general, likely have the potential to play a role in weed management decisions in agricultural systems.

In **Chapter 5**, I delved into the mechanisms and spatio-temporal dynamics of microarthropod-plant pathogen interactions. The dominant mechanism in the *Rhizoctonia solani* and Collembola interactions was consumption of the pathogen, however there was potential for the collembolans to disperse the pathogen as there was viable pathogen structures on the cuticle and in the frass. Increasing Collembola abundances decreased the growth of *R. solani*. In a soil environment with no organic matter, the Collembola decreased the pathogen growth. In a soil environment with organic matter present the Collembola did not affect the pathogen growth. Our findings suggest that it is not the physical soil environment diminishing the collembolan control of pathogens, but that it is the presence of alternative food resources in the form of organic matter.

From this work it is evident that soil microarthropods play a role in all aspects of crop management. The studies presented in the following chapters span applied and mechanistic research to begin creating a foundation for utilizing soil microarthropods in crop management.

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CHAPTER 1

SOIL MICROARTHROPOD EFFECTS ON PLANT GROWTH AND DEVELOPMENT[1]

Abstract

Soil microarthropods influence many soil processes that support plant growth and development. In this paper we review the current understanding of direct microarthropod-plant interactions, how microarthropod-microbe interactions indirectly impact plant growth, and key areas for future study. Microarthropod impacts on plants are primarily routed through their interactions with microbial communities, mediating organic matter decomposition, nutrient cycling and allocation, and plant-pathogen dynamics in soils. The research investigating how microarthropod-saprotrophic microbe interactions affect plants through decomposition and nutrient cycling indicates a generally positive relationship, though this relationship is influenced by the overall diversity or species richness observed in the microarthropod communities. The effects of microarthropod-plant symbionts interactions on plants are varied and there is no clear benefit or detriment to plants via this mechanism. The effects of microarthropod-plant pathogen interactions on plants suggest that, in most cases, microarthropods will reduce disease incidence and severity. The limited diversity of the study taxa in this area of research is a major limitation to our understanding of how microarthropods impact plant health. Our review revealed that while much is known about microarthropod impacts on the intermediate processes that influence plants, only a subset of studies have quantified plant responses to microarthropod activity. Overall, existing evidence indicates that the overall effects of microarthropods on plants is positive. Future research should aim to incorporate more plant metrics and consider both

[1] Jernigan, A., Kao-Kniffin, J., Pethybridge, S. & Wickings, K. 2022. Soil microarthropod effects on plant growth and development. *Plant and Soil*. https://doi.org/10.1007/S11104-022-05766-X

microarthropod and microbial community dynamics in designed and observational studies.

1. Introduction

The effects of soil processes on plant growth and development have long been studied, leading to the current soil health concepts that dominate conversations in the field of sustainable agriculture. Soil health schemas recognize the importance of soil biological processes in maintaining the soil functions that support crop production (NRCS; Barrios 2007; Briones 2018). Soil microarthropods, a diverse group of soil fauna dominated by springtails (Collembola) and mites (Acari), are known to mediate many soil biological processes (Lavelle et al. 2006). While our understanding of the effects of microarthropods on these processes has increased greatly (Wagg et al. 2014; Filser et al. 2016; Beretta et al. 2022; Gergócs et al. 2022; Potapov 2022), we still have a limited understanding of how these effects manifest in plant growth and development.

The interactions of microarthropods within soil environments help connect smaller and larger scale activities due to their intermediate size. Microarthropods fall in the category of soil mesofauna (0.1-2 mm), the intermediate size category between microfauna (<0.1 mm) and macrofauna (>2 mm) (Briones 2018). Microarthropods can alter both the composition and function of soil microbial communities by feeding on microbes, while simultaneously being an important food source for larger fauna (Briones 2014).

Through their interactions within the soil environment and other biota, microarthropods affect plants both indirectly and directly. Microarthropods indirectly impact plants through their influence on soil organic matter decomposition, nutrient cycling, pathogen density, and plant-soil feedbacks, all of which converge to have nuanced impacts on plant health (Neher and

Barbercheck 2019). Microarthropods may also impact plants directly through interacting with plant roots (Eerpina *et al*., 2017), though there is comparatively less evidence of these interactions in the literature. Synthesizing the literature on the direct and indirect effects microarthropods have on plants will aid in clarifying knowledge gaps and provide direction for utilizing soil microarthropods as a tool to improve plant productivity.

Our objectives for this review are to both summarize the body of research conducted on soil microarthropod effects on plants and to highlight new areas of emerging research. BIOSIS Previews Database and Google Scholar were used to obtain relevant literature. Search terms targeting microarthropods included: microarthropod, soil arthropods, soil invertebrates, soil fauna, Collembola, Acari, mite. Search terms targeting plants included: plant biomass, plant yield, crop yield, primary productivity, plant growth. We have chosen to focus on papers that incorporate measurements or manipulations of at least one plant and microarthropod metric, although we cite other literature where relevant to illustrate microarthropod impacts on intermediate processes important for plant productivity. Within this scope, we discuss the current understanding of pathways by which microarthropods affect plants, highlight knowledge gaps within these pathways, and propose directions that warrant future study.

2. Microarthropod Effects on Plants

Soil microarthropods can affect living plants through their relationships with the plants themselves and with other abiotic and biotic soil factors. Here we posit that microarthropods exert the majority of their effects on plants via two primary activities: 1) feeding – consumption of microbial biomass and living or senesced plant matter, and 2) movement – passive external (cuticle) or internal (gut) transport of microbes throughout the soil profile (Coleman et al. 2018). Many of the indirect effects that microarthropods have on plants are mediated through their

relationships with soil microbial communities (Wall et al. 2012). A summary graphic for understanding these interactions is illustrated in **Figure 1**. This graphic highlights the interactions where there is strong existing evidence that microarthropods are impacting plant growth and development, as well as areas where there is emerging evidence for interactions (Figure 1).

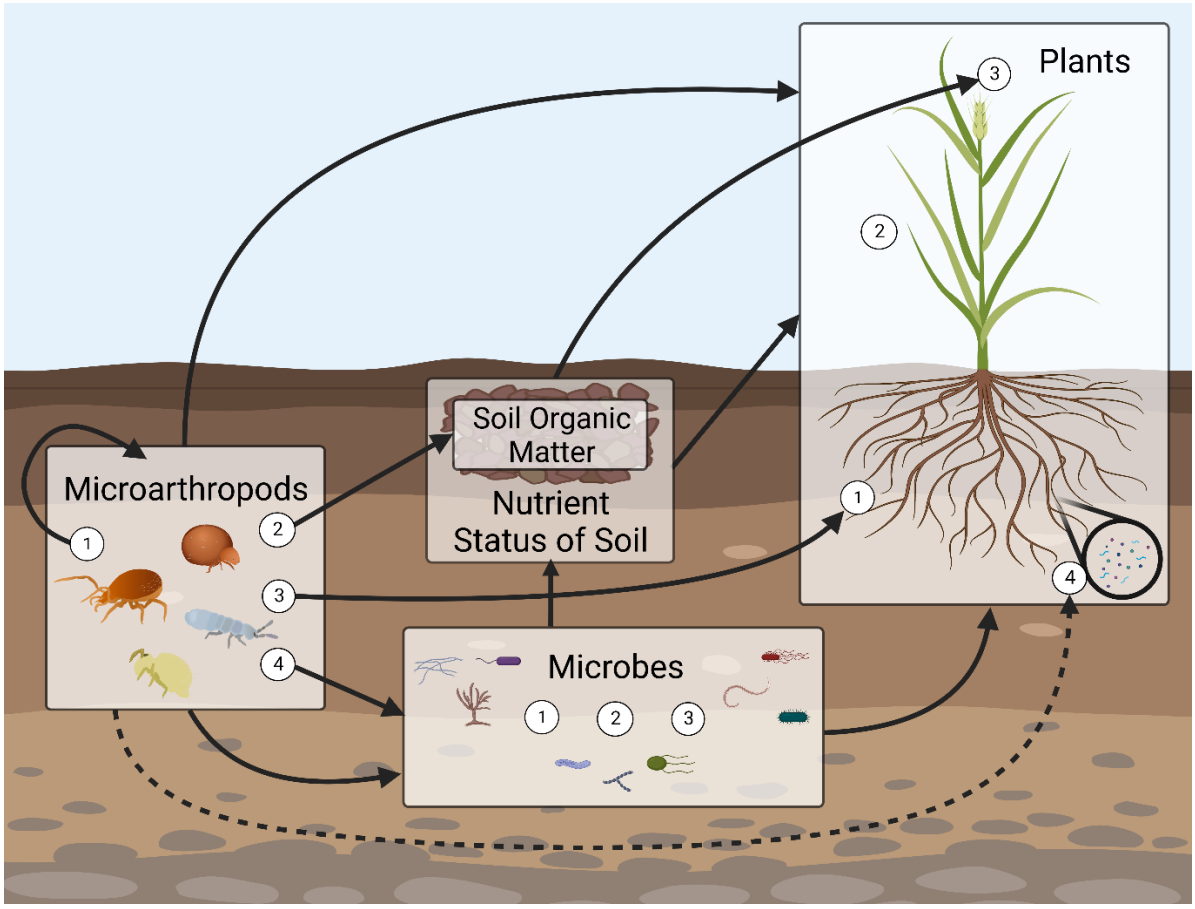

Fig. 1 Overview of pathways by which microarthropods affect plants. The microarthropods group has been divided into four primary feeding groups: (1) predators, (2) detritivores, (3) herbivores, and (4) microbivores. The plants group has been divided into three primary areas: (1) roots, (2) shoots and leaves, and (3) seeds and reproductive structures, in addition to (4) signaling molecules produced in the plant. Soil microbes are subdivided into (1) saprotrophs, (2) symbionts, and (3) pathogens. The nutrient status of soil encompasses soil organic matter to

indicate time since entering the soil environment. Solid arrows illustrate relationships between microarthropods and plants that have been validated in research studies. The dashed arrow illustrates a relationship between microarthropods and plants where there is growing evidence in the literature. Created with BioRender.com

2.1. Direct Effects of Microarthropods on Plants

The amount of direct interaction between plants and soil microarthropods is not well understood. Some research suggests that when plant roots are present, Collembola switch their diet almost exclusively to roots or root-derived products (Endlweber *et al.*, 2009). Though in many experiments it has proven difficult to distinguish among roots, rhizodeposits, and root-associated microbes as the actual food source for Collembola (Eerpina, *et al.*, 2017). It is evident that rhizodeposits are an important resource fueling soil food webs generally (Pollierer et al. 2007, 2012). However, their relative importance for Collembola appear to be generally low and the exact mechanisms driving the assimilation of freshly fixed carbon by microarthropods remains unclear (Potapov et al. 2016).

As with rhizodeposits, direct contribution of plant roots and seeds to the diet of microarthropods and how this feeding manifests in plant growth outcomes remains ambiguous. Ulber (1978) found that in lab experiments, *Onychiurus fimatus* Gisin damaged sugar beet seedlings. Later, researchers connected Collembola presence to feeding injury on germinating lettuce (Joseph et al. 2015; Joseph 2017) and spinach (Getzin 1985) by manipulating Collembola abundances with insecticides. Nietschke et al. (2011) provided photographic evidence of *Folsomia candida* Willem feeding on the mucilaginous seed coats and seed embryos of *Plantago major* L., though this did not result in changes in germination rates. Interestingly, this study also found the presence of *F. candida* resulted in greater germination rates for *Hypericum perforatum*

L. (Nietschke et al. 2011).

The disparity in plant growth outcomes due to Collembola herbivory may be due to feeding preferences of different collembolan species and the availability of alternative food resources. Investigations into the food selection of the Collembola, *O. fimatus*, revealed a preference for feeding on sugar beet seedlings over other weed species, though this preference for plant seedlings was diminished in the presence of fungi and other organic materials in soil (Ulber 1980). Further feeding preference research found mixed preferences for the collembolan species *F. candida* and *Folsomia fimetaria* L. (Buse and Filser 2014). The different Collembola fed on a broad range of resources, though *F. fimetaria* preferred mucilaginous seeds to soilborne fungi (Buse and Filser 2014).

The research investigating root herbivory by soil microarthropods focuses intensely on Collembola, with little investigation of mites or other microarthropods. Other microarthropod taxa (e.g., Oribatida), have been strongly associated with fine root biomass of trees (Doblas-Miranda *et al.*, 2014). However, it is unclear if and how these microarthropod taxa directly affect plant roots. The existing literature suggests that the primary direct effect microarthropods have on plants is occasionally feeding on their roots when other food sources are not present.

2.2. Indirect Effects of Microarthropods on Plants

2.2.1. Microarthropods, Soil Organic Matter, and Nutrient Cycling

Microarthropod feeding is known to generally enhance decomposition and increase soil nutrient availability (Seastedt 1984). Though we know the effects of microarthropods on soil nutrient status are dominated by their impacts on both organic matter decomposition and saprotrophic microbes (Soong and Nielsen, 2016), it is often difficult to determine if their effects on soil nutrient status are mediated through litter fragmentation and feeding or microbivory of

saprotrophic microbes. Thus, in many studies these effects are grouped together. Developing knowledge does however suggest that microarthropods play a lesser role in litter fragmentation than in microbivory (Potapov 2022).

Soil organic matter (SOM) and its decay determine the physical stability, water holding capacity, and nutrient status of soil, and, subsequently, the ability to support plant life (Kampichler and Bruckner, 2009; Lal, 2020; Minasny and McBratney, 2018; Onemli, 2004; Seastedt, 1984). Microarthropods can influence SOM-plant interactions in many ways. By fragmenting plant residues, they change the physical structure of particulate soil organic matter (Seastedt 1984; González 2002). Additionally, by translocating plant residues from the soil surface, they alter organic matter vertical distributions in soil (Chamberlain *et al.*, 2006). Microarthropod waste is rich in nitrogen and other nutrients, which generally mobilizes nutrients (Lussenhop 1992; Bardgett and Chan 1999) and can alter microbial activity in soils (Wickings and Grandy 2011). Ecosystem modelers have begun to highlight the importance of the effects of fauna in C and N cycling models (Grandy et al. 2016; Zhang et al. 2021). Through these activities, microarthropods can exert many indirect effects on plant health. An overview of studies that have explored this connection are highlighted in **Table 1**.

Table 1. An overview of the studies investigating microarthropod effects on plants via their impacts on SOM decomposition and nutrient cycling.

Microarthropod Metric	Plant Metric	Effect	Environment	Paper
total microarthropods	net primary plant productivity	positive	tallgrass prairie	*Soong et al., 2016*
total microarthropods	grain weight	positive	cropping system - sweet corn (*Zea mays* L.)	*Kaneda et al., 2012*
total microarthropods	shoot biomass	negative	microcosms - perennial ryegrass (*Lolium perenne* L.)	*Cole et al., 2004a*
species richness	shoot biomass	positive		
species richness	primary production of tree seedlings	mixed[a]	microcosms - birch tree seedings (*Betula*)	*Liiri et al., 2002*
decomposer diversity	wheat shoots	positive	cropping system – wheat (*Triticum aestivum* L.)	*Eisenhauer et al., 2018*
	wheat spikes	positive		
	wheat roots	positive		
mite abundance	plant cover	positive	semiarid temperate steppe (grassland) in the Mongolian Plateau, China	*Wu et al., 2014*
	plant species richness	positive		
predatory mites	plant complementarity effects	positive	microcosms - mixed plant community and monoculture plant communities (included *Trifolium pratense* L. (legume), *Poa pratensis L.* (grass), and *Rumex acetosa* L. (herb))	*Thakur et al., 2015*
	interspecific plant competition	negative		
	vegetation	positive		

three fungivorous springtail species (*Proisotoma minuta* Tullberg, *Folsomia candida* Willem, and *Sinella curviseta* Brook) and a predatory mite (*Hypoaspis aculeifer* Canestrini)	seedling establishment	mixed[b]	microcosms - *Phleum pratense* L. and *Poa pratensis* L.	*Kutakova et al., 2018*
	below-ground plant biomass	mixed[b]		
	plant biomass allocation	mixed[b]		
Collembola (natural assemblage)	flowering time	positive	microcosms - annual bluegrass (*Poa annua* L.)	*Forey, Coulibaly, and Chauvat, 2015*
	flowering abundance	positive		
	number of leaves	positive		
	root biomass	positive		
	chemical traits of plants	mixed[c]		
Collembola (mixed assemblages)	number of leaves	positive	microcosms - perennial ryegrass (*Lolium perenne* L.)	*Winck et al. 2020*
	shoot biomass	positive		
	root biomass	negative		
	foliar carbon content	positive		
	foliar nitrogen content	positive		
Collembola (*Parisotoma notabilis* Schaffer + other morphospecies)	number of flowers	mixed[d]	microcosms - annual bluegrass (*Poa annua* L.)	*Chauvet and Forey, 2021*
	first flowering date	mixed[d]		
	root biomass	positive		
	shoot:root ratio	negative		
	leaf P content	positive		
	leaf Mg content	negative		

Collembola (*Heteromurus nitidus* Templeton and *Onychiurus scotarius* Gisin)	root biomass	negative[e]	microcosms - two plant species from different functional groups (*Poa annua* L. and *Trifolium repens* L.)	*Scheu, Theenhaus, and Jones, 1999*
	shoot biomass	negative[e]		
	root N content	negative[e]		
	shoot N content	positive		
	shoot C content	positive		
Collembola (*Protaphorura fimata* Gisin, *Heteromurus nitidus* Templeton and *Folsomia candida* Willem)	shoot biomass	positive[f]	microcosms - ten plant individuals (height 2-6 cm) of a total of 43 common species of Central European Arrhenatherion grasslands	*Partsch, Milcu, and Scheu, 2006*
	root biomass	negative[g]		
	total N concentration	positive		
	^{15}N enrichment	positive		
	shoot:root ratio	positive		
Collembola (*Onychiurus procampatus* Gisin)	shoot and root biomass	negative	microcosms – grassland species (*Nardus stricta* L.)	*Bardgett and Chan, 1999*
	shoot N and P	positive[h]		
Collembola (*Protaphorura fimata* Gisin)	wheat leaf biomass	negative	microcosms – wheat (*Triticum aestivum* L.)	*Schutz, Bonkowski, and Scheu, 2008*
	wheat ear biomass	negative		
	leaf N concentration	mixed[i]		

[a]Primary production and nutrient uptake of tree seedlings increased as microarthropod species richness increased, however only at low levels of microarthropod diversity.
[b]Seedling establishment, below-ground plant biomass, and plant biomass allocation were affected by soil conditioning treatment interactions.
[c]The presence of Collembola increased N, decreased C:N, increased K, decreased Mg, and decreased chlorophyll in plant tissue.
[d]At higher temperatures, Collembola increased the number of flowers produced and decreased the number of days to first flowering.
[e]Collembola generally reduced root biomass, but especially in the *P. annua* treatments with earthworms (by 55%).Collembola also reduced shoot biomass when earthworms were present (by 16% and 7% for *P. annua* and *T. repens*, respectively). Collembola reduced root N content, especially for P. annua when earthworms were present.

[f]Magnitude of effect varied by plant species.
[g]Root biomass increased when both Collembola and earthworms were present.
[h]Relationship only present when nematodes were present.
[i]When fertilized with N fertilizer, Collembola reduced leaf N concentration by 9%, but when fertilized with NPK fertilizer the Collembola increased leaf N concentration by 20%.

The presence of Collembola generally increases soil nutrient availability, however this leads to mixed plant growth outcomes and nutrient uptake in annual plant species. The presence of Collembola (*Protaphorura fimata* Gisin) has been found to decrease wheat (*Triticum aestivum* L.) leaf biomass and ear biomass. This study also revealed that Collembola reduced leaf N concentrations by 9% when fertilized with N alone ($NaNO_3$), but when fertilized with NPK (1:1:2.5) were associated with increases in leaf N concentration by 20% *(*Schütz *et al.* 2008). Forey *et al.* (2015) showed the presence of Collembola (as a mixed assemblage) increased soil nutrient availability (NO_3- and P_2O_5) and fungal biomass in soil. This increased soil nutrient availability corresponded to Collembola decreasing shoot to root ratios, and increasing root biomass, leaf number, and a 6.5-fold increase in flowering and advanced flowering time by two weeks (Forey *et al.* 2015). Collembola also had mixed effects on *Poa annua* L. tissue chemistry, increasing N and K, and decreasing the C:N ratio, and levels of Mg and chlorophyll (Forey *et al.* 2015). Further research by Chauvat and Forey (2021) found flower production in *P. annua* increased by up to 150% in the presence of the Collembola (*Parisotoma notabilis* Schaffer + other morphospecies). In this study Collembola also increased root biomass by an average of 87% and decreased the shoot to root ratio by 49% (Chauvat and Forey, 2021). Collembola presence also increased foliar P content by 23%, while decreasing leaf Mg content by 16% (Chauvat and Forey, 2021). Based on these studies with annual species, we generally see a decreased shoot to root ratio, often caused by increasing root biomass, and increased N uptake.

Collembola presence had clearer effects on perennial plant species, with general trends in contrast to those observed for annual plant species. The presence of Collembola (mixed assemblages) induced increases in perennial ryegrass (*Lolium perenne* L.) leaf production (47-68%) and shoot biomass, but a decrease in root biomass by up to a third of the biomass produced

without Collembola (Winck *et al.,* 2020). The N content in the *L. perenne* leaves increased an average of 36-67% dependent of the Collembola type (Winck *et al.,* 2020). Collembola (*Protaphor urafimata* Gisin, *Heteromurus nitidus* Templeton, and *F. candida*) increased shoot biomass for grassland plants, though the magnitude of this effect varied by plant species, and they generally decreased root biomass except in the presence of earthworms (Partsch *et al.* 2006). This study also found that Collembola increased the shoot to root ratios and total N concentration and ^{15}N enrichment (Partsch *et al.* 2006). Bardgett and Chan (1999) found the presence of Collembola (*Onychiurus procampatus* Gisin) reduced shoot and root biomass by 28% and 39%, respectively, for the grassland species *Nardus stricta* L. This study also found the presence of Collembola and nematodes (communities, predominately bacterial feeders) increased shoot N and P content (Bardgett and Chan 1999). These findings suggest that the increase in N availability caused by Collembola leads to a decrease in root biomass and increase in shoot biomass in perennial species though these effects may be somewhat mitigated at high NH_4^+–N concentrations in the soil solution.

While it appears that Collembola generally affect annual and perennial plants differently, interactions with additional soil fauna may alter observed effects. A study investigating the impact of the Collembola *H. nitidus* and *Onychiurus scotarius* Gisin on *P. annua* (annual) and *Trifolium repens* L. (perennial), identified that earthworms can impact these trends. Collembola generally reduced root biomass, but especially in the *P. annua* treatments with earthworms (by 55%). Collembola also reduced shoot biomass when earthworms were present (16% and 7% for *P. annua* and *T. repens*, respectively). Collembola additionally caused an increase in the shoot to root ratio, particularly that of *P. annua* (from 2.34 to 4.42 and from 5.10 to 5.41 for *P. annua* and *T. repens*, respectively). Collembola presence increased shoot N (on average by 2.6% for *P.*

annua and 7.5% for *T. repens*) and C content (44.1-46.5%) (Scheu *et al.* 1999). Collembola reduced root N content, especially for *P. annua* when earthworms were present (Scheu *et al.* 1999). The activity of some mites and collembolans have been negatively related to earthworm activity, though the relative importance of microarthropods in the soil environment could be determined by soil moisture content (Porazinska et al. 2022).

Many studies have investigated how Collembola impact plant growth and nutrient uptake strategies through changes in soil nutrient status. Plant biomass allocation patterns are dependent on both soil nutrient levels (Glimskar and Ericsson, 1999; Müller *et al.* 2000) and forms (Cambui *et al.,* 2011). Annual and perennial plants also exhibit different nutrient uptake and growth patterns (Weih et al. 2011; Lundgren and Des Marais 2020) and may respond differently to biologically driven shifts in soil nutrient availability. The variable impacts of microarthropods on plant biomass allocation therefore likely reflect other differences in these studies beyond presence/absence such as species-specific feeding rates and resource use efficiency, as well as microarthropod abundance and diversity.

Changes in microarthropod abundance are well known for impacting soil biological process rates including litter decomposition and nutrient mineralization (Seastedt 1984; Verhoef and Brussaard 1990). Microarthropods generally stimulate litter decomposition and nutrient mineralization, however at greater abundances, over-grazing of microbes can hinder these processes (Lussenhop 1992; Heneghan et al. 1998; Kampichler and Bruckner 2009). A handful of studies have also quantified these impacts to explore subsequent plant responses. In general, increases in microarthropod abundance have been shown to increase plant growth metrics. Within a tallgrass prairie, a 38% increase in microarthropod abundance, increased C and N mineralization and primary plant productivity by about 30% (Soong *et al.,* 2016). Similarly,

increased abundances of Collembola, oribatid and prostigmatid mites in a sweet corn cropping system were associated with increased corn yields (Kaneda *et al.,* 2012). These findings suggest that microarthropods support greater plant productivity by increasing soil nutrient availability, however, other research indicates that at relatively greater microarthropod abundances these effects may change. For example, Cole et al. (2004a) found that while increasing microarthropod densities led to an increase in N availability, they also resulted in a decrease in shoot biomass of *L. perenne* (Cole et al. 2004a). However, the effects documented in this study may have been related due to greater microarthropod abundances causing an increase in N release earlier in plant growth when the plants' demand for N was lower.

Relationships between soil biodiversity and plant productivity have been studied extensively. The loss of soil biodiversity and simplification of soil community composition reduces ecosystem multifunctionality and can impair decomposition and nutrient cycling (Wagg et al. 2014). Fewer studies have explored the linkages specifically between microarthropod diversity and plant productivity, however, in most cases, the relationship appears to be positive. Cole et al. (2004a) found that increasing microarthropod species richness by 3.6x increased shoot biomass of *L. perenne* by 1.4x. Increasing decomposer diversity was also found to increase the biomass of wheat shoots (+11%), spikes (+7%), and roots (+56%), through increasing nutrient mineralization (Eisenhauer *et al.,* 2018).

Yet, there is evidence that, in some contexts, the benefits of increased microarthropod diversity for plant productivity may saturate at low diversity levels. Liiri et al. (2002) found that increasing microarthropod species richness resulted in elevated productivity in *Betula pendula* Roth seedlings, but only at low levels of diversity. This saturation may be attributed to the functional redundancy of different microarthropod taxa. Nielsen et al.'s review of soil

biodiversity-ecosystem functioning observed that the effects of increasing species richness were more pronounced at low-diversity levels compared to high-diversity levels. They also found that community composition often had greater effects on ecosystem functioning compared to species richness (Nielsen et al. 2011). This effect on community composition could highlight the importance of niche differentiation and multi-trophic interactions to support ecosystem functioning (Eisenhauer et al. 2019). This explanation is supported by research investigating specific multitrophic interactions. Thakur et al. (2015) found that increasing predatory mite densities led to cascading effects on their collembolan prey, soil microbes and nutrient mineralization rates which ultimately decreased interspecific plant competition. There is also evidence that multitrophic interactions can impact seedling establishment and plant root-to-shoot ratios indirectly by changing soil nutrient availability (Kuťáková *et al.*, 2018).

Overall, the research that explicitly investigates how microarthropods affect plants through decomposition and nutrient cycling (Table 1), indicates a generally positive relationship between microarthropods and plant metrics such as aboveground plant biomass, plant nutrient content, and plant reproduction. This general trend related to microarthropod presence and abundance appears to be greatly influenced by the overall diversity or species richness observed in the microarthropod communities, suggesting that understanding interspecific interactions and multitrophic interactions may be the key to understanding the variability of this mechanism.

2.2.2. Microarthropods and Plant Symbionts

Plant symbionts promote plant growth through improved nutrient acquisition, plant defense, and abiotic stress tolerance (Dodd 2000; Neumann and George 2010). Microarthropods can influence the processes that plant-symbiotic microbes control through feeding and movement (Anderson *et al.* 1981; Gange, 2000), ultimately impacting plant growth. Across different

ecosystems, collembolan abundances are positively correlated with root biomass, which has been attributed to collembolan grazing on root-associated microorganisms (Potapov et al. 2017). Positive associations between microarthropod densities and both fine and mycorrhizal root biomass (Lussenhop et al. 1998), further confirms these interactions. Many studies exploring how microarthropods influence plant growth and function via interactions with plant symbionts focus on mycorrhizal fungi (Frey 2003; Nadeem et al. 2014; Ganugi et al. 2019). An overview of the studies that have explored how the interaction between microarthropods and plant symbionts affect plant growth are highlighted in **Table 2** and discussed in the subsequent paragraphs

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Table 2. An overview of the studies that researched how microarthropod effects on plant symbionts impacts plants.

Microarthropod Metric	Plant Metric	Effect	Environment	Paper
Collembola abundance	soybean nodule numbers	negative	field – soybeans (*Glycine max* L.)	*Hansen et al., 2018*
three fungivorous springtail species (*Proisotoma minuta* Tullberg, *Folsomia candida* Willem, and *Sinella curviseta* Brook) and a predatory mite (*Hypoaspis aculeifer* Canestrini)	mycorrhizal colonization of roots	no effect	microcosm - *Phleum pratense* and *Poa pratensis*	*Kutakova et al., 2018*
Collembola (*Folsomia candida* Willem)	number of nodules per plant	positive	microcosms – soybean (*Glycine max* L.)	*Lussenhop, 1996*
Collembola (*Folsomia candida* Willem and *Tullbergia granulate* Mills)	mycorrhizal root length	positive	field – cylinders in soil – soybean (Glycine max L.)	
	leaf tissue N	positive		
Collembola (*Protaphorura fimata* Gisin)	proportion of seeds that were still ungerminated and viable	positive	petri dish - grassland species: *Centaurea nigra* L., *Dactylis glomerata* L., *Origanum vulgare* L. and *Taraxacum officinale* L.	*Mitschunas, Wagner and Folser, 2006*
	seed mortality	negative		
Collembola (*Protaphorura fimata* Gisin)	seedling emergence	positive	field - mesocosms buried in a ruderal grassland - species *Anthriscus sylvestris* L., *Centaurea nigra* L., and *Origanum vulgare* L.	*Mitschunas, Wagner and Filser, 2008*
Collembola (*Protaphorura fimata* Gisin)	plant nutrient sequestration	positive	mesocosm - maize (*Zea mays L.*)	*Ngosong, Gabriel and Ruess, 2014*

Collembola (*Protaphorura fimata* Gisin)	shoot biomass, root volume, root diameter of *L. perenne*	negative	microcosm - *Lolium perenne* L. (perennial ryegrass) and *Trifolium repens* L. (white clover)	*Endlweber & Scheu, 2007*
	root length and number of root tips of *L. perenne*	positive		
	length of roots of *T. repens*	positive		
	number of root tips of *T. repens*	negative		
	colonization of roots of *T. repens* by mycorrhizal fungi	negative		
	mycorrhizal infection of roots of *L. perenne*	no effect		
Collembola (*Folsomia candida* Willem)	seed germination	mixed[a]	microcosm - grassland plant species (*Agrostis capillaris* L., *Hypericum perforatum* L., *Plantago major* L. and *Vicia cracca* L.)	*Nietschke et al., 2011*
Collembola (*Folsomia candida* Willem)	plant dry weight	negative	microcosm – leek (*Allium porrum* L.)	*Warnock, Fitter, and Usher, 1982*
	mycorrhizal infection	no effect		
	plant phosphate content	negative[b]		
Collembola (*Folsomia candida* Willem)	average hyphal length in root-free soil compartment	negative	microcosms – clover (*Trifolium subterraneum* L.)	*Larsen and Jakobsen, 1996*
	average hyphal ^{32}P transport from the RFSC	negative		
	root dry weights of mycorrhizal plants	negative		
	shoot yields	no effect		
	leaflet ^{32}P content	no effect		

Collembola (*Folsomia candida* Willem)	*P. virgatum* mass	no effect	microcosms - mycorrhizal perennial grass *Panicum virgatum* L. and the non-mycorrhizal annual crucifer *Brassica nigra* L.	*Boerner and Harris, 1991*
	P. virgatum P uptake	no effect		
	P. virgatum tissue N concentration	negative		
	P. virgatum root:shoot ratio	negative		
	differences in nutrient uptake between plant species in competition	positive		
Collembola (*Folsomia candida* Willem)	root mass	no effect	microcosms – soybean (*Glycine max* L.)	*Kaiser and Lussenhop, 1991*
	shoot mass	no effect		
	number of bean pods	no effect		
	mycorrhizal root length	negative		
	mycorrhizal infection sites	negative		
Collembola (*Folsomia candida* Willem)	total and aboveground growth	mixed[c]	microcosms – forest herb (*Geranium robertianum* L.)	*Harris and Boerner, 1990*
	root biomass	no effect		
	total infected root length	negative		
Collembola (*Mesaphorura macrochaeta* Rusek)	arbuscular mycorrhizal colonization of roots	positive	mesocosm - grassland plant (*Agrostis capillaris* L.)	*Cole et al., 2004b*

[a] *H. perforatum* showed a positive increase in germination rate in the presence of the Collembola, however the three other species tested showed no effects.
[b] Collembola had a negative effect for the mycorrhizal inoculated plants.
[c]Total and aboveground plant growth were greater at lower collembola density compared to the higher and no collembola densities [densities: 0, 5, 15, or 25 animals per pot (0, 15, 40, and 70 animals.dm-3)].

The effects of microarthropods on mycorrhizal colonization of plant roots are mixed. Mycorrhizal infection of leek (*Allium porrum* L.) was not affected by the Collembola *F. candida* (Warnock *et al.* 1982). Similarly, research using a mixture of Collembola species (*Proisotoma minuta* Tullberg, *F. candida*, and *Sinella curviseta* Brook) with a predatory mite (*Hypoaspis aculeifer* Canestrini), found that the microarthropods had no effect on the mycorrhizal colonization of the grasses, *Phleum pratense* L. and *Poa pratensis* L. (Kuťáková et al. 2018). In contrast, Cole et al. (2004b) observed that a specific Collembola species, *Mesaphorura macrochaeta* Rusek, enhanced arbuscular mycorrhizal root colonization of the grassland plant, *Agrostis capillaris* L. (Cole et al. 2004b). Moreover, Endlweber and Scheu (2007) found the Collembola species *P. fimata* had a negative effect on the mycorrhizal colonization of *T. repens* (Endlweber and Scheu 2007). The Collembola species, *F. candida,* also had a negative impact on mycorrhizal infection of soybeans (*Glycine max* L.) (Kaiser and Lussenhop 1991) and the forest herb, *Geranium robertianum* L. (Harris and Boerner 1990). These differential effects may be due to variation in the target Collembola species and grazing pressure, or root structures between different plant species (Treseder 2013), such as those between grasses and leguminous plants.

The effects of microarthropods on mycorrhizal colonization of plant roots and mycorrhizal growth can translate into impacts on plant nutrient acquisition. Collembola grazing on the extra-radical mycelia of arbuscular mycorrhizae can influence fungal phenology by favoring colonization phases of hyphal proliferation over reproductive phases, therefore increasing plant nutrient acquisition (Ngosong *et al.* 2014). Though in some cases the presence of Collembola can reduce P and N uptake, likely due to the over-grazing of the mycorrhizae limiting the effectiveness of the fungi (Harris and Boerner, 1990; Warnock *et al.* 1982). However, microarthropod grazing on mycorrhizae does not always affect plant nutrient uptake of

P (Boerner and Harris 1991) or the functioning of mycorrhizal fungi (Larsen and Jakobsen 1996).

The impact that microarthropod mycorrhizal grazing has on plant nutrient acquisition can have mixed effects on plant growth outcomes. Collembola presence can reduce (Larsen and Jakobsen 1996; Endlweber and Scheu 2007), or have no effect (Harris and Boerner 1990; Kaiser and Lussenhop 1991) on root growth. Plant biomass of *Panicum virgatum* L. and shoot biomass of clover (*Trifolium subterraneum* L.) were unaffected by the presence of the Collembola, *F. candida* (Boerner and Harris 1991; Larsen and Jakobsen 1996). However, the presence of *F. candida* resulted in decreased plant dry weight for leeks (Warnock *et al.* 1982). Collembola presence did not affect soybean root, shoot or number of bean pods, even though they had negative effects on mycorrhizal associations (mycorrhizal root length and infection sites) (Kaiser and Lussenhop 1991). These discrepancies may be attributed to a difference in collembolan density, as Harris and Boerner (1990) found that the total and aboveground plant growth of *G. robertianum* were greater at lower collembola density compared to the higher and no collembola densities.

In addition to the work focusing on mycorrhizal fungi, some studies have investigated how the relationship between microarthropods and symbiotic bacteria impact plants. Lussenhop (1996) found that high densities of the Collembola, *F. candida*, increased the number of nodules on soybean roots that contain the nitrogen-fixing bacteria *Bradyrhizobium japonicum* Buchanan by 52% per plant in pots. However, this relationship was not observed in a soybean field at moderate collembolan densities (Lussenhop 1996). These interactions may be impacted further by environmental factors including insecticides that can alter collembolan and bacterial populations. In an experiment where insecticides reduced collembolan densities there was

increased P inflow into roots of the perennial grass *Holcus lanatus* L. (McGonigle and Fitter 1988). In contrast, Hansen et al. (2018) showed that greater Collembola densities in a soybean field led to decreased nodule numbers in the following season (Hansen et al. 2018). The authors proposed this relationship may be due to altered soil arthropod-microorganism interactions induced by insecticides (Hansen et al. 2018).

There is also evidence that microarthropods may influence microbial associations with plant seeds. The effects of microarthropod grazing on fungal seed coats appears to be generally positive due to stimulatory and protective effects. Collembola have been associated with reduced seed mortality (Mitschunas *et al*., 2006) and increased plant germination by feeding on the fungi associated with seed coats (Mitschunas *et al*., 2008; Nietschke *et al.*, 2011). The addition of the fungivorous collembolan, *P. fimata,* resulted in greater seedling emergence for *Centaurea nigra* L. and *Origanum vulgare* L., most likely by decreasing the seed mortality caused by fungi (Mitschunas *et al.* 2008).

Overall, the research that explicitly investigates how microarthropods affect plants through their relationships with plant symbionts (Table 2) illustrates these relationships are variable and there is no clear benefit or detriment to plants via this mechanism. The mixed findings of these studies are highly dependent upon the microarthropod and plant measurements chosen for each study, as well as the context of the experiment and availability of alternative food sources for the microarthropods (Klironomos *et al.* 1999; Klironomos and Kendrick, 1995). The microarthropod taxa identity and density levels are likely important determinants of the effects these soil fauna have on the root symbiont processes that impact plant growth and development.

2.2.3. Microarthropods and Plant Pathogens

Microarthropods primarily impact plant-pathogen interactions by dispersing or feeding on pathogen propagules (Innocenti and Sabatini, 2018; Visser *et al.* 1987), however most studies that have explored these interactions have focused on the latter (Friberg *et al.* 2005). An overview of the studies is provided in **Table 3**.

Table 3. An overview of the studies that researched how microarthropod effects on plant pathogens impacts plants.

Microarthropod Metric	Plant Pathogen	Plant Metric	Effect	Environment	Paper
Collembola	stem canker (*Rhizoctonia solani*)	disease infection on potato sprouts	negative	pots - potato (*Solanum tuberosum* L.)	*Bollen, Middelkoop, and Hofman, 1991*
Mites	stem canker (*Rhizoctonia solani*)	disease infection on potato sprouts	negative		
Collembola and Mites	stem canker (*Rhizoctonia solani*)	disease infection on potato sprouts	negative		
Collembola	stem canker (*Rhizoctonia solani*)	disease infection	no effect	field – corn (*Zea mays* L.), cotton (*Gossypium* L.), peanut (*Arachis hypogaea* L.) and soybean (*Glycine max* L.)	*Rickerl, Curl and Touchton, 1989*
Collembola	take-all and brown foot rot (*Gaeumannomyces graminis var. tritici and Fusarium culmorum*)	disease severity on plants	negative	microcosms – wheat (*Triticum* L.)	*Sabatini and Innocenti, 2001*
		shoot and root dry weight	positive		
Collembola (*Folsomia fimetaria* L.)	stem canker (*Rhizoctonia solani*)	disease infection on plants	negative	microcosms - potato (*Solanum tuberosum* L.)	*Lootsma and Scholte, 1997a*
Collembola (*Folsomia fimetaria* L.)	stem canker (*Rhizoctonia solani*)	disease infection on plants	negative	microcosms - potato (*Solanum tuberosum* L.)	*Lootsma and Scholte, 1998*
Collembola (Folsomia fimetaria L.)	stem canker (*Rhizoctonia solani*)	disease infection on plants	negative	microcosms - potato (*Solanum tuberosum* L.)	*Lootsma and Scholte, 1997b*

Collembola (*Proisotoma minuta* Tullberg)	stem canker (*Rhizoctonia solani*)	disease infection on plants	negative	microcosms – cotton (*Gossypium* L.)	*Lartey, Curl and Peterson, 1994*
		plant growth - dry weight	no effect		
Collembola (*Sinelli curviseta*)	*Furarim, oxysporum* f.sp. *cucumerinum*	cucumber seedling infection	negative	pots - cucumbers (*Cucumis sativus* L.)	*Nakamura, Matsuzaki and Itakura, 1992*
Collembola (*Onychiurus fimatus* Gisin and *Folsomia candida* Willem)	*Pythium ultimum*	disease infection	negative	microcosms – sugar beets (*Beta vulgaris* L.)	*Koleva, Ulber, and Wolf, 2009*
		Seedling length, root length, and root weight	positive		
Collembola (*Hypogastrura perplexa* Christiansen and Bellinger and *Sinella curviseta* Bellinger, Christiansen, and Janssens)	*Pythium ultimum*	disease infection[a]	negative	microcosms – tomatoes (*Solanum lycopersicum* L.)	*Zhang, Zhang, and Hu, 2022*
		growth suppression of *P. ultimum*	positive		

[a]*H. perplexa* reduced disease infection more than *S. curviseta*.

Microcosm studies have demonstrated that collembolan activity can decrease pathogen infection and disease severity on different crops. Collembola (*S. curiseta)* grazing on *Fusarim oxysporum* f. sp. *cucumerinum*, decreased virulence on cucumber seedlings (Nakamura *et al.* 1992). Collembolan feeding activity also significantly reduced the severity of the diseases, take-all (caused by *Gaeumannomyces graminis var. tritici*) and brown foot rot (caused by *Fusarium culmorum*) on wheat (Sabatini and Innocenti 2001). Different collembolan species (*Hypogastrura perplexa* Christiansen and Bellinger and *Sinella curviseta* Bellinger, Christiansen, and Janssens) have been shown to cause varying reductions in infection by *Pythium ultimum* on tomatoes (Zhang et al. 2022). Interestingly, Koleva *et al.* (2009) found that the incidence of infection by *P. ultimum* was decreased and sugar beet survivability and growth outcomes were improved by Collembola disseminating the fungal antagonist *Pseudomonas fluorescens*.

The effects of microarthropod grazing on *Rhizoctonia solani* has been studied in depth. Research aiming to determine the ability of different soil fauna to reduce potato infection by *R. solani* found that mites (from field communities, predominately *Pygmephorus sellnicki*) were not as effective in reducing disease incidence as Collembola (Bollen *et al.* 1991). Feeding by the Collembola, *F. fimetaria*, has been shown to decrease *R. solani* disease severity in microcosms (Lootsma and Scholte 1997a, 1998). Additionally, these authors found greater disease suppression under dry soil conditions when fungal growth was stimulated (Lootsma and Scholte 1997b), and diminished disease suppression when there was an alternative food source (dried rape biomass) for the Collembola (Lootsma and Scholte 1998). A study by Lartey et al. (1994) found that the Collembola-mediated control of *R. solani* did not lead to increases in plant biomass (Lartey *et al.* 1994). These findings suggest that the impact of Collembola on the control of selected soilborne plant pathogenic fungi primarily results in improved plant populations.

Multiple microcosm studies found that at typical field densities, microarthropods can suppress *R. solani* (Bollen *et al.* 1991; Lootsma and Scholte, 1997b), however there are limited field studies to validate these results at larger scales. Rickerl *et al.* (1989) did not observe any effects of Collembola on *R. solani* in their field study. The authors suggested that this may be attributable to the peak populations of Collembola not occurring when disease control was most critical at the time of planting due to deleterious tillage effects on microarthropods (Rickerl *et al.* 1989).

The presence of diverse microbial communities in field soils may impact the effects that microarthropods have on soilborne fungal plant pathogens. While lab assays have demonstrated that some collembola preferentially feed on plant pathogenic fungi (Sabatini and Innocenti 2000), the gut-content analysis of field-collected Collembola suggest they are less selective than the results from the laboratory assays (Tebbe *et al.* 2006). These discrepancies are likely due to the variation in settings (lab vs. field) altering the chemical and contact cues that collembolans use to make food choices (Hedlund *et al.* 1995).

Overall, this area of research is biased towards specific Collembola species and specific plant pathogens. Despite the limited diversity in the study taxa, this research indicates that microarthropods can reduce disease incidence and severity in plants. Taken collectively, these studies suggest that microarthropods may be best considered as a longer-term control measure for the management of plant pathogen densities in soils. However, more long-term field studies are needed to understand the influence that microarthropods can have on plant disease management.

3. Knowledge Gaps and Future Directions

3.1. Microarthropod-Microbe-Plant Interaction Knowledge Gaps

Existing soil ecology literature is dominated by research investigating how microarthropod-microbe interactions affect soil biological processes. Relatively few studies take the next step to determine how these manifest in plants, which has left many pertinent knowledge gaps and opportunities. Connecting soil processes to specific plant growth outcomes is crucial for understanding the role of these processes in broader ecosystem functioning and to enable us to capitalize on ecosystem services in managed ecosystems.

When studies include plant metrics, they often find significant relationships between microarthropods and plants that appear to be mediated by microbes (Wardle et al. 2004; Eo 2010; Wu et al. 2014). However, the studies that report these relationships rarely identify a mechanism driving the relationship. In the area of soil animal ecology alone there are multiple mechanistic knowledge gaps that warrant further research including microarthropod feeding and movement behaviors, species specificity of interactions and effects, diversity-function saturation, and trophic effects. A limitation of our understanding of microarthropod-microbe-plant interactions is that much of the research in this area has focused on broader microarthropod taxonomic groups and has not accounted for the complexities of the interactions within microarthropod communities.

Additionally, studies that investigate how microarthropod-microbe interactions impact plant growth directly rarely account for microarthropod interactions with the microbial community, instead focusing on a single microbial species ([reviewed by] Innocenti and Sabatini 2018). Research on beneficial microbe-microarthropod-plant interactions has been limited to primarily mycorrhizal fungi and other root symbionts, neglecting to explore how microarthropod grazing on saprotrophic microbes manifests in plants. Similarly, research on pathogenic microbe-microarthropod-plant interactions has been limited to fungal pathogens, especially *Rhizoctonia*

solani, while ignoring other plant pathogens such as bacteria and plant-parasitic nematodes. The limited diversity in the study taxa for the microarthropod, microbe, and plant species in this area of research is a major limitation to our understanding of how microarthropods impact plant health. As climate change progresses and causes plant disease ranges to further expand, our understanding of how microarthropods mediate plant pathogen dynamics will become increasingly important in managing plant diseases to reduce crop losses (Guzmán 2021).

A general limitation to our understanding of microarthropod-microbial mechanisms is that most studies that measure both fauna and plant metrics manipulate the plants or the conditions that impact plant growth such as tillage or fertilization. These treatment conditions simultaneously alter microbial communities, making disentangling specific mechanisms more challenging. The treatments used in many experiments are too much of a blunt hammer approach that limits our ability to connect findings from the laboratory to natural field observations.

3.2. Future Directions

Our understanding of how microarthropods impact plant growth and development can be further expanded by delving into rhizosphere interactions. Studying belowground plant interactions *in situ* remains difficult, as early methods in this area were developed to study root architecture and rely upon destructive sampling (Weaver 1919; Stoeckeler and Kluender 1938). Less destructive methods have been developed in recent decades to study root system architecture such as using x-ray and radar and those broadly used to study root interactions such as coring and rhizotrons (Huck and Taylor 1982; Centenaro et al. 2018). While these techniques may be able to provide insight into soil microarthropod-root interactions, new methods need to be developed to better understand the underlying mechanisms behind these interactions.

One such method that has helped to develop our understanding of these interactions is

isotopic labeling. Carbon isotopic labeling used to trace freshly fixed carbon assimilation from trees into soil animals revealed that both euedaphic and epigeic Collembola often consume freshly fixed carbon, though likely by different pathways via plant roots or aboveground sources (Potapov et al. 2016). Carbon isotope tracing in arable soil food webs has also found that root-derived carbon is the greatest contributor to soil arthropod body carbon, though this varied greatly by the soil fauna species (Scheunemann et al. 2015). Advances in isotope tracing now allows for more specific tracing to targeted fauna groups and species (Scheunemann et al. 2015). The mechanisms driving these interactions warrant further exploration to better understand the value of rhizodeposits in soil food webs.

Advances in molecular biology and chemical ecology indicate that microarthropod effects on plants are more complex than we currently understand. Signal molecules, primarily hormones, in the environment can impact plant growth and development (Santner and Estelle 2009; Eichmann et al. 2021). There have been several studies investigating how soil microbes impact plant growth and development through their effects on signaling pathways, yet very little work has explored the effects of soil animals on hormone-related signaling pathways and how these effects manifest in plant gene expression (Blouin 2018).

Detritivores may also impact secondary metabolites and defense gene expression in aboveground parts of plants, which could have further potential impacts on aboveground plant–herbivore interactions. Driving mechanisms may include defense induction by passive or active ingestion of living plant roots, nutrient mobilization effects, or impacts on soil microorganisms (Wurst 2013).

Earlier work investigating the effect of soil animals on hormone-related signaling pathways in plants focused on the influence of earthworms on indole acetic acid, jasmonic acid

and ethylene (Canellas et al. 2002; Jana et al. 2010; Puga-Freitas et al. 2012). Earthworms have also been found to modulate plant genes and hence the plant response to biotic and abiotic stress (Puga-Freitas et al. 2012). Research then explored how a Collembola species impacted plant gene expression through indole acetic acid and ethylene pathways using the model plant *Arabidopsis thaliana* L. (Endlweber et al. 2011). Researchers later studied how collembolans can affect oak tree resource allocation and genome expression within the context of multitrophic interactions, finding that the collembolans increased gene expression in relation to primary growth and nutrient (N and C) uptake into aboveground plant tissues (Herrmann et al. 2016; Graf et al. 2019). Alterations in gene expression also affected plant secondary metabolism, physical fortification, and plant defense genes which help prime oak shoots against attack by fungi or herbivores (Graf et al. 2019).

The building evidence in this area suggests that hormone signaling pathways that influence plant growth, development, and defense may be an important mechanism by which soil microarthropods impact plants. There are other hormone signaling pathways to be explored beyond indole acetic acid, jasmonic acid and ethylene; including cytokinins, gibberellins, abscisic acid, and salicylic acid pathways warrant further research (Puga-Freitas and Blouin 2015). These studies provide insight into the ways in which microarthropod can possibly influence plant metabolic responses and defense pathways. We argue more studies should explore these pathways to improve our understanding of the roles that microarthropods play in plant ecology and crop production.

3.3. Conclusions

Microarthropods impact plant growth and development through many interactions, though most of the relationships are indirect and cascading. By further developing our

understanding of these primary pathways, we may begin managing soil microarthropods to improve plant growth and development. Our current understanding is that microarthropods generally enhance plant growth and development through improved nutrient availability and control of plant antagonists. Current evidence has not reported that soil dwelling microarthropods have any significant negative impacts on plants, though indirect negative effects of species not benefitted by microarthropods will inevitably occur. There are still many knowledge gaps and opportunities surrounding the dissection of microarthropod effects on plants, however new methodological advancements in both chemical ecology and molecular biology suggest transformational steps can be taken to elucidate these interactions further.

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CHAPTER 2

SOIL BIOLOGICAL DRIVERS OF CROP PRODUCTION UNDER DIFFERENT COVER CROP MANAGEMENT STRATEGIES

ABSTRACT

Soil microarthropods, a group of fauna dominated by mites and collembolans, mediate multiple microbial-driven soil processes. The effects that soil microarthropods have on crop production are typically explored with a focus on one microbial driven process, such as nutrient cycling or plant pathogen disease incidence, though their behaviors influence these processes simultaneously. The goal of this research was to develop a greater understanding of how microarthropods affect plant growth through their effects on multiple interconnected processes in a field setting under different management strategies. In 2019 and 2020 the drivers of crop productivity were investigated in both soybeans and dry beans under three different cover cropping treatments *[1) no cover crop with tillage (control treatment), 2) cereal rye with tillage, and 3) rolled cereal rye with no tillage]*. Within this experiment we measured microarthropod communities, multiple microbial metrics (biomass, five enzymes, community DNA analysis), and soil characteristics that impact biological processes (soil carbon and nitrogen, aggregate stability, soil protein). We also measured select plant pathogen metrics for white mold (*Sclerotinia sclerotiorum*) and root rot [*Fusarium* spp.], along with crop production metrics (cereal rye biomass, weed suppression, and crop performance). Multi-model piecewise structural equation modeling was used to investigate the relationships driving crop production. Soil nutrient status was an important determinant of total bean weight. Microbial biomass nitrogen was an important soil metric, consistently having a negative effect on total bean weight. The microarthropods had more positive effects on bean production when there are more food

resources available, as in the rolled cereal rye treatment.

INTRODUCTION

The aboveground and belowground biota in ecosystems interact to effect biological processes and ecosystem services (van der Putten *et al.*, 2001; Wardle *et al.*, 2004). Soil biological process are important drivers of many ecosystem services, including crop production in agricultural systems (Bender and van der Heijden, 2014; Bender, Wagg and van der Heijden, 2016). To capitalize on the soil biological processes that enhance crop production, there has been a push for producers to improve their soil health (Chaparro *et al.*, 2012; NRCS, undated; Rinot *et al.*, 2019).

Soil health initiatives have primarily focused on soil microbes because plant-microbe interactions are known determinants of plant growth. However, in emerging models of soil processes, microarthropods, an important group of fauna that includes collembolans and mites, are shown to mediate the activities of soil microbial communities (Soong and Nielsen, 2016). There is growing evidence that the impacts of soil microarthropods on microbial communities can affect plant growth (Forey, Coulibaly and Chauvat, 2015; Innocenti and Sabatini, 2018; Kuťáková *et al.*, 2018). Previous work has found that specific groups of soil microarthropods can explain significant amounts of variation within crop biomass production, highlighting the impact microarthropods can have on crop yields (Jernigan *et al.*, 2020). However, it remains unclear which mechanisms are driving this relationship. The roles of microarthropods in agroecosystems are complex and interconnected. Plant growth is impacted by many processes simultaneously, including biological nitrogen cycling and pathogen dynamics.

Microarthropods play important roles in organic matter decomposition and nutrient

cycling through the liberation of carbon and nutrients during the fragmentation of plant residues and predation on soil microbes (Carrillo *et al.*, 2011; Filser *et al.*, 2016). Across a variety of landscapes, soil fauna have been estimated to contribute between 10-49% to total net nitrogen mineralization (Verhoef and Brussaard, 1990a). Furthermore, research in a native short grass steppe in Colorado found that even though total faunal biomass was only 2.5% of that of saprophytic microbes, fauna still accounted for 37% of nitrogen mineralization. While the importance of soil microarthropods in nitrogen cycling is established, a greater understanding is needed to inform the management of these soil biological processes.

Plant pathogen life cycles, and therefore disease incidence and severity in agroecosystems, are also influenced by the biota in the soil. Microarthropods can move plant pathogens throughout the soil which can increase disease incidence (Friberg, Lagerlöf and Rämert, 2005); however, they can also reduce plant pathogen loads in soil by consuming the pathogens (Curl, Lartey and Peterson, 1988; Dromph, 2001). Lab assays have demonstrated that some Collembola preferentially feed on plant pathogenic fungi (Sabatini and Innocenti, 2000b). Though gut-content analysis of field-collected Collembola indicate that they are less selective in their diet than the results from laboratory assays suggest (Tebbe, Czarnetzki and Thimm, 2006). While there has been successful pathogen control by microarthropods in controlled microcosm experiments, it is still unclear what level of microarthropod abundances or community composition is necessary to impact pathogen suppression in field settings (Lootsma and Scholte, 1997a; Rickerl, Curl and Touchton, 1989; Sabatini and Innocenti, 2001). Overall, relatively few studies have investigated how microarthropods influence pathogens, and even fewer have incorporated plant metrics (Innocenti and Sabatini, 2018). There is a need for a greater mechanistic understanding of how microarthropods influence plant pathogen loads in soil, which

can then be used to inform crop management decisions.

One management practice, cover cropping, has increasingly been incorporated into crop management systems in an effort to manage multiple aspects of crop management including weed competition, pathogen pressure, and soil fertility. The practice of roller-crimping a cereal rye cover crop to create a mulch has had greater adoption by farmers in the northeastern United States over the last few years because of its reported benefits for weed control, due to the mulch, and soil health, due to the decreased tillage (Crowley, 2017; Ryan *et al.*, 2011). This mulching practice has also been shown to reduce white mold incidence in bean crops (Pethybridge *et al.*, 2020).

Understanding nitrogen dynamics within this no-till system is essential for farmers to achieve their weed suppression and soil health standards. The timing of nitrogen mobilization in this system is essential for cereal rye establishment and spring growth to allow the cereal rye cover crop to produce enough biomass to be roller-crimped into a thick mulch for optimal weed suppression during the bean growing season. Nitrogen availability when the subsequent crop is planted is also important since inadequate nitrogen supplies can cause the plants to wither and stunt before reaching maturity. The mobilization of nitrogen in this system is significantly influenced by soil biota. However, we are limited in how we can optimize this and other organic cropping systems by our lack of understanding of how crop management practices (i.e. cover crops and tillage) impact soil biota and the consequences of these effects on the role of soil biota in nitrogen cycling.

The lack of knowledge about microarthropod-microbe interactions has limited the ability to predict or manage crop production outcomes. Many studies focus on one aspect of crop management, limiting our systems-level understanding of management decisions. While there is

evidence that microarthropods play a role in nitrogen cycling and affect pathogen life cycles in soils, it is unclear whether the effects of microarthropods lead to overall positive or negative impacts on crop production (Osler and Sommerkorn, 2007a; Sabatini and Innocenti, 2000a). Building this foundational knowledge will help strengthen the linkage between soil and plant health.

The goal of this research was to find ways to improve crop health and productivity by developing a greater understanding of how microarthropods affect plant growth. We hypothesized that the different cover cropping strategies would affect the microarthropod communities, which would influence the biological processes driving crop production.

METHODS

The foundation of this experiment was designed to test the effect of rolled cereal rye on white mold and weed suppression. The experiment was conducted at Cornell University Geneva, NY, and implemented a split-block randomized complete block design with four replicates. Individual plots were 10 x 20 m and crops were managed with farm scale equipment. Soybeans or dry beans were the main plot treatments, and the sub plot treatments were: 1) no cover crop (control treatment), 2) cereal rye with tillage, and 3) cereal rye mulch. The no cover crop treatment did not have cereal rye planted in the fall and used shallow tillage to control weeds as needed. The cereal rye with tillage and cereal rye mulch treatments had cereal rye planted in the fall at a rate of 200 kg seed ha^{-1}. The cereal rye with tillage treatment and the no cover crop treatment were both plowed prior to stem elongation in the cereal rye in the spring. The cereal rye mulch treatment was instead mechanically terminated and flattened using a roller-crimper.

Prior to planting the soybeans and dry beans in the spring, poultry manure and potassium sulfate were applied based on needs as determined by soil testing. The original measurements

within this experiment included cereal rye biomass, soybean and dry bean establishment, carpogenic germination of *Sclerotinia sclerotiorum, Sclerotinia sclerotiorum* ascorporic inoculum density, microclimate conditions, white mold disease incidence, weed suppression, and cash crop performance. Results of these metrics and additional details on experimental design are published by Pethybridge et al. (in prep).

Soil collection

Soil samples were collected on June 25th and September 30th in 2019 and on June 8th, July 18th, and in September of 2020. In 2020 the dry beans matured faster and were harvested before the soybeans. The September soil sampling in 2020 was timed based on the bean harvest, therefore the dry bean plot soil was collected on September 8th and the soybean plot soil was collected on September 23rd. All soil was kept in coolers on ice packs until processed or placed in a refrigerator or freezer.

Three composite soil samples, each comprised of 3 soil cores, were collected in each plot for microarthropod extraction. These cores were taken using a golf corer (10.8 cm diameter) to a depth of 10 cm. One composite soil sample, comprised of 10 soil cores, was collected in each plot for all other soil metric analyses. These cores were taken using a soil fertility probe (1.75 cm diameter) to a depth of 15 cm.

At the harvest time point each growing season, soil was also collected to send to the Cornell Soil Health lab for analysis of aggregate stability and soil protein. For these samples three composite soil samples, each comprised of 3 hand trowels of soil to a depth of 15 cm, were collected in each plot.

Soil microarthropods

Each composite soil sample was placed on a Berlese funnel to extract the

microarthropods. Over the course of the 3-day extraction, temperature was gradually increased from 30°C to 50°C. Invertebrates were extracted into 70% ethanol, then were topped off with 95% ethanol and stored until the samples were processed. In this study soil fauna include mites, collembola, and other taxa within Arthropoda. Extracted fauna were identified to family using published taxonomic keys (Borror and DeLong, 1964; Dindal, 1990; Krantz and Walter, 2009). After the soil samples were removed from the Berlese funnels, soil mass was determined from the air-dried weights of the soil samples. All arthropod abundances are reported as the number of individuals kg^{-1} dry soil.

Microbial biomass

The fresh soil was passed gently through a 2 mm sieve and 5 g of soil was weighed to determine gravimetric soil moisture content.

A modified chloroform fumigation/extraction was used to quantify microbial biomass in each pot, using two 5 g subsamples of soil (Jenkinson and Powlson, 1976). Half of all samples were fumigated by adding 3 ml of chloroform to 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 carbon and nitrogen on a Shimadzu TOC-TN analyzer (Shimadzu Scientific Instruments, INC., Columbia, MD). Microbial biomass carbon was determined by subtracting non-fumigated from fumigated carbon values and by applying a k_{EC} value of 0.45 (Joergensen, 1996). Microbial biomass nitrogen was derived using the same calculations and applying a k_{EC} value of 0.54. Biomass carbon and nitrogen is presented as μg g^{-1} dry soil.

Microbial enzyme activity

Potential soil microbial extracellular enzyme activity was assessed using protocols outlined by previous studies (Grandy *et al.*, 2008; Saiya-Cork, Sinsabaugh and Zak, 2002; Wickings and 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 (POX) 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 and 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 phenol oxidase or L-DOPA plus hydrogen peroxide (0.3%) for peroxidase. 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, Winooski, VT, United States). Potential enzyme activity for each substrate was calculated as nmol of substrate h^{-1} g^{-1} dry soil.

Soil carbon and nitrogen

Dried soil was pulverized using a ball mill grinder (8000D Mixer/Mill, SPEX SamplePrep, Metuchen, NJ, USA), weighed into tin capsules, and combusted to determine carbon (C) and nitrogen (N) concentration. Soil C and N was measured by the Cornell Stable

Isotope Lab through elemental analysis (Costech EA 4010 CHNS-O Analyzer, Costech Analytical Technologies, Valencia CA, USA) using acetanilide, organic rye flour, and certified soil reference material (Elemental Microanalysis, Ltd, UK) as standards and quality controls.

Soil protein

Soil protein content was measured using an extraction process with a citrate buffer under high temperature and pressure, following the standard operating procedures for the Cornell Comprehensive Assessment of Soil Health (Moebius-Clune *et al.*, 2016).

Soil aggregate stability

Soil aggregate stability was measured using a wet sieving technique to determine the percent of stable aggregates(Moebius *et al.*, 2007), following the standard operating procedures for the Cornell Comprehensive Assessment of Soil Health (Moebius-Clune *et al.*, 2016).

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. Bean treatment, cover crop treatments, and their interaction were included as fixed effects, and a random block effect was included to account for potential variability in field 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 LSD method, with Tukey adjustment and significance was declared for $P \leq 0.05$.

To analyze the microarthropod community composition, permutation-based multivariate ANOVAs (Anderson, 2001) were ran using the *Adonis2* function of the 'Vegan' package

(Oksanen *et al.*, 2010) in R software. This data was then subjected to nonmetric multidimensional scaling (NMDS) with Bray-Curtis distance metric implemented in the 'Vegan' package.

Multi-model piecewise structural equation modeling (SEM) was used to determine how the response variables effected crop production. For each sampling date, multiple regressions techniques were run on the microarthropod, soil, and weeds datasets to determine which variables had the strongest relationships with total bean weight. Stepwise multiple regressions were ran using the *stepAIC* function in the 'MASS' package. All subsets regressions were ran using the *regsubsets* function in the 'leaps' package. Variables that were significantly related to total bean weight were included in the modeling process.

For each sampling date, structural equation models were created using the selected variables from the multiple regression process. Models were ran using the *sem* function in the 'lavaan' package, grouped by the tillage treatments with all variables standardized. Unconstrained and constrained models were compared to determine if the significant paths varied between the tillage treatments. Models were then ran using the *psem* function in the 'piecewiseSEM' package. Each model was modified using fit indices (AIC, BIC, Fisher's C, and p-value) until optimized.

RESULTS

Soil microarthropods

In 2019, total microarthropod abundances were affected by the bean type at both sampling dates (Table 1 & 2). In June the soybeans had greater microarthropod abundances, which was driven by increases in astigmatid mite abundances. By September the dry beans had greater microarthropod abundances, which was driven by increases in all Orders of

microarthropods.

Tillage affected most of the microarthropod Orders in June 2019 (Table 1). The presence of the rye cover crop increased Collembola abundances. The increased tillage intensity in the absence of the rye cover crop increased Oribatid mite abundances. Astigmatid mite abundances were greatest in the treatment with the rye cover crop with tillage. The rye-no till treatment had the greatest prostigmatid mite abundances. In September of 2019, tillage affected Collembola and mesostigmatid mite abundances, with greater abundances in the rye-no till plots (Table 2). In 2020, total microarthropod abundances were affected by tillage in June and July but were affected by the bean type in September (Tables 3, 4, & 5). In both June and July, the rye-plowed plots had the greatest microarthropod abundances, which was driven in by increases in oribatid, astigmatid, and mesostigmatid mite abundances. In July 2020 the Collembola were affected by the interaction of the bean type and tillage treatments, with the greatest abundances in the rye-plowed plots of both bean types (Table 4).

In September 2020, total microarthropod abundances were greatest in the dry bean plots, which was driven by increases in Collembola, oribatid mites, prostigmatid mites, and mesostigmatid mites. The rye-plowed plots had the greatest Collembola abundances (Table 5). Bean type and the tillage treatments did not affect soil microarthropod community composition at any of the sampling dates ($p>0.05$).

Microbial biomass

In June 2019 microbial biomass C:N was greatest in the no rye plowed plots (Table 1). In September 2019 both microbial biomass C and N were greatest in the dry bean plots (Table 2). In July 2020 there was greater microbial biomass C and N in the dry bean plots (Table 4). In September 2020 there was greater microbial biomass C and a higher C:N ratio in the soybean

plots, but greater microbial biomass N in the dry bean plots (Table 5).

Microbial enzyme activity

In June 2019, the soybeans had greater peroxidase activity and less PHOS activity compared to the dry beans (Table 1). Increased tillage intensity led to greater LAP and PHOS activity in June 2019 (Table 1). In September 2019 there was greater LAP activity and less PHOS activity in the dry beans compared to the soybeans. In September 2019 there was also less PHOS activity in the rye-no till plots (Table 2).

In June 2020, there was less PHOS activity in the no rye-plowed plots compared to the rye-plowed plots (Table 3). In June 2020 the interaction of the bean variety and tillage treatment affected NAG, BG, and LAP activity (Table 3). In the soybean plots there was less activity of these three enzymes in the no-rye plowed plots. In July 2020, NAG activity was greatest in the rye-no till plots (Table 4). In July 2020, there was greater PHOS activity and less peroxidase activity in the soybeans compared to the dry beans. There was also the greatest BG activity in the rye-no till plots with soybeans (Table 4). In September 2020 there was great NAG and peroxidase activity in the rye-no till plots. There was also greater NAG activity in the soybeans compared to the dry beans (Table 5).

Soil carbon and nitrogen

In June 2019, the rye-plowed plots in dry beans had the greatest soil C and soil C:N ratios (Table 1). In September 2020 the soil C:N ratio was greatest in the no rye-plowed and rye-plowed plots with dry beans. Soil C was also greater under dry beans and in the no rye-plowed plots (Table 2).

In July 2020, the soil C:N ratio was greater in the rye-plowed plots with dry beans compared to the no-rye plowed plots with soybeans (Table 4). In September 2020, the soil C:N

ratio was greater in the rye-plowed and rye-no till plots with soybeans compared to the no-rye plowed plots with soybeans and the rye-no till plots with dry beans (Table 5).

Soil protein

Soil protein was not affected by the treatments in September 2019 (Table 2). However, in September 2020 there was greater soil protein in the rye-no till plots than the rye-plowed plots (Table 5).

Soil aggregate stability

In September 2019, there was greater soil aggregate stability in the rye-no till plots with soybeans compared to the no rye-plowed plots under both bean types and the rye-plowed plots under soybeans (Table 2). In September 2020, the no rye-plowed plots had less soil aggregate stability than plots with the rye cover crop (Table 5).

Table 1. Significance levels from the ANOVAs performed on the soil metrics from June 2019 with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$). Interaction means not shown in table.

					Main Effect Means				
		P-Values			Crop		Management System		
Metrics	Units[1]	Crop	Management System	Interaction	Dry Bean	Soybean	No Rye - plowed	Rye - plowed	Rye - No till
Microbial Biomass Carbon	µg g −1 dry soil	0.7082	0.0995	0.7069	245.5	239.9	274.8	233.9	228.6
Microbial Biomass Nitrogen		0.8755	0.1552	0.1153	7.6	7.6	7.0	7.8	8.0
Microbial Biomass C:N		0.7762	**0.0225**	0.5906	33.9	33.1	41.0 a	30.9 ab	30.1 b
NAG	nmol of substrate h -1 g -1 dry soil	0.6259	*0.0571*	8.6810	16.0	16.6	15.0	15.3	18.6
BG		0.2045	0.7689	0.6029	95.1	101.3	96.2	100.5	97.8
LAP		0.6263	**0.0102**	0.4776	166.4	162.3	182.0 a	161.7 ab	149.4 b
PHOS		**0.0012**	**0.0008**	0.3890	77.6 B	101.6 A	93.5 a	105.0 a	72.9 b
NETPEROX		*0.0438*	0.1096	0.6269	1.6 A	1.5 B	1.6	1.6	1.5
Soil Nitrogen	%	0.6014	0.2183	0.6215	1.2	1.2	1.2	1.2	1.2
Soil Carbon	%	**0.0098**	**0.0288**	**0.0469**	2.0 A	1.9 B	1.9 ab	2.0 a	1.9 b
Soil C:N		**6.17E-06**	**0.0001**	**7.36E-06**	10.3 A	9.8 B	9.9 b	10.3 a	9.9 b
Microarthropods	# individuals / kg dry soil	*0.0561*	0.4262	0.1672	97.9 B	121.3 A	113.6	116.3	98.5
Total Collembola		0.5472	**0.0002**	0.1893	22.7	24.9	14.4 b	25.6 a	33.2 a
Total Mites		**0.0312**	**0.0208**	0.3370	71.4 B	93.3 A	97.0 a	87.2 ab	63.7 b
Oribatid Mites		0.1809	**0.0003**	0.3532	48.2	58.0	73.5 a	52.8 ab	36.0 b
Astigmatid Mites		**0.0056**	**0.0117**	0.4406	8.7 B	16.5 A	7.9 b	18.2 a	11.9 ab
Prostigmatid Mites		**0.0465**	**3.49E-05**	0.7246	0.6	1.4	0.4 b	0.4 b	3.0 a
Mesostigmatid Mites		0.2240	0.3357	0.8488	9.5	11.7	10.2	12.4	9.2

[1] Soil microbial and chemical metrics were log transformed when necessary and invertebrate data square root transformed prior to data analysis to meet ANOVA assumptions.

Table 2. Significance levels from the ANOVAs performed on the soil metrics from September 2019 with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$). Interaction means not shown in table.

					Main Effect Means				
		P-Values			Crop		Management System		
Metrics	Units[1]	Crop	Management System	Interaction	Dry Bean	Soybean	No Rye - plowed	Rye - plowed	Rye - No till
Aggregate Stability	%	0.7139	**5.64E-08**	**0.0427**	16.6	16.3	14.2 b	15.8 b	19.4 a
Soil Protein	mg / g dry soil	0.8188	0.5999	0.3917	5.1	5.1	5.0	5.2	5.2
Microbial Biomass Carbon	μg g −1 dry soil	**0.0011**	0.2537	0.1199	218.8 A	191.0 B	195.0	209.4	208.9
Microbial Biomass Nitrogen		**4.65E-07**	0.3537	0.1788	10.0 A	8.8 B	9.2	9.4	9.6
Microbial Biomass C:N		0.8623	0.6437	0.3204	22.0	22.1	21.5	22.8	22.3
NAG	nmol of substrate h -1 g -1 dry soil	0.4120	0.4179	0.1216	1.7	1.8	1.7	1.7	1.9
BG		0.8126	0.2349	0.3293	10.1	10.0	10.6	9.7	9.8
LAP		**0.0173**	*0.0765*	0.2014	7.8 A	6.6 B	8.0	6.5	7.1
PHOS		**0.0016**	**0.0287**	0.6692	6.5 B	8.6 A	7.2 ab	8.7 a	6.6 b
NETPEROX		0.1782	0.3366	0.8940	0.3	0.4	0.3	0.4	0.4
Soil Nitrogen	%	*0.0659*	0.2457	0.7319	1.2	1.2	1.2	1.2	1.2
Soil Carbon	%	**1.69E-06**	**0.0201**	*0.0756*	2.0 A	1.9 B	2.0 a	1.9 ab	1.9 b
Soil C:N		**3.12E-06**	**0.0280**	**0.0015**	10.2 A	9.7 B	10.0 ab	10.0 a	9.8 b
Microarthropods	# individuals / kg dry soil	**8.71E-06**	0.3785	0.9167	507.3 A	324.9 B	393.3	391.9	449.4
Total Collembola		**0.0016**	**0.0238**	0.1557	109.2 A	72.7 B	72.7 b	88.6 ab	110.8 a
Total Mites		**1.85E-05**	0.6734	0.8438	392.3 A	246.8 B	316.7	297.9	332.0
Oribatid Mites		**0.0001**	*0.0632*	0.3248	98.8 A	66.9 B	82.2	93.6	71.2
Astigmatid Mites		**0.0084**	0.1389	0.6732	142.9 A	93.1 B	117.5	94.8	139.9
Prostigmatid Mites		**2.89E-06**	0.7560	0.3561	107.5 A	56.8 B	82.6	83.0	74.9
Mesostigmatid Mites		**0.0015**	**0.0008**	0.8047	30.1 A	16.9 B	18.0 b	17.5 b	35.7 a

[1] Soil microbial and chemical metrics were log transformed when necessary and invertebrate data square root transformed prior to data analysis to meet ANOVA assumptions.

Table 3. Significance levels from the ANOVAs performed on the soil metrics from June 2020 with means (P < 0.05, bolded). Means with the same letters are not significantly different (Fisher's LSD, P > 0.05). Interaction means not shown in table.

					Main Effect Means				
		P-Values			Crop		Management System		
Metrics	Units[1]	Crop	Management System	Interaction	Dry Bean	Soybean	No Rye - plowed	Rye - plowed	Rye - No till
Microbial Biomass Carbon	μg g −1 dry soil	0.4634	0.5755	0.6391	181.6	191.3	178.7	185.2	195.5
Microbial Biomass Nitrogen		0.4412	0.7200	0.3326	7.5	8.0	7.5	8.2	7.7
Microbial Biomass C:N		0.9733	0.7612	0.3796	21.9	21.8	21.1	21.5	23.1
NAG	nmol of substrate h -1 g -1 dry soil	0.3926	**0.0005**	**0.0286**	16.3	15.2	12.5	16.5	18.7
BG		0.5529	**0.0025**	**0.0289**	90.5	88.4	80.7	91.5	96.1
LAP		0.6731	**0.0013**	**0.0289**	101.4	97.8	79.3	114.9	108.4
PHOS		0.8527	**0.0283**	0.2898	90.3	91.7	78.6 b	103.2 a	93.0 ab
NETPEROX		0.1579	0.7186	0.9029	1.6	1.5	1.5	1.6	1.5
Microarthropods	# individuals / kg dry soil	0.9720	**2.26E-05**	0.2625	326.5	324.7	239.9 b	523.6 a	248.5 b
Total Collembola		0.9931	**0.0033**	0.4177	27.3	27.2	17.4 b	32.4 a	33.6 a
Total Mites		0.9660	**1.96E-05**	0.3049	294.4	292.4	220.3 b	486.5 a	209.9 b
Oribatid Mites		0.8725	**1.22E-05**	0.3017	149.2	154.1	122.5 b	279.1 a	84.0 b
Astigmatid Mites		0.8302	**1.99E-05**	0.3469	68.0	65.2	43.3 b	121.8 a	47.0 b
Prostigmatid Mites		0.4833	0.5521	0.2823	39.9	34.4	32.8	43.2	35.7
Mesostigmatid Mites		0.9277	**7.25E-10**	0.2712	11.3	11.5	3.0 c	21.9 a	13.9 b

[1] Soil microbial and chemical metrics were log transformed when necessary and invertebrate data square root transformed prior to data analysis to meet ANOVA assumptions.

Table 4. Significance levels from the ANOVAs performed on the soil metrics from July 2020 with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$). Interaction means not shown in table.

		P-Values			Main Effect Means				
					Crop		Management System		
Metrics	Units[1]	Crop	Management System	Interaction	Dry Bean	Soybean	No Rye - plowed	Rye - plowed	Rye - No till
Microbial Biomass Carbon	μg g −1 dry soil	**0.0341**	0.5354	0.9996	323.3 A	288.6 B	318.4	297.3	302.3
Microbial Biomass Nitrogen		**0.0466**	*0.0541*	0.6092	6.7 A	6.2 B	6.0	6.5	6.8
Microbial Biomass C:N		0.4167	*0.0609*	0.6090	47.0	44.3	51.4	44.0	42.0
NAG	nmol of substrate h -1 g -1 dry soil	0.4176	**0.0007**	0.8995	17.5	18.3	17.1 b	15.9 b	21.0 a
BG		**0.0041**	**0.0006**	*0.0560*	84.7	91.8	86.5	83.4	95.0
LAP		*0.0869*	0.1929	0.1709	60.2	66.4	61.3	68.0	60.7
PHOS		**0.0325**	**0.0762**	0.4149	88.4 B	100.3 A	91.9	88.0	103.2
NETPEROX		**0.0009**	0.6990	0.6377	1.8 A	1.6 B	1.7	1.7	1.7
Soil Nitrogen	%	0.3579	0.4095	0.3260	1.2	1.2	1.1	1.2	1.2
Soil Carbon	%	0.3351	0.4693	0.4121	2.6	2.5	2.5	2.5	2.7
Soil C:N		0.1269	**0.0249**	**0.0269**	11.0	10.8	10.8	11.1	10.9
Microarthropods	# individuals / kg dry soil	0.6999	**1.81E-07**	0.2630	736.6	714.2	580.8 b	1005.2 a	624.5 b
Total Collembola		0.5955	**5.24E-13**	**0.0338**	215.7	204.3	115.2	369.3	182.8
Total Mites		0.9247	**0.0029**	0.7688	504.8	500.4	456.8 b	626.2 a	435.1 b
Oribatid Mites		0.8003	0.2449	0.4045	116.1	112.1	106.9	102.9	133.5
Astigmatid Mites		0.6072	**7.07E-12**	0.9750	90.0	84.2	42.8 c	169.3 a	71.3 b
Prostigmatid Mites		0.8126	**0.0011**	0.3871	220.7	226.7	263.7 a	255.6 a	159.8 b
Mesostigmatid Mites		0.3400	**1.03E-05**	0.4427	39.7	44.8	30.2 b	63.9 a	36.0 b

[1] Soil microbial and chemical metrics were log transformed when necessary and invertebrate data square root transformed prior to data analysis to meet ANOVA assumptions.

Table 5. Significance levels from the ANOVAs performed on the soil metrics from September 2020 with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$). Interaction means not shown in table.

					Main Effect Means				
		P-Values			Crop		Management System		
Metrics	Units[1]	Crop	Management System	Interaction	Dry Bean	Soybean	No Rye - plowed	Rye - plowed	Rye - No till
Aggregate Stability	%	0.3757	**0.0012**	0.5914	10.8	11.3	9.6 b	12.4 a	11.4 a
Soil Protein	mg / g dry soil	0.7852	**0.0084**	0.2553	4.1	4.0	4.0 ab	3.9 b	4.2 a
Microbial Biomass Carbon	µg g −1 dry soil	**0.0028**	0.6649	0.2616	302.0 B	350.0 A	326.0	317.4	334.6
Microbial Biomass Nitrogen		**2.42E-11**	0.5193	*0.0574*	7.8 A	5.5 B	6.4	6.4	6.8
Microbial Biomass C:N		**4.91E-17**	0.9122	0.7997	38.3 B	62.1 A	49.3	48.3	48.6
NAG	nmol of substrate h - 1 g -1 dry soil	**0.0009**	**2.24E-05**	0.9088	24.6 B	30.1 A	22.9 b	26.8 b	32.9 a
BG		*0.0637*	0.1629	0.6464	128.5	138.7	131.0	128.9	140.9
LAP		0.2385	0.5552	0.5009	93.4	102.9	100.9	101.4	92.1
PHOS		0.1643	0.1057	0.2737	144.9	160.2	144.6	169.8	144.1
NETPEROX		0.3259	**0.0059**	*0.0863*	1.7	1.7	1.6 b	1.7 ab	1.8 a
Soil Nitrogen	%	0.7249	0.7090	0.9516	1.2	1.2	1.2	1.2	1.2
Soil Carbon	%	0.1997	0.1548	*0.0570*	2.5	2.5	2.5	2.5	2.5
Soil C:N		**0.0255**	**0.0138**	**0.0022**	10.8	11.0	10.7	11.1	10.9
Microarthropods	# individuals / kg dry soil	**3.17E-05**	0.8341	*0.0822*	878.2 A	597.3 B	723.0	712.9	757.4
Total Collembola		**6.85E-08**	**0.0166**	0.1231	88.8 A	35.5 B	43.6 b	74.8 a	61.2 ab
Total Mites		**0.0004**	0.7025	*0.0973*	781.3 A	557.9 B	674.6	631.1	689.8
Oribatid Mites		**6.00E-07**	0.3620	0.3736	209.5 A	116.4 B	157.1	146.5	175.8
Astigmatid Mites		0.6236	0.5769	**0.0417**	262.4	246.0	279.6	241.0	242.7
Prostigmatid Mites		**0.0014**	0.8969	*0.0740*	217.8 A	149.6 B	188.9	178.9	178.6
Mesostigmatid Mites		**0.0010**	0.6583	0.7280	42.4 A	26.1 B	30.8	34.6	36.0

[1] Soil microbial and chemical metrics were log transformed when necessary and invertebrate data square root transformed prior to data analysis to meet ANOVA assumptions.

Agroecosystem models

At all sampling dates in 2019 and 2020 the paths in the agroecosystem models were affected by the tillage treatments, regardless of the microarthropod grouping level used in the models (Family, Order, total microarthropods). Results from the order-level microarthropod group modeling are presented in the results section and focused on in the discussion section. Order-level microarthropod groupings are focused on since this level of taxonomic identification separates common functional groups within the microarthropod communities. Details of the family-level and total microarthropod grouping models are included in the appendices.

In June 2019, PHOS directly affected bean weight and collembolans and astigmatid mites indirectly affected bean weight in the no-rye plowed plots, explaining 63% of the variation in bean weight (Figure 1; Appendix C). Microbial biomass and soil C:N ratios directly affected bean weight, and mesostigmatid mites indirectly affected bean weight in the rye-plowed plots, explaining 85% of bean weight variation (Figure 1; Appendix C). BG, astigmatid mites, and prostigmatid mites directly affected bean weight, and microbial biomass C:N and PHOS indirectly affected bean weight, in the rye-no till plots explaining 81% of the variation in bean weight (Figure 1; Appendix C).

In September 2019, prostigmatid mites, mesostigmatid mites, microbial biomass N, PHOS, BG, and soil C:N directly affected total bean weight in the no-rye plowed plots (Figure 2; Appendix C). PHOS and BG also indirectly affected bean weight via their effect on the prostigmatid mites. In the no rye-plowed plots 85% of bean weight variation was explained. In the rye-plowed plots, PHOS, BG, volunteer rye, and root rot severity directly affected total bean weight, and BG also indirectly affected bean weight through its effects on the volunteer rye (Figure 1; Appendix C). In the rye-plowed plots 95% of bean weight variation was explained. In

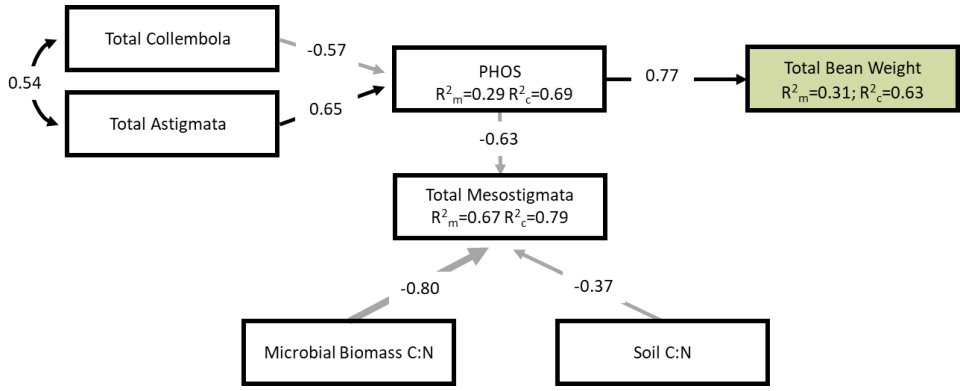
the rye-no till plots, Collembola, oribatid mites, astigmatid mites, soil C:N, peroxidase, PHOS, BG, root rot severity, volunteer rye, and other monocot weeds directly affected bean weight (Figure 1; Appendix C). Oribatid mites and PHOS also indirectly affected bean weight through their effects on the weeds. In the rye-no till plots 100% of the variation in bean weight was explained.

In June 2020, mesostigmatid mites, prostigmatid mites, astigmatid mites, Collembola, BG, LAP, and microbial biomass C:N directly affected bean weight in the no-rye plowed (Figure 3; Appendix C). LAP, BG, and NAG had indirect effects on bean weight via the mites. In the no rye-plowed plots 99% of bean weight variation was explained. In the rye-plowed plots, oribatid mites directly affected bean weight, and the model explained 99% of bean weight variation (Figure 3; Appendix C). In the rye-no till plots BG directly affected bean weight, and the model explained 49% of the bean weight variation (Figure 3; Appendix C).

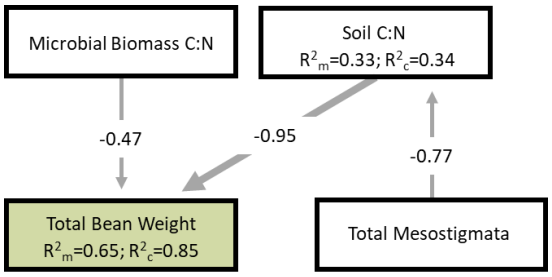
In July 2020, Collembola, oribatid mites, prostigmatid mites, LAP, microbial biomass C:N, soil N and soil C directly affected bean weight in the no-rye plowed plots (Figure 4; Appendix C). Microbial biomass C:N, microbial biomass C, soil N, soil C, and LAP all had indirectly effects on bean weight routed through different microarthropod groups. In the no-rye plowed plots 92% of the variation in bean weight was explained. In the rye-plowed plots, oribatid mites, LAP, soil N and soil C directly affected bean weight, while prostigmatid mites and LAP indirectly affected bean weight (Figure 4; Appendix C). In the rye-plowed plots 100% of bean weight variation was explained. In the rye-no till plots, astigmatid mites, LAP, microbial biomass C, soil N and soil C directly affected bean weight (Figure 4; Appendix C). LAP, soil N, and Soil C also indirectly affected bean weight through their effects on astigmatid mites. In the rye-no till plots 72% of bean weight variation was explained.

In September 2020, prostigmatid mites, mesostigmatid mites, microbial biomass C and N, soil N, and volunteer rye directly affected bean weight in the no rye-plowed plots (Figure 5; Appendix C). Soil N, microbial biomass N, and microbial biomass C all indirectly affected bean weight through different microarthropod groups. Mesostigmatid mites also indirectly affected bean weight through their effects on the volunteer rye. In the no rye-plowed plots 95% of the variation in bean weight was explained. In the rye-plowed plots, Collembola and oribatid mites directly affected bean weight, while microbial biomass N indirectly affected bean weight via the oribatid mites (Figure 5; Appendix C). In the rye-plowed plots 90% of the variation in bean weight was explained. In the rye-no till plots, Collembola, prostigmatid mites, mesostigmatid mites, microbial biomass C and N, soil N, and volunteer rye directly affected bean weight (Figure 5; Appendix C). Soil N, microbial biomass N, and collembolans indirectly affected bean weight. In the rye-no till plots 98% of the variation of bean weight was explained.

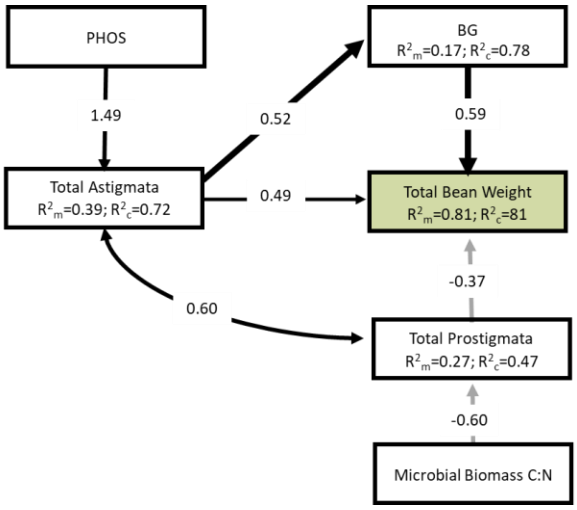
Figure 1. Piecewise structural equation models (SEM) from June 2019 for each cover crop treatment. Black arrows represent positive relationships, and grey arrows represent negative relationships. Arrow thickness indicates p-values; thick arrows are for p-values <0.01, thin arrow are for p-values <0.05. Standardized path coefficients are shown for significant relationships. Marginal (R^2_m) and conditional (R^2_c) coefficients of determination are shown for each component model, which describes the proportion of response variance associated with the fixed effects (marginal) and the fixed effects with random effects included (conditional).



No Rye – Plowed

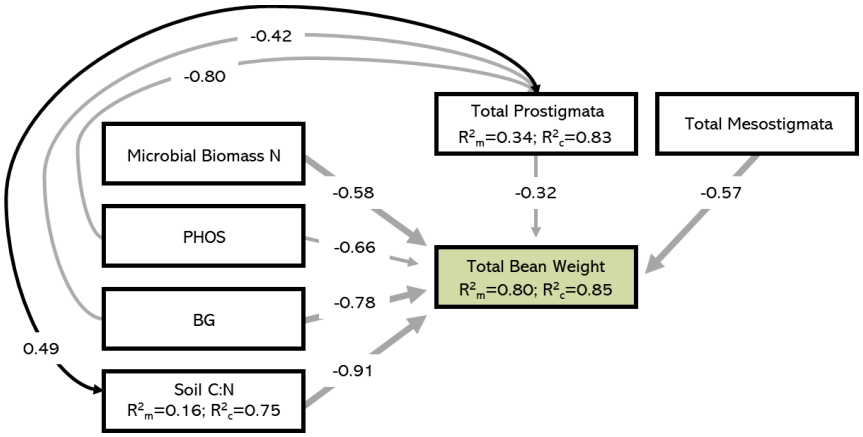


Rye – Plowed

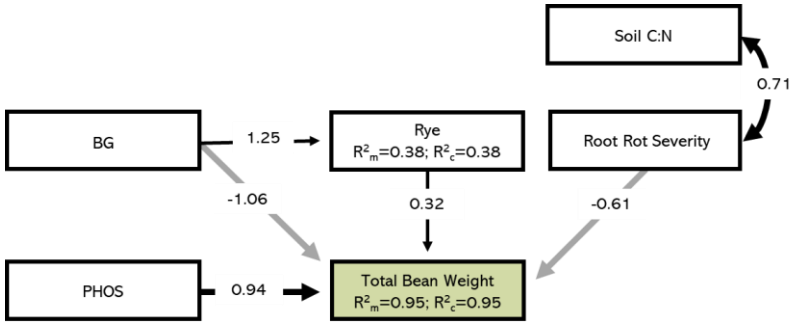

PHOS
BG
R^2_m=0.17; R^2_c=0.78
1.49
0.52
0.59
Total Astigmata
R^2_m=0.39; R^2_c=0.72
0.49
Total Bean Weight
R^2_m=0.81; R^2_c=81
-0.37
0.60
Total Prostigmata
R^2_m=0.27; R^2_c=0.47
-0.60
Microbial Biomass C:N

Rye – No Till

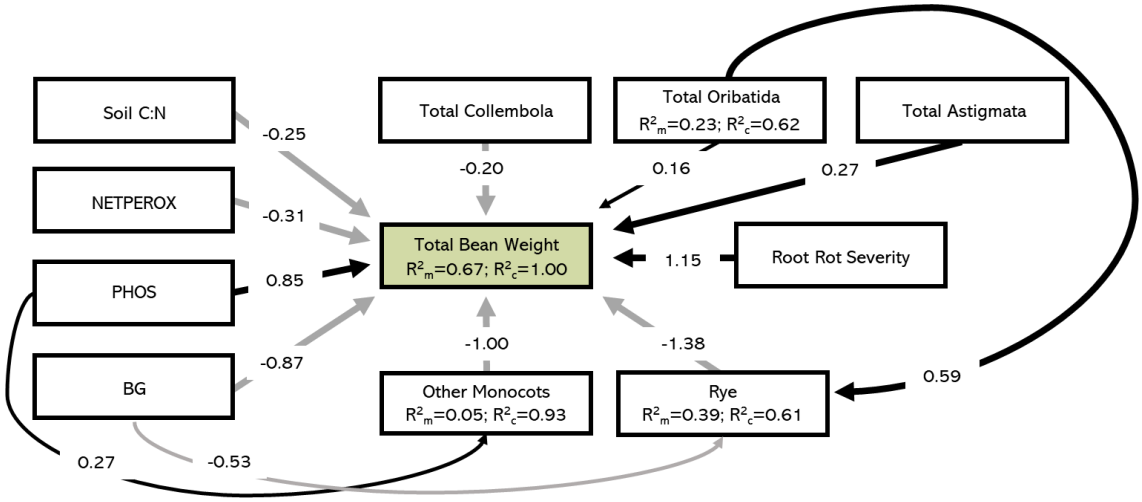
Figure 2. Piecewise structural equation models (SEM) from September 2019 for each cover crop treatment. Black arrows represent positive relationships, and grey arrows represent negative relationships. Arrow thickness indicates p-values; thick arrows are for p-values <0.01, thin arrow are for p-values <0.05. Standardized path coefficients are shown for significant relationships. Marginal (R^2_m) and conditional (R^2_c) coefficients of determination are shown for each component model, which describes the proportion of response variance associated with the fixed effects (marginal) and the fixed effects with random effects included (conditional).



No Rye – Plowed

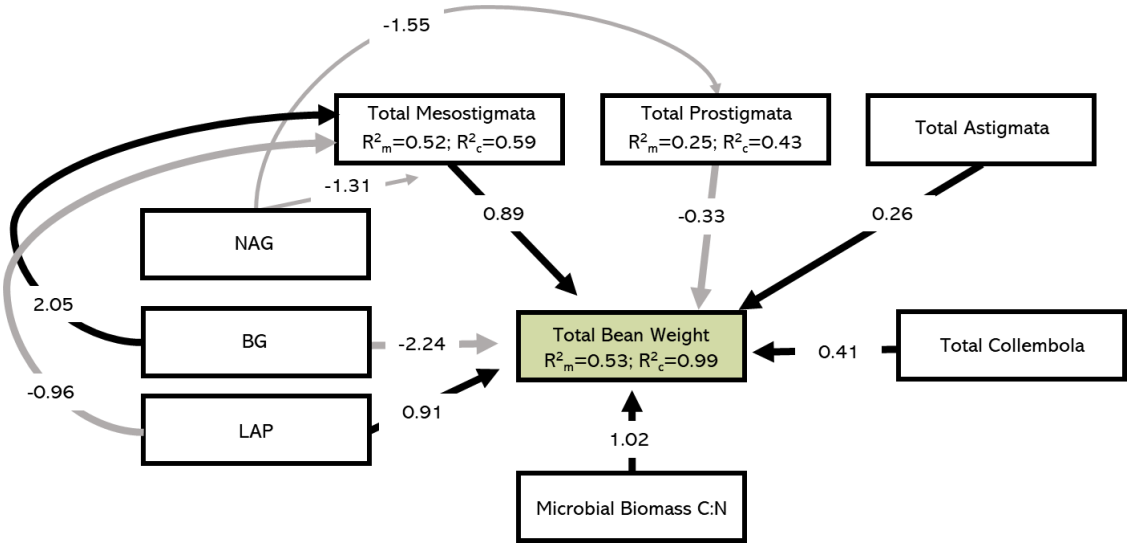


Rye – Plowed

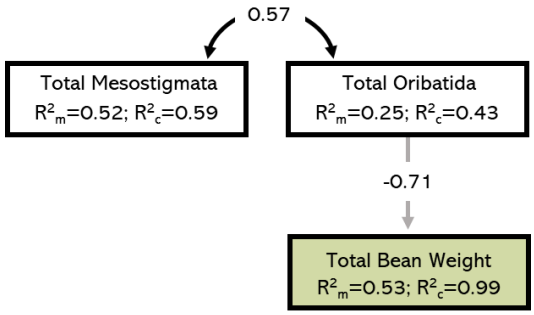

Soil C:N
NETPEROX
PHOS
BG
Total Collembola
Total Oribatida
R^2_m=0.23; R^2_c=0.62
Total Astigmata
Total Bean Weight
R^2_m=0.67; R^2_c=1.00
Root Rot Severity
Other Monocots
R^2_m=0.05; R^2_c=0.93
Rye
R^2_m=0.39; R^2_c=0.61
-0.25
-0.31
0.85
-0.87
-0.20
0.16
0.27
1.15
-1.00
-1.38
0.59
0.27
-0.53

Rye – No Till

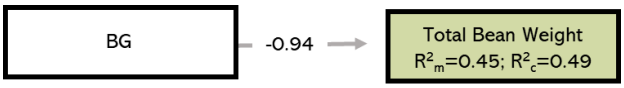
Figure 3. Piecewise structural equation models (SEM) from June 2020 for each cover crop treatment. Black arrows represent positive relationships, and grey arrows represent negative relationships. Arrow thickness indicates p-values; thick arrows are for p-values <0.01, thin arrow are for p-values <0.05. Standardized path coefficients are shown for significant relationships. Marginal (R^2_m) and conditional (R^2_c) coefficients of determination are shown for each component model, which describes the proportion of response variance associated with the fixed effects (marginal) and the fixed effects with random effects included (conditional).



No Rye – Plowed

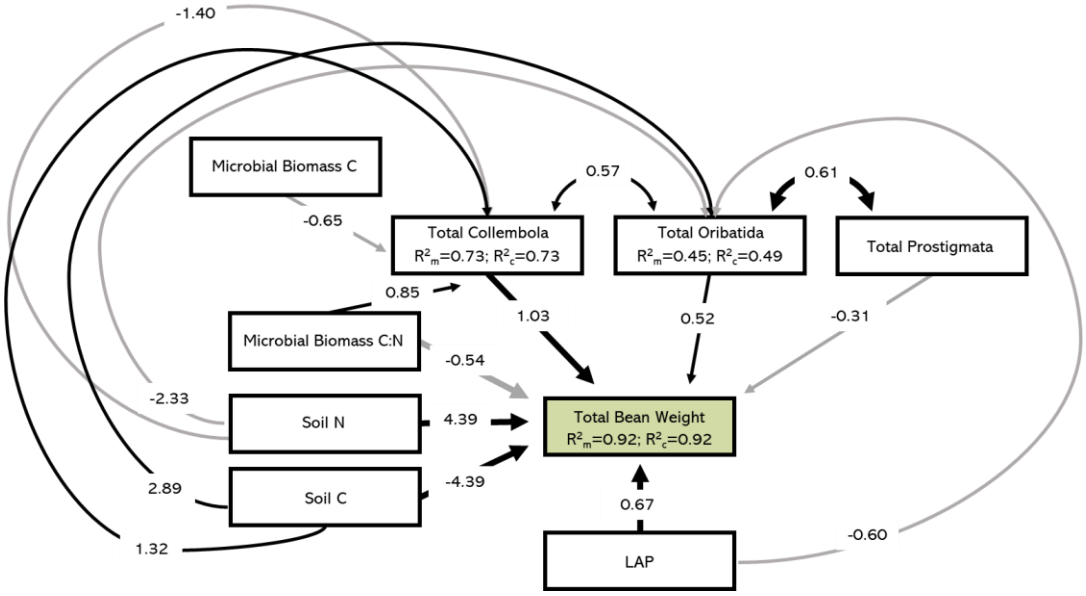


Rye – Plowed

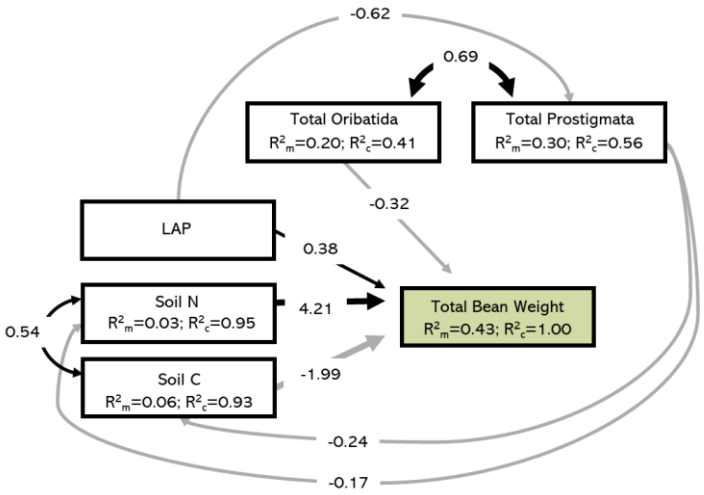


Rye – No Till

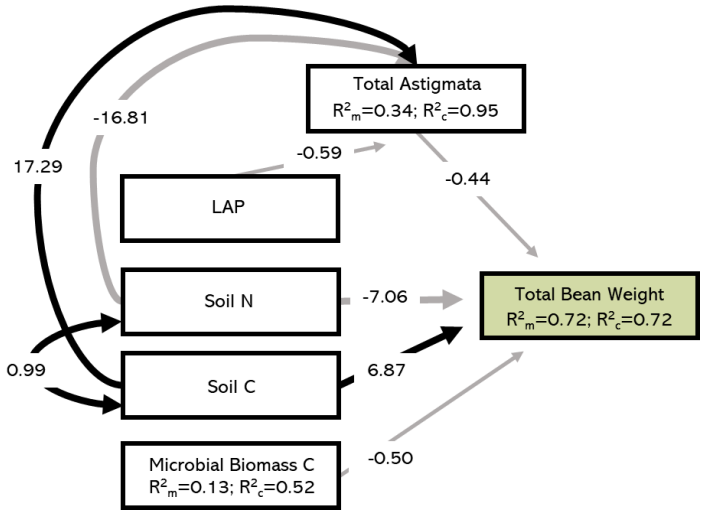
Figure 4. Piecewise structural equation models (SEM) from July 2020 for each cover crop treatment. Black arrows represent positive relationships, and grey arrows represent negative relationships. Arrow thickness indicates p-values; thick arrows are for p-values <0.01, thin arrow are for p-values <0.05. Standardized path coefficients are shown for significant relationships. Marginal (R^2_m) and conditional (R^2_c) coefficients of determination are shown for each component model, which describes the proportion of response variance associated with the fixed effects (marginal) and the fixed effects with random effects included (conditional).



No Rye – Plowed

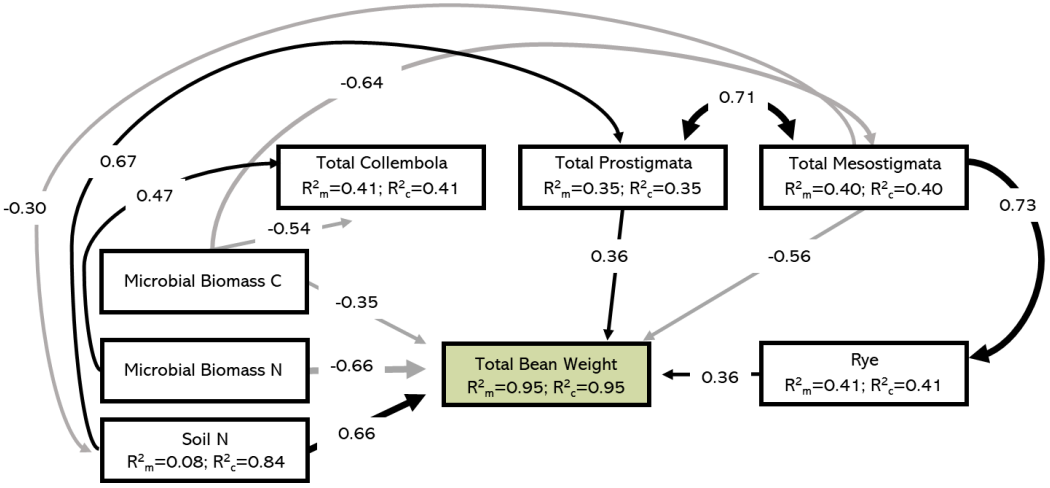


Rye – Plowed

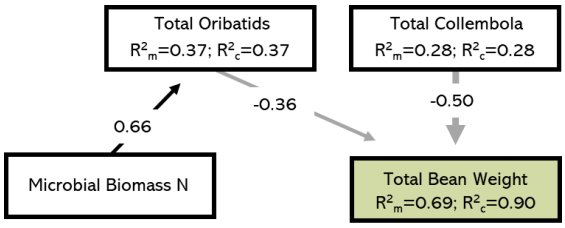


Rye – No Till

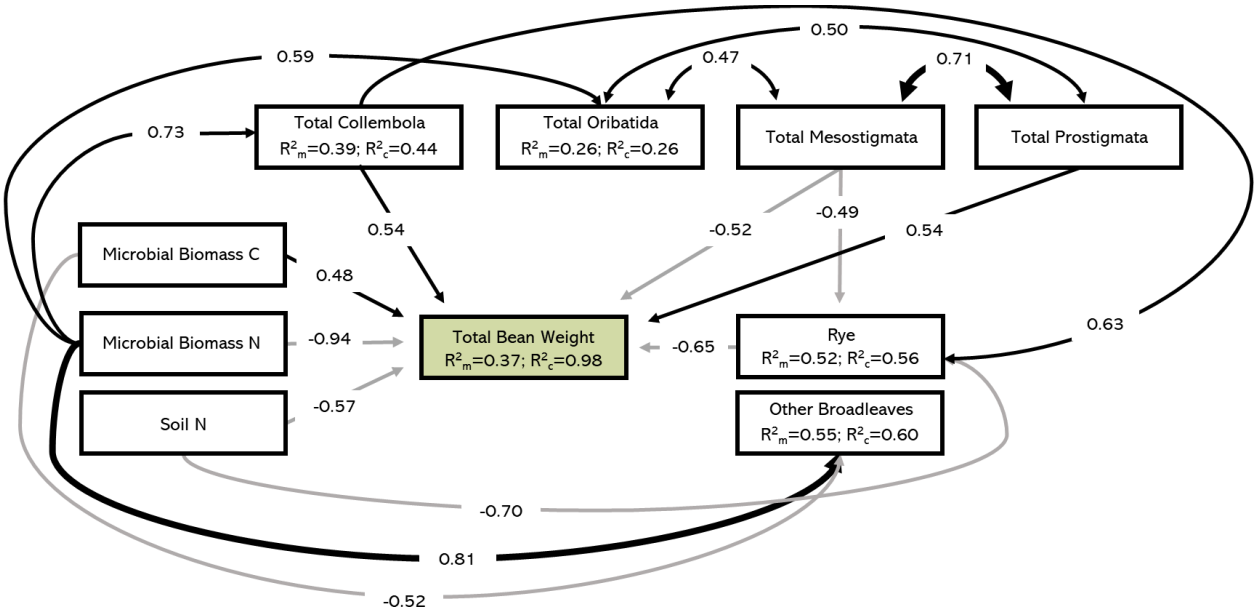
Figure 5. Piecewise structural equation models (SEM) from September 2020 for each cover crop treatment. Black arrows represent positive relationships, and grey arrows represent negative relationships. Arrow thickness indicates p-values; thick arrows are for p-values <0.01, thin arrow are for p-values <0.05. Standardized path coefficients are shown for significant relationships. Marginal (R^2_m) and conditional (R^2_c) coefficients of determination are shown for each component model, which describes the proportion of response variance associated with the fixed effects (marginal) and the fixed effects with random effects included (conditional).



No Rye – Plowed



Rye – Plowed


0.59
0.50
0.47
0.71
0.73
Total Collembola
R^2_m=0.39; R^2_c=0.44
Total Oribatida
R^2_m=0.26; R^2_c=0.26
Total Mesostigmata
Total Prostigmata
0.54
-0.52
-0.49
0.54
Microbial Biomass C
0.48
Microbial Biomass N
-0.94
Total Bean Weight
R^2_m=0.37; R^2_c=0.98
-0.65
Rye
R^2_m=0.52; R^2_c=0.56
0.63
Soil N
-0.57
Other Broadleaves
R^2_m=0.55; R^2_c=0.60
-0.70
0.81
-0.52

Rye – No Till

DISCUSSION

Cover Crop Effects

The presence of the rye cover crop, regardless of tillage, increased Collembola abundances at every sampling date both years. Collembola abundances can be increased using cover crops (Bedano *et al.*, 2016; Dulaurent *et al.*, 2023), though this is not always the case (de Pedro *et al.*, 2020). In cases where the cover crop also increased predator populations in this study, there were no increases in Collembola abundance due to the top-down controls on the Collembola (Carmona *et al.*, 2022). The different effects of cover crops on Collembola may be attributed to the cover crop species, tillage practices, or soil arthropod community compositions in the different studies.

Early in the 2020 growing season, the rye increased the activity of four out of the five enzymes measured. The microbial community likely produced more enzymes early in the growing season to break down the rye for its nutrients. Research consistently finds that the introduction of additional food resources via cover crops increases microbial enzyme activity (Calderón *et al.*, 2016; dos Santos Cordeiro, Echer and Araujo, 2021; Thapa *et al.*, 2021), though these results can be short lived in some cases as with our study.

The introduction of cover crop residues can alter soil carbon and nitrogen (Pan, Tang and Chen, 2022), though these effects are highly dependent on the cover crop species and residue composition (Chen *et al.*, 2014; Mueller and Thorup-Kristensen, 2012). The cover crop increased soil C:N ratios in 2020. Cover crops with higher C:N ratios and lignin content, like the cereal rye in this experiment, decompose slower due to the immobilization of soil N (Gentile *et al.*, 2009). This effect is driven by the increased demand of soil available N by the microbial community as they metabolize residues rich in C but poor in N (Geisseler *et al.*, 2010). The incorporation of the

high C content residue by the microbial community can therefore increase soil C:N ratios.

The cover crop increased soil aggregate stability both years. Cover crops can increase soil aggregate stability (Khan *et al.*, 2022), typically through the growth of roots (Stegarescu, Reintam and Tõnutare, 2021), or by increasing the polysaccharides in the soil which help bind soil particles together (Liu, Ma and Bomke, 2005). Cover crops do not always increase aggregate stability, which may be due to lack of root growth or soil moisture (Rojas *et al.*, 2018).

Reduced Tillage Effects

In 2019, reducing tillage led to increased soil aggregate stability and increased Collembola and mesostigmatid mite abundances. Several studies have shown that reducing tillage can increase soil aggregate stability and improve soil structure (BELMONTE *et al.*, 2018; Bilibio *et al.*, 2023; Hermawan and Bomke, 1997; Obalum, Uteau-Puschmann and Peth, 2019; Rubio, Sawchik and van Es, 2022b). Improvements in soil structure creates habitats that are more suitable for soil fauna such as the collembolans and mesostigmatid mites. Previous research further confirms that reduced tillage cropping systems can lead to increases in Collembola and mesostigmatid mite abundances (Jernigan *et al.*, 2020).

Reducing tillage can also affect the activities of the soil microbial community. In reduced tillage systems fungal hyphae can grow undisturbed and more microbial extracellular polysaccharides can be produced which aids in soil aggregation (Tang *et al.*, 2011). We observed reducing tillage decreased PHOS activity in 2019, and increased NAG in 2020, which is likely due to shifts in the activities of the microbial communities caused by the reduction in soil disturbance.

Bean Type Effects

Earlier in the growing season each year the bean type had fewer effects on the soil

environment compared to the end of season. Interestingly, in 2019 and 2020 the beans had opposing effects on microbial biomass and C:N ratios, as well as the enzymatic activities of the microbial communities. The opposing responses between years suggests an important role of field conditions and weather variability in these responses, as is the case in many studies (Hu *et al.*, 2021; Huygens *et al.*, 2011; Jiao *et al.*, 2011; Mayr, Miller and Insam, 1999; Miura *et al.*, 2019). The soil conditions of the fields used in 2019 and 2020 differed considerably in their biological communities from the start, especially their microarthropod communities, which could also explain the opposing effects of the beans (Jernigan *et al.*, 2022).

The soybeans generally performed better than the dry beans, but this effect was more pronounced in 2019. In 2019 the dry beans had higher microbial biomass C and C:N ratios, indicating a larger microbial community with more fungi (Jenkinson and Ladd, 1981; McGill *et al.*, 1982). This likely reflected an increase in fungal pathogens, like the white mold and roots rot, which harmed the dry beans (Pethybridge et al., *in prep*). At the end of the growing season in both years the soybeans had less microarthropods of all different orders compared to the dry beans. It is possible that the microarthropods flourished in the dry beans because there were more pathogenic microbes which they prefer as a food source (Innocenti and Sabatini, 2018).

Agroecosystem Modeling

Soil nutrient status was an important determinant of total bean weight. The main drivers of bean production were the C and N in both the microbial biomass and soil both years, across the growing season. This trend was unsurprising given that soil fertility is known to be an important determinant in crop productivity (Shang *et al.*, 2014; Watson *et al.*, 2006).

Microbial biomass N was an important soil metric, consistently having a negative effect on total bean weight. This suggests that plant-microbe competition for nutrients may be a central

driver of crop production outcomes relative to other factors in agroecosystems. Competition between plants and microbes for limiting nutrient can negatively affect plant growth (Fitzpatrick, Mustafa and Viliunas, 2019; Johnson *et al.*, 2010; VIMAL *et al.*, 2017). In this experiment N was likely a limiting factor since the cereal rye introduced a large C source, binding up the N in the systems.

The importance of microbial enzymes varied between the growing seasons, with the enzymes measured, primarily PHOS (phosphorus enzyme) and BG (cellulose enzyme), only being significant in 2019. Microbes produce extracellular enzymes in response to their metabolic needs and their environments (Alster *et al.*, 2020; Burns *et al.*, 2013; Sinsabaugh and Moorhead, 1994; Sorouri and Allison, 2022). The seasonal variability of the importance of microbial enzymes for crop productivity is likely related to the differences between the fields used each year, which would likely vary in the amount of available nutrients.

The microarthropods often affected bean production indirectly through their interactions with the microbial community. The close interactions of these two communities influence many of the soil biological process that affect plant growth (Lartey, 2006; Soong and Nielsen, 2016; Tejada *et al.*, 2008), validating this observation in these models.

Collembola, mesostigmatid mites, and prostigmatid mites were the most important microarthropods across the models. Interestingly, the microarthropods switched between having positive and negative effects on crop production across the growing season and between cropping systems. Microarthropod community composition can change dramatically throughout a growing season, which was observed in this study. These temporal shifts in the effects of the microarthropods may reflect changing dynamics with these communities (Wu *et al.*, 2014). Similarly, the cropping system practices implemented can alter microarthropod communities

(Carmona *et al.*, 2022; de Pedro *et al.*, 2020; Reeleder *et al.*, 2006), therefore altering the dominant groups and their influence over the community dynamics.

The microarthropods had more direct effects on bean production when there was a cover crop and tillage was reduced, likely because there was greater microarthropod abundances under these conditions. The microarthropods have more positive effects when there are more food resources available, as observed in the rolled cereal rye treatment. Since there were greater microarthropod abundances this would result in increased feeding on both soil microbes and the decomposing cereal rye roots (Cole, Buckland and Bardgett, 2005; Heneghan *et al.*, 1998; Kampichler and Bruckner, 2009; Lussenhop, 1992). These interactions likely led to increased nutrient cycling and plant available nutrients.

The models using different levels of microarthropod taxonomic resolution (Appendix C, D, E) highlight that measuring total microarthropod appears to be sufficient to obtain a general understanding of the overall effects of the microarthropod community on crop production. Other studies have found that coarser level identification of microarthropods can be sufficient indicators of other factors, such as disturbance and land use changes (Meehan *et al.*, 2019; Menta *et al.*, 2018). As the taxonomic resolution is refined, we observed more nuanced relationships between the microarthropods and bean production, with some taxa having more positive effects and others having more negative effects. Finer taxonomic resolution will be necessary for understanding the mechanisms underlying the relationships between microarthropods and crop production (Potapov, 2022; Potapov, Tiunov and Scheu, 2019).

Relative to the soil metrics, the pathogens played a less important role in determining bean production. Root rot severity appeared sporadically in the models with mixed effects, and white mold was not significant in any of the models. White mold and root rot can significantly

reduce crop yields (Bolton, Thomma and Nelson, 2006; Chekali *et al.*, 2016; Demissie, Momen and Everts, 2022). The insignificance of these pathogens in these models likely do not reveal that these were not important factors in these cropping systems, instead revealing their relative importance in these growing seasons was less relative to soil fertility.

Aside from the volunteer rye, weed competition also did not play a major role in the models. In the rolled cereal rye plots, volunteer rye was a major problem because of competition (Ryan *et al.*, 2011; Zimdahl, 2004). However, it had a positive effect in other treatments, possibly by providing an additional food source for the soil food web that was complementary to the beans (Bradford, 2016; de Vries *et al.*, 2013).

Overall, the soil fertility related metrics were the dominant drivers of crop productivity in these systems, in comparison with plant pathogen pressure and weed competition. Within biological nutrient cycling, soil microarthropods appear to be a central determinant of crop production. The effects of crop management practices on soil microarthropods should therefore be considered an important factor in crop management decisions.

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APPENDICES

Appendix A. Microarthropod taxa ANOVA tables for 2019.

Table A.1. June 2019 Microarthropod taxa ANOVAs

	P-Values			Main Effect Means				
				Crop		Management System		
Metrics	Crop	Management System	Interaction	Dry Bean	Soybean	No Rye - plowed	Rye - plowed	Rye - No till
Onychuridae	0.1499	0.1786	0.4219	8.1	11.2	7.4	9.3	12.3
Entomobryidae	0.9830	**0.0307**	0.8750	3.9	3.9	1.9 b	4.1 ab	6.2 a
Isotomidae	0.7620	**0.0005**	0.1711	4.8	5.3	1.8 b	6.7 a	7.9 a
Sminthuridae	0.7738	**0.0302**	0.6058	0.8	0.7	0.2 b	0.8 ab	1.6 a
Astig_5_OO	0.1616	**6.99E-06**	**0.0323**	6.7	9.5	6.8 b	16.8 a	3.2 b
Oribatid_2_T	*0.0979*	0.2400	**0.0327**	4.0	2.6	3.2	4.2	2.4
Oribatid_2_S	0.1090	*0.0652*	0.6761	2.0	3.6	3.7	3.6	1.4
Oribatid_3	0.2722	**0.0221**	0.7836	1.5	0.7	1.1 ab	2.7 a	0.2 b
Oribatid_4	0.9548	0.5932	0.2154	0.0	0.0	0.0	0.0	0.0
Prostig_1	0.3210	0.3735	0.3735	0.0	0.0	0.0	0.0	0.0
Prostig_2	*0.0794*	**0.0001**	0.6449	0.6	1.3	0.4 b	0.4 b	2.8 a
Oribatid_6_OA	0.5848	**0.0053**	0.6961	2.9	3.5	3.1 ab	5.8 a	1.5 b
Oribatid_7_OA	0.0870	**0.0001**	0.4132	29.6	39.8	55.2 a	30.2 b	22.1 b
Astig_3	0.8726	**0.0201**	0.8028	0.0	0.0	0.2 a	0.0 ab	0.0 b
Hypopi	**0.0129**	**2.80E-07**	*0.0648*	0.6 B	2.3 A	0.1 b	0.4 b	5.8 a
Mesostig_1	0.1849	0.3335	0.8658	9.2	11.6	10.1	12.2	9.0
Mesostig_2	0.4853	0.8769	0.8047	0.0	0.0	0.0	0.0	0.0
Carabid Larvae	*0.0690*	0.2121	**0.0109**	0.8	1.7	1.0	0.8	1.9
Larva_1	0.5970	**0.0004**	0.5627	0.8	0.5	0.0 b	0.2 b	3.4 a
Larva_2	0.3912	**0.0256**	0.1123	0.5	0.8	1.2 a	0.9 ab	0.1 b
Larva_4	0.5435	0.3835	0.5155	0.0	0.1	0.0	0.1	0.0
Enchytraid	0.1565	0.8391	0.7668	1.1	0.6	1.0	0.8	0.7
Staphinalid_Beetle	**0.0309**	0.5436	0.9998	0.0 B	0.1 A	0.0	0.1	0.0
Ant	0.7764	0.1838	**0.0270**	0.0	0.0	0.1	0.0	0.0
Diplura	0.1675	0.3463	0.2144	0.0	0.1	0.0	0.0	0.1
Thrips	0.1423	**0.0030**	0.1182	0.0	0.0	0.0 b	0.0 b	0.1 a
Chilopoda	0.3235	0.2240	0.2549	0.1	0.0	0.0	0.0	0.1

Table A.2. September 2019 Microarthropod taxa ANOVAs

	P-Values			Main Effect Means				
				Crop		Management System		
Metrics	Crop	Management System	Interaction	Dry Bean	Soybean	No Rye - plowed	Rye - plowed	Rye - No till
Onychuridae	**0.0338**	0.4442	0.2267	48.5 A	35.5 B	36.6	45.2	43.9
Entomobryidae	**0.0009**	**0.0010**	0.5374	32.0 A	15.9 B	16.4 b	18.3 b	37.7 a
Isotomidae	**0.0002**	**0.0105**	0.6353	12.6 A	4.0 B	4.8 b	6.3 b	13.2 a
Sminthuridae	**0.0352**	*0.0944*	0.3991	8.2 B	11.5 A	8.7	12.4	8.6
Astig_5_OO	**0.0164**	0.5104	0.7981	124.0 A	80.9 B	108.8	87.4	108.5
Oribatid_2_T	**0.0005**	*0.0931*	0.1723	6.8 A	3.0 B	3.2	5.5	5.6
Oribatid_2_S	**0.0126**	**0.0491**	0.4542	7.7 A	3.3 B	2.7 b	6.4 ab	7.3 a
Oribatid_3	**0.0040**	**0.0042**	0.8631	58.4 A	42.1 B	56.7 a	56.8 a	37.4 b
Prostig_2	**0.0000**	0.3163	0.2230	69.7 A	33.6 B	46.4	46.9	57.2
Prostig_3	**0.0034**	**0.0006**	0.5302	34.1 A	19.6 B	33.9 a	33.5 a	14.4 b
Prostig_4	0.6177	0.8215	0.1098	0.0	0.0	0.0	0.0	0.0
Oribatid_6_OA	0.2122	0.5249	0.5661	0.2	0.1	0.1	0.1	0.3
Oribatid_7_OA	0.1098	0.4238	0.2857	18.3	14.3	16.0	18.4	14.4
Astig_3	*0.0544*	**0.0382**	0.2701	0.1 A	0.0 B	0.2 a	0.0 b	0.0 ab
Hypopi	*0.0855*	**0.0000**	**0.0419**	11.6	6.9	3.8	5.6	22.4
Astig_4	0.5836	**0.0045**	0.4041	0.1	0.0	0.0 ab	0.0 b	0.4 a
Mesostig_1	**0.0028**	**0.0202**	0.8998	27.4 A	15.6 B	17.6 b	17.2 b	29.5 a
Mesostig_2	0.2399	*0.0913*	0.2848	0.2	0.1	0.0	0.0	0.3
Mesostig_3	0.4203	**0.0000**	0.7698	0.4	0.2	0.0 b	0.0 b	2.6 a
Carabid Larvae	0.2186	0.2360	0.3659	0.3	0.1	0.1	0.2	0.3
Larva_1	**0.0264**	0.4133	0.3925	0.2 A	0.0 B	0.2	0.0	0.0
Larva_2	0.1345	*0.0851*	0.1883	3.2	1.7	3.7	1.2	2.7
Enchytraid	0.7047	*0.0710*	0.5102	1.3	1.1	1.7	1.8	0.4

Appendix B. Microarthropod taxa ANOVA tables for 2020.

Table B.1. June 2020 Microarthropod taxa ANOVAs

	P-Values			Main Effect Means				
				Crop		Management System		
Metrics	Crop	Management System	Interaction	Dry Bean	Soybean	No Rye - plowed	Rye - plowed	Rye - No till
Onychuridae	0.3884	**0.0020**	0.1027	8.0	6.7	4.0 b	8.4 a	10.5 a
Entomobryidae	0.8636	**9.45E-11**	0.4248	4.0	4.2	1.0 b	2.2 b	12.8 a
Isotomidae	0.1631	**0.0015**	0.5551	7.3	10.5	6.0 b	15.9 a	6.1 b
Sminthuridae	**0.0417**	**0.0007**	0.7058	2.4 A	1.2 B	2.5 a	2.9 a	0.5 b
Astig_5_OO	0.8121	**2.10E-05**	0.3341	67.0	63.9	42.1 b	119.8 a	46.7 b
Oribatid_2_T	0.1153	0.8370	0.8485	0.0	0.1	0.0	0.0	0.1
Oribatid_2_S	0.8510	0.3079	0.9867	2.3	2.2	1.5	3.0	2.4
Oribatid_3	0.9436	**1.33E-05**	0.3501	126.4	124.5	98.6 b	235.7 a	69.2 b
Oribatid_5	0.2542	0.1682	0.3875	0.1	0.4	0.1	0.6	0.2
Prostig_1	0.3211	0.3736	0.3736	0.0	0.0	0.0	0.0	0.0
Prostig_2	**0.0297**	**0.0219**	0.1240	9.4 A	5.9 B	5.1 b	7.3 ab	10.6 a
Prostig_3	0.8344	0.3766	0.5183	28.3	26.9	26.5	34.1	22.7
Prostig_4	0.2509	0.7477	0.8616	0.0	0.0	0.0	0.0	0.0
Prostig_5	0.1623	0.6080	0.6080	0.0	0.0	0.0	0.0	0.0
Oribatid_6_OA	**0.0900**	**1.68E-05**	0.2517	5.0	9.9	6.9 b	19.2 a	1.2 c
Oribatid_7_OA	0.6160	**0.0125**	0.1658	9.9	9.0	9.2 ab	13.1 a	6.5 b
Astig_3	0.3064	**0.0349**	0.9996	0.2	0.4	0.3 ab	0.9 a	0.1 b
Hypopi	0.3684	0.1401	0.6913	5.5	7.1	6.4	4.2	8.6
Astig_4	0.3211	0.3736	0.3736	0.0	0.0	0.0	0.0	0.0
Mesostig_1	0.9369	**7.53E-10**	0.2622	11.3	11.4	3.0 c	21.8 a	13.8 b
Mesostig_2	0.9796	0.6086	0.2307	0.0	0.0	0.0	0.0	0.0
Carabid_Beetle_Larvae	0.7573	**0.0103**	0.2424	0.6	0.7	0.2 b	1.5 a	0.6 ab
Larva_1	0.7626	**0.0064**	0.4280	0.0	0.0	0.0 b	0.1 a	0.0 b
Larva_2	0.4813	0.1390	0.9562	0.1	0.1	0.0	0.2	0.1
Enchytraid	0.8559	**0.0086**	0.5609	0.6	0.7	0.2 b	0.5 ab	1.5 a
Spider	0.0969	0.1484	0.7672	0.0	0.0	0.0	0.1	0.0
Thrips	0.8721	0.2244	0.3528	5.3	5.0	3.4	7.0	5.4

Table B.2. July 2020 Microarthropod taxa ANOVAs

	P-Values			Main Effect Means				
				Crop		Management System		
Metrics	Crop	Management System	Interaction	Dry Bean	Soybean	No Rye - plowed	Rye - plowed	Rye - No till
Onychuridae	0.9998	**0.0008**	*0.0534*	63.1	63.1	44.0 b	90.9 a	58.8 b
Entomobryidae	0.9911	**6.42E-07**	0.7572	39.1	39.2	19.7 b	56.9 a	46.0 a
Isotomidae	0.3268	**8.82E-15**	*0.0643*	98.0	85.8	45.8 b	207.4 a	57.4 b
Sminthuridae	0.7914	**6.42E-08**	0.7189	4.0	4.2	1.5 b	2.6 b	10.5 a
Astig_5_OO	0.6354	**7.08E-12**	0.9749	88.5	83.1	41.9 c	167.5 a	70.2 b
Oribatid_2_T	0.3831	0.7711	0.4597	4.3	5.4	5.1	4.3	5.2
Oribatid_2_S	**0.0171**	**1.18E-07**	0.2194	8.5 A	4.6 B	11.6 a	9.5 a	1.2 b
Oribatid_3	0.9443	**0.0129**	0.5045	74.0	73.1	57.9 b	63.0 b	103.8 a
Oribatid_5	*0.0624*	0.2439	0.7606	0.6	0.1	0.6	0.1	0.4
Prostig_1	0.0894	0.4647	0.4647	0.0	0.0	0.0	0.0	0.0
Prostig_2	0.6201	**0.0008**	0.3738	39.7	37.4	27.6 b	50.2 a	39.5 ab
Prostig_3	0.6390	**0.0002**	0.2655	173.9	184.7	231.4 a	201.3 a	115.8 b
Prostig_4	0.2265	0.4077	0.9571	0.0	0.2	0.2	0.1	0.0
Prostig_5	0.5631	0.3520	*0.0894*	0.0	0.0	0.0	0.0	0.0
Prostig 6	0.2348	0.5551	0.1466	0.0	0.0	0.0	0.0	0.0
Oribatid_6_OA	0.4843	**0.0292**	0.9795	0.5	0.3	0.7 a	0.7 a	0.1 b
Oribatid_7_OA	*0.0597*	0.1331	0.1645	15.9	21.0	22.4	16.9	16.1
Astig_3	0.9072	0.2983	0.4465	0.5	0.4	0.2	0.7	0.5
Hypopi	0.7077	**0.0005**	0.9573	9.5	8.4	2.7 b	16.0 a	11.3 a
Astig_4	0.3211	0.3735	0.3736	0.0	0.0	0.0	0.0	0.0
Mesostig_1	0.3386	**1.03E-05**	0.4428	39.6	44.8	30.2 b	63.8 a	35.9 b
Mesostig_2	0.9898	0.5941	0.2151	0.0	0.0	0.0	0.0	0.0
Carabid Larvae	0.2704	0.2192	0.1912	2.4	3.2	2.6	2.2	3.7
Larva_1	0.3291	0.4725	0.2321	0.1	0.3	0.4	0.1	0.2
Larva_2	0.4760	0.9059	0.2056	0.7	0.5	0.6	0.5	0.7
Catapillar	0.8987	0.2090	0.4636	0.2	0.2	0.5	0.1	0.1
Enchytraid	0.1307	0.1448	0.2099	0.4	1.0	1.0	0.9	0.2
Staphinalid_Beetle	0.1929	0.6555	0.7754	0.0	0.1	0.0	0.1	0.1
Spider	0.2466	**0.0090**	0.9979	0.1	0.0	0.0 b	0.0 b	0.2 a
Thrips	**0.0427**	*0.0617*	0.8099	1.1 A	0.4 B	1.4	0.3	0.7
Chilopoda	0.9262	0.5429	0.4021	0.1	0.1	0.1	0.0	0.1
Small_Beetle	0.8665	0.3263	0.5305	0.2	0.3	0.3	0.5	0.1
Aphid	0.7941	*0.0842*	0.3154	0.1	0.1	0.2	0.0	0.0
Tiny_Wasp	0.9449	0.9788	0.3783	0.1	0.1	0.1	0.1	0.1
Pauropoda	*0.0866*	0.9456	0.5619	0.0	0.2	0.1	0.1	0.1

Table B.3. September 2020 Microarthropod taxa ANOVAs

	P-Values			Main Effect Means: Crop		Main Effect Means: Management System		
Metrics	Crop	Management System	Interaction	Dry Bean	Soybean	No Rye - plowed	Rye - plowed	Rye - No till
Onychuridae	**1.40E-05**	**0.0021**	0.1745	40.0 A	16.2 B	15.6 b	36.8 a	30.5 a
Entomobryidae	**9.00E-06**	0.2862	0.1914	27.8 A	11.5 B	17.0	22.8	16.8
Isotomidae	**3.21E-05**	**0.0350**	0.5513	14.0 A	4.5 B	5.4 b	12.1 a	9.0 ab
Sminthuridae	**0.0007**	**0.0081**	0.3593	0.8 A	0.0 B	0.9 a	0.0 b	0.3 ab
Astig_5_OO	0.7385	0.5075	**0.0417**	256.7	245.6	279.1	234.7	240.7
Oribatid_2_T	**0.0005**	**0.0417**	**0.0486**	21.8 A	11.1 B	13.1 b	13.7 ab	21.8 a
Oribatid_2_S	**0.0027**	**0.0030**	0.1085	10.0 A	3.4 B	10.0 a	8.4 a	2.1 b
Oribatid_3	**6.84E-06**	0.8416	0.6936	133.3 A	77.0 B	107.1	98.9	103.6
Oribatid_4	0.3211	0.3736	0.3736	0.0	0.0	0.0	0.0	0.0
Oribatid 5	0.1122	**0.0009**	0.6894	3.4	1.3	4.3 a	0.1 b	4.5 a
Prostig_1	0.1474	0.2564	0.4290	0.1	0.3	0.3	0.3	0.1
Prostig_2	0.1369	*0.0661*	0.4468	63.1	51.1	48.8	52.1	70.9
Prostig_3	**0.0018**	0.3157	**0.0113**	146.1 A	94.6 B	134.1	119.2	104.4
Prostig_5	0.5344	0.5108	0.7888	0.0	0.0	0.1	0.0	0.0
Oribatid_6_OA	0.1544	**0.0026**	0.2982	0.2	0.0	0.0 b	0.0 b	0.5 a
Oribatid_7_OA	**0.0005**	**0.0003**	*0.0791*	26.1 A	13.8 B	13.8 b	15.6 b	30.9 a
Astig_3	**3.79E-06**	**1.27E-05**	**0.0009**	2.2 A	0.0 B	0.1 b	3.1 a	0.2 b
Hypopi	**0.0190**	**7.56E-06**	0.2964	13.6 A	6.0 B	2.6 b	7.3 b	24.0 a
Astig_4	0.3211	0.3736	0.3736	0.0	0.0	0.0	0.0	0.0
Mesostig_1	**0.0006**	0.7362	0.8244	42.3 A	25.4 B	30.8	34.3	34.9
Mesostig_2	**0.0460**	**0.0434**	*0.0671*	0.0 B	0.1 A	0.0 b	0.0 b	0.2 a
Carabid Larvae	**0.0001**	0.5579	0.6545	1.9 A	0.2 B	1.2	0.8	0.6
Larva_2	**0.0003**	**0.0280**	0.2358	1.9 A	0.2 B	1.6 a	0.2 b	1.1 ab
Catapillar	**0.0038**	**0.0279**	0.6741	3.5 A	1.1 B	3.5 a	2.3 ab	0.9 b
Enchytraid	0.1720	**0.0001**	0.6621	0.3	0.1	0.0 b	0.1 b	0.8 a
Staphinalid_Beetle	0.1134	0.8453	0.4250	0.2	0.5	0.4	0.3	0.2
Ant	0.2897	*0.0845*	0.1298	0.0	0.1	0.0	0.2	0.0
Diplura	0.3211	0.3736	0.3736	0.0	0.0	0.0	0.0	0.0
Spider	0.9819	0.8202	0.7403	0.3	0.3	0.2	0.4	0.3
Thrips	0.8948	0.9572	0.2993	0.6	0.5	0.6	0.5	0.5
Chilopoda	**0.0163**	*0.0895*	0.1213	0.2 A	0.0 B	0.0	0.3	0.0
Small_Beetle	0.1334	0.9306	0.7223	0.5	1.2	0.9	0.8	0.7
Aphid	**0.0093**	**0.0063**	0.9002	1.3 B	5.1 A	5.3 a	0.6 b	4.2 a
Pauropoda	0.7184	0.3119	**0.0434**	0.0	0.0	0.0	0.0	0.0
Hemiptera	0.9975	0.7531	0.1133	0.2	0.2	0.2	0.3	0.2
Large_Beetle	0.8391	0.4414	0.5040	0.2	0.1	0.1	0.1	0.3

Appendix C. Table with details of each SEM model for all dates/years

Table C.1. June 2019

		Model Indicators					Coefficients								Individual R-squared		
Management System	**Microarthropod Grouping**	**AIC**	**BIC**	**Fisher's C**	**P-value**	**DF**	**Response**	**Predictor**	**Estimate**	**Std. Error**	**DF**	**Crit. Value**	**P-value**	**Std. Estimate**	**Response**	**Marginal**	**Conditional**
No Rye - Plowed	Total	20.28	28.01	0.288	0.866	2	Total Berry Weight	microbial biomass C:N	-74.08	32.02	11	-2.31	0.0411	-0.53	Total Berry Weight	0.26	0.26
							Total Microarthropods	microbial biomass C:N	-7.03	2.4	11	-2.93	0.0138	-0.64	Total Microarthropods	0.4	0.49
	Order	59.05	75.28	17.05	0.76	22	Total Berry Weight	PHOS	174.97	57.61	10	3.04	0.0125	0.77	Total Berry Weight	0.31	0.63
								mesostigmatid mites	7.94	6.58	10	1.21	0.2556	0.28			
							Mesostigmatid Mites	microbial biomass C:N	-4.04	1.09	7	-3.68	0.0079	-0.79	Mesostigmatid Mites	0.67	0.79
								PHOS	-5.12	4.52	7	-3.37	0.0119	-0.63			
								BG	0.04	0.02	7	2.08	0.0758	0.35			
								soil C:N	-40.17	15.94	7	-2.51	0.0398	-0.37			
								Soil C	-14.89	6.76	7	-2.2	0.0635	-0.57			
							PHOS	Collembola	-0.06	0.02	10	-2.95	0.0145	-0.57	PHOS	0.29	0.69
								Astigmatid Mites	0.06	0.02	10	3.13	0.0107	0.65			
							Astigmatid Mites	Collembola	0.54	-	14	2.38	0.032	0.54			
							PHOS	microbial biomass C:N	-0.31	-	16	-1.18	0.1286	-0.31			
	Family	43.17	57.85	5.167	0.88	10	Total Berry Weight	microbial biomass C:N	-57.65	25.66	8	-2.25	0.0549	-0.41	Total Berry Weight	0.67	0.67
								soil C:N	-1456.48	594.67	8	-2.25	0.4	-0.48			
								soil C	303.32	161.96	8	1.87	0.098	0.41			
								Oribatid 2-T	-23.38	5.46	8	-4.28	0.0027	-0.98			
							Oribatid 2-T	soil C:N	-64.91	24.89	10	-2.61	0.0261	-0.51	Oribatid 2-T	0.48	0.48
								soil C	15.02	5.95	10	2.52	0.0302	0.49			
							Microbial biomass C:N	Oribatid 7-OA	-0.06	0.02	11	-3.77	0.0031	-0.73	Microbial Biomass C:N	0.54	0.63
Rye - Plowed	Total	28.96	38.24	4.96	0.548	6	Total Berry Weight	soil C:N	-1657.73	229.41	10	-7.23	0.00001	-1.51	Total Berry Weight	0.47	0.93
								soil C	539.69	138.38	10	3.9	0.003	1.07			
							Total Microarthropods	BG	-0.06	0.03	10	-2.08	0.0644	-0.61	Total Microarthropods	0.24	0.47
								soil C	20.46	10.6	10	1.93	0.0824	0.63			
	Order	53.25	67.93	15.25	0.645	18	Total Berry Weight	microbial biomass C:N	-74.34	26.92	9	-2.76	0.0221	-0.47	Total Berry Weight	0.65	0.85
								soil C:N	-1042.55	140.92	9	-7.39	0.00001	-0.95			
								Prostigmatid Mites	10.88	6.14	9	1.77	0.1103	0.2			
							Prostigmatid Mites	PHOS	1.15	0.89	11	1.28	0.2257	0.32	Prostigmatid Mites	0.1	0.1
							Soil C:N	Astigmatid Mites	0.01	0.006	9	1.97	0.0809	0.6	Soil C:N	0.33	0.34
								Oribatid Mites	0.01	0.005	9	1.39	0.1963	0.4			
								Mesostigmatid	-0.02	0.01	9	-2.37	0.0417	-0.77			

							Mesostigmatid Mites	Mites										
							Mesostigmatid Mites	Oribatid Mites	0.58	-	14	2.65	0.019	0.58				
							Prostigmatid Mites	Astigmatid Mites	0.66	-	14	3.31	0.0052	0.66				
							Prostigmatid Mites	soil C:N	0.46	-	16	1.02	0.1624	0.27				
	Family	32.48	44.85	0.484	0.975	4	Total Berry Weight	microbial biomass C:N	-63.98	16.13	6	-3.97	0.0074	-0.4	Total Berry Weight	0.92	0.92	
								BG	-0.25	0.15	6	-1.68	0.1436	-0.15				
								PHOS	30.87	18.12	6	1.7	0.1394	0.16				
								soil C:N	-1074.61	99.47	6	-10.8	0.00001	-0.98				
								Isotomidae	-14.11	2.06	6	-6.84	0.0005	-0.61				
								Astig 5-OO	8.5	2	6	4.25	0.0054	0.35				
							Isotomidae	microbial biomass C:N	-3.22	1.83	10	-1.76	0.1089	-0.47	Isotomidae	0.27	0.81	
								BG	-0.04	0.01	10	-3.29	0.008	-0.69				
							Astig 5-OO	Isotomidae	0.49	-	16	2.01	0.033	0.49				
Rye - No Till	Total	39.34	51.7	7.335	0.119	4	Total Berry Weight	microbial biomass C:N	42.33	31.03	10	1.36	0.2025	0.2	Total Berry Weight	0.72	0.72	
								BG	1.58	0.26	10	6.18	0.0001	0.91				
							BG	Total Microarthropods	3.12	1.71	11	1.82	0.0963	0.36	BG	0.13	0.62	
							Microbial biomass C:N	Total Microarthropods	-0.03	0.02	11	-1.82	0.0969	-0.44	Microbial Biomass C:N	0.18	0.23	
							BG	PHOS	0.6	-	16	2.69	0.0092	0.6				
	Order	57.7	77.79	5.703	0.997	18	Total Berry Weight	BG	1.03	0.25	8	4.18	0.0031	0.59	Total Berry Weight	0.81	0.81	
								Astigmatid Mites	13.63	4.52	8	3.01	0.0167	0.49				
								Prostigmatid Mites	-12.66	5.61	8	-2.26	0.054	-0.37				
								mesostigmatid mites	9.27	4.92	8	1.88	0.0963	0.24				
							Astigmatid Mites	microbial biomass C:N	-3.56	2.19	9	-1.62	0.1388	-0.47	Astigmatid Mites	0.39	0.72	
								PHOS	13.36	4.51	9	3.08	0.0132	1.49				
								Soil C	-23.07	13.25	9	-1.74	0.1157	-1.07				
							Prostigmatid Mites	microbial biomass C:N	-3.68	1.5	11	-2.45	0.0322	-0.6	Prostigmatid Mites	0.27	0.47	
							BG	Astigmatid Mites	8.42	2.52	10	3.34	0.0075	0.52	BG	0.17	0.78	
								Prostigmatid Mites	-6.15	3.2	10	-1.92	0.084	-0.31				
							Prostigmatid Mites	Astigmatid Mites	0.6	-	16	2.74	0.0085	0.6				
							BG	PHOS	0.42	-	16	1.69	0.0575	0.42				
							BG	Soil C	0.29	-	16	1.11	0.1444	0.29				
							BG	Soil C:N	-0.24	-	16	-0.89	0.1948	-0.24				
	Family	49.7	66.7	5.712	0.839	10	Total Berry Weight	microbial biomass C:N	84.51	43.12	7	1.96	0.0908	0.4	Total Berry Weight	0.68	0.81	
								PHOS	195.6	82.05	7	2.38	0.0486	0.75				
								Soil C	-154.04	250.84	7	-0.61	0.5586	-0.26				
								Isotomidae	9.22	7.54	7	1.22	0.261	0.22				
								Oribatid 7-OA	8.36	3.27	7	2.56	0.0376	0.58				

Isotomidae	microbial biomass C:N	-3.05	0.98	9	-3.11	0.0124	-0.6	Isotomidae	0.4	0.91
	BG	0.04	0.01	9	3.3	0.0093	0.97			
Oribatid 7-OA	Soil C	-23.76	6.18	9	-3.85	0.0039	-1.64	Oribatid 7-OA	0.42	0.75
	microbial biomass C:N	-5.2	2.39	10	-2.18	0.054	-0.36			
	PHOS	8.38	3.62	10	2.31	0.0432	0.46			
Astig 5-OO	Isotomidae	-0.09	-	16	-0.35	0.3651	-0.1			
Oribatid 7-OA	Astig 5-OO	0.27	-	16	1.02	0.1641	0.27			
Oribatid 7-OA	Oribatid 2-T	0.41	-	16	1.63	0.0635	0.41			
Oribatid 2-T	Isotomidae	-0.49	-	16	-2.01	0.0328	-0.49			

Table C.2. September 2019

Management System	Microarthropod Grouping	Model Indicators: AIC	BIC	Fisher's C	P-value	DF	Coefficients: Response	Predictor	Estimate	Std. Error	DF	Crit. Value	P-value	Std. Estimate	Individual R-squared: Response	Marginal	Conditional
No Rye - Plowed	Total	78.91	103.64	14.914	0.923	24	Total Berry Weight	PHOS	-178.94	41.88	5	-4.27	0.0079	-0.98	Total Berry Weight	0.6	0.96
								Microbial Biomass N	-15.94	2.42	5	-6.59	0.0012	-0.72			
								BG	-13.94	1.54	5	-9.05	0.0003	-0.86			
								Soil C:N	-1762.72	295.73	5	-5.96	0.0019	-1.02			
								Total Microarthropods	-3.12	0.84	5	-3.72	0.0137	-0.47			
								Other Monocot Weeds	17.53	5.01	5	3.50	0.0174	0.29			
								Volunteer Rye	-80.33	31.9	5	-2.52	0.0533	-0.24			
							Total Microarthropods	PHOS	-19.88	6.97	10	-2.85	0.0172	-0.72	Total Microarthropods	0.26	0.86
								BG	-0.85	0.45	10	-1.87	0.0903	-0.34			
							Other Monocot Weeds	Soil C:N	-14.35	6.6	11	-2.17	0.0526	-0.50	Other Monocot Weeds	0.24	0.24
							Volunteer Rye	Total Microarthropods	0.01	0.05	11	2.31	0.0411	0.53	Volunteer Rye	0.26	0.26
							Soil C:N	Total Microarthropods	0.002	0.0008	11	1.93	0.0801	0.41	Soil C:N	0.1	0.72
							Soil C:N	PHOS	-0.44	-	16	-1.75	0.0518	-0.44			
	Order	44.84	61.07	2.844	0.985	10	Total Berry Weight	PHOS	-119.82	41.84	6	-2.86	0.0287	-0.66	Total Berry Weight	0.8	0.85
								Microbial Biomass N	-12.9	3.21	6	-4.02	0.007	-0.58			
								BG	-12.73	2.12	6	-6.00	0.001	-0.78			
								Soil C:N	-1581.91	358.26	6	-4.42	0.0045	-0.91			
								Prostigmatid Mites	-4.29	1.76	6	-2.44	0.0508	-0.32			
								Mesostigmatid Mites	-11	2.67	6	-4.11	0.0063	-0.57			
							Prostigmatid Mites	PHOS	-10.8	3.54	10	-3.05	0.0122	-0.80	Prostigmatid Mites	0.36	0.84
								BG	-0.51	0.23	10	-2.20	0.0526	-0.42			
							Soil C:N	Prostigmatid Mites	0.004	0.001	11	2.80	0.0174	0.49	Soil C:N	0.16	0.75
							Soil C:N	PHOS	-0.38	-	16	-1.50	0.0789	-0.38			
	Family	81.08	106.58	15.081	0.978	28	Total Berry Weight	PHOS	-82.01	25.51	4	-3.21	0.0324	-0.45	Total Berry Weight	0.66	0.99
								BG	-14.49	0.85	4	-17.03	0.0001	-0.89			
								Soil C:N	-1608.69	221.55	4	-7.26	0.0019	-0.93			
								Prostig 2	-14.82	1.64	4	-9.04	0.0008	-0.99			
								Oribatid 2-S	4.08	1.12	4	3.64	0.0219	0.18			
								Other Broadleaf Weeds	-28.06	5.88	4	-4.77	0.0088	-0.32			
								Volunteer Rye	150.17	29.88	4	5.03	0.0074	0.45			
								Root Rot Rating	39.76	4.64	4	8.57	0.001	0.89			
							Prostig 2	PHOS	-10.01	3.41	11	-2.94	0.0135	-0.82	Prostig 2	0.26	0.8
							Other Broadleaf Weeds	Soil C:N	13.93	4.92	11	2.83	0.0163	0.71	Other Broadleaf Weeds	0.35	0.58
							Volunteer Rye	Prostig 2	0.04	0.01	10	4.98	0.0006	0.79	Volunteer Rye	0.64	0.64

								PHOS	0.17	0.09	10	1.97	0.0775	0.31				
							Soil C:N	Prostig 2	0.00	0.00	11	2.51	0.0291	0.47	Soil C:N	0.13	0.76
							Volunteer Rye	Root Rot Rating	-0.50	-	16	-2.07	0.0297	-0.50			
							Soil C:N	PHOS	-0.39	-	16	-1.50	0.0781	-0.39			
							Soil C:N	Root Rot Rating	0.40	-	16	1.57	0.0701	0.40			
Rye - Plowed	Total	39.77	53.68	3.768	0.708	6	Total Berry Weight	PHOS	231.86	17.54	5	13.22	0.00001	1.06	Total Berry Weight	0.97	0.97
								Microbial Biomass N	6. 8	2.56	5	2.65	0.0452	0.20			
								BG	-18.78	2.07	5	-9.07	0.0003	-0.75			
								NETPEROX	-76.31	21.22	5	-3.60	0.0156	-0.31			
								Soil C:N	-454.98	126.63	5	-3.59	0.0157	-0.30			
								Volunteer Rye	59.64	10.51	5	5.68	0.0024	0.33			
								Root Rot Rating	-23.38	4.38	5	5.34	0.0031	-0.41			
							Volunteer Rye	PHOS	-0.35	0.34	5	-1.04	0.3262	-0.30	Volunteer Rye	0.21	0.21
								Microbial Biomass N	-0.06	0.05	5	-1.14	0.2823	-0.34			
								BG	0.08	0.04	5	1.99	0.0774	0.61			
							Soil C:N	Microbial Biomass N	0.48	-	14	2.05	0.0597	0.48			
							Soil C:N	Root Rot Rating	0.71	-	14	3.72	0.0023	0.71			
	Order	55.72	75.8	3.717	0.715	6	Total Berry Weight	PHOS	205.51	20.26	5	10.15	0.0002	0.94	Total Berry Weight	0.95	0.95
								Microbial Biomass N	8.34	3.91	5	2.13	0.0861	0.25			
								BG	-26.45	3.94	5	-6.71	0.0011	-1.06			
								Soil C:N	-381.13	172.15	5	2.21	0.0777	-0.25			
								Oribatid Mites	4.01	2.36	5	1.70	0.1494	0.16			
								Volunteer Rye	58.50	14.92	5	3.92	0.0112	0.32			
								Root Rot Rating	-35.19	5.84	5	6.03	0.0018	-0.61			
							Oribatid Mites	PHOS	-8.34	2.85	10	-2.92	0.0152	-0.93	Oribatid Mites	0.49	0.86
								BG	1.16	0.25	10	4.62	0.0009	1.13			
							Volunteer Rye	Oribatid Mites	-0.06	0.04	7	-1.47	0.1841	-0.46	Volunteer Rye	0.38	0.38
								PHOS	-0.73	0.36	7	2.03	0.0818	-0.61			
								Microbial Biomass N	-0.15	0.07	7	-2.18	0.0652	-0.81			
								BG	0.17	0.06	7	2.99	0.0203	1.25			
								Soil C:N	5.72	2.91	7	1.97	0.0897	0.68			
							Oribatid Mites	Root Rot Rating	0.39	-	16	1.51	0.0769	0.39			
							Soil C:N	Microbial Biomass N	0.48	-	14	2.05	0.0597	0.48			
							Soil C:N	Root Rot Rating	0.71	-	14	3.72	0.0023	0.71			
	Family	64.3	85.93	8.301	0.761	12	Total Berry Weight	PHOS	239.11	11.03	3	21.68	0.0002	1.09	Total Berry Weight	0.99	0.99
								Microbial Biomass N	9.23	1.61	3	5.73	0.0106	0.28			
								BG	-21.93	1.23	3	-17.79	0.0004	-0.88			
								NETPEROX	-69.45	10.41	3	-6.67	0.0069	-0.28			
								Soil C:N	-492.78	60.70	3	-8.12	0.0039	-0.32			
								Carabid Beetle Larvae	-5.24	1.41	3	-3.70	0.0342	-0.09			
								Prostig 2	3.11	0.73	3	4.26	0.0237	0.16			
								Volunteer Rye	60.52	5.57	3	10.87	0.0017	0.33			
								Root Rot Rating	-32.80	2.71	3	-12.09	0.0012	-0.57			
							Prostig 2	PHOS	-11.00	4.76	10	-2.31	0.0432	-0.96	Prostig 2	0.27	0.56
								NETPEROX	9.29	4.78	10	1.94	0.0808	0.71			

							Volunteer Rye	Prostig 2	-0.04	0.03	7	-1.62	0.1502	0.42	Volunteer Rye	0.4	0.4
								PHOS	-0.74	0.35	7	-2.10	0.0739	-0.62			
								Microbial Biomass N	-0.15	0.07	7	-2.31	0.0539	-0.86			
								BG	0.14	0.05	7	3.03	0.0190	1.03			
								Soil C:N	6.08	2.92	7	2.09	0.0754	0.72			
							Prostig 2	Root Rot Rating	0.52	-	16	2.17	0.0246	0.52			
							Prostig 2	Soil C:N	0.35	-	16	1.35	0.1007	0.35			
Rye - No Till	Total	52.56	68.79	10.564	0.72	14	Total Berry Weight	PHOS	176.73	22.08	6	8.00	0.0002	0.77	Total Berry Weight	0.64	0.99
								Microbial Biomass N	-10.48	2.98	6	-3.52	0.0125	-0.26			
								BG	-10.27	1.98	6	-5.17	0.0021	-0.50			
								Other Monocot Weeds	-68.17	13.47	6	-5.06	0.0023	-1.16			
								Volunteer Rye	-213.31	20.11	6	-10.60	0.00001	-1.30			
								Root Rot Rating	135.18	22.16	6	6.10	0.0009	1.31			
							Other Monocot Weeds	PHOS	0.79	0.40	11	1.96	0.0763	0.20	Other Monocot Weeds	0.03	0.92
							Volunteer Rye	Total Microarthropods	0.03	0.01	10	2.23	0.0495	0.51	Volunteer Rye	0.34	0.41
								BG	-0.06	0.03	10	-1.97	0.0768	-0.44			
							Volunteer Rye	Root Rot Rating	0.26	-	16	0.99	0.1709	0.26			
							Other Monocot Weeds	Root Rot Rating	-0.19	-	16	-0.69	0.2497	-0.19			
	Order	84.15	108.87	20.149	0.859	28	Total Berry Weight	PHOS	195.35	5.92	2	33.02	0.0009	0.85	Total Berry Weight	0.67	1
								BG	-17.84	0.40	2	-44.98	0.0005	-0.87			
								NETPEROX	-59.86	4.24	2	-14.11	0.005	-0.31			
								Soil C:N	-1244.02	77.99	2	-15.95	0.0039	-0.25			
								Collembola	-1.78	0.15	2	-11.99	0.0069	-0.20			
								Oribatid Mites	4.68	0.65	2	7.20	0.0187	0.16			
								Astigmatid Mites	4.68	0.2197	2	21.31	0.0022	0.27			
								Other Monocot Weeds	-58.86	2.65	2	-22.22	0.002	-1.00			
								Volunteer Rye	-226.51	4.95	2	-45.74	0.0005	-1.38			
								Root Rot Rating	118.60	7.99	2	14.85	0.0045	1.15			
							Oribatid Mites	NETPEROX	3.74	1.87	10	2.00	0.0728	0.55	Oribatid Mites	0.23	0.62
								Soil C:N	92.74	44.37	10	2.09	0.0631	0.52			
							Other Monocot Weeds	Oribatid Mites	-0.08	0.04	10	-1.91	0.0852	-0.17	Other Monocot Weeds	0.05	0.93
								PHOS	1.04	0.39	10	2.67	0.0235	0.27			
							Volunteer Rye	Oribatid Mites	0.10	0.03	10	3.22	0.0092	0.59	Volunteer Rye	0.39	0.61
								BG	-0.07	0.03	10	-2.65	0.0242	-0.53			
							Other Monocot Weeds	Root Rot Rating	-0.03	-	16	-0.12	0.4545	-0.03			
							Astigmatid Mites	Collembola	0.36	-	14	1.46	0.1653	0.36			
							Oribatid Mites	Root Rot Rating	0.12	-	16	0.44	0.3339	0.12			
							Oribatid Mites	Astigmatid Mites	0.40	-	16	1.60	0.0672	0.40			

						Volunteer Rye	Collembola	0.32	-	16	1.21	0.1244	0.32				
Family	123.14	159.45	29.141	0.898	40	Total Berry Weight	PHOS	61.00	17.63	2	3.46	0.0743	0.27	Total Berry Weight	0.91	0.97	
							Microbial Biomass N	-24.40	4.16	2	-5.87	0.0278	-0.61				
							NETPEROX	139.86	17.94	2	7.80	0.0161	0.72				
							Soil C:N	3009.46	598.63	2	5.03	0.0374	0.60				
							Prostig 2	14.13	3.37	2	4.20	0.0523	0.80				
							Oribatid 2-S	18.67	4.30	2	4.34	0.0492	0.69				
							Mesostig 1	-15.38	2.74	2	-5.61	0.0303	-0.86				
							Other Broadleaf Weeds	-79.46	15.88	2	-5.00	0.0377	-0.81				
							Other Monocot Weeds	-81.33	10.60	2	-7.67	0.0166	-1.39				
							Volunteer Rye	-81.89	15.58	2	-5.26	0.0343	-0.50				
						Oribatid 2-S	Soil C:N	95.81	36.62	11	2.62	0.024	0.51	Oribatid 2-S	0.22	0.58	
						Mesostig 1	Soil C:N	112.24	57.39	11	1.96	0.0764	0.40	Mesostig 1	0.15	0.5	
						Other Broadleaf Weeds	Prostig 2	0.13	0.04	7	3.79	0.0068	0.75	Other Broadleaf Weeds	0.43	0.76	
							Oribatid 2-S	0.17	0.08	7	2.13	0.0712	0.61				
							Mesostig 1	-0.07	0.05	7	-1.28	0.2411	-0.38				
							NETPEROX	0.89	0.42	7	2.13	0.0707	0.45				
							Soil C:N	18.86	11.79	7	1.60	0.1537	0.37				
						Other Monocot Weeds	Prostig 2	0.07	0.03	7	2.46	0.0432	0.22	Other Monocot Weeds	0.06	0.95	
							Oribatid 2-S	0.09	0.06	7	1.53	0.1694	0.19				
							Mesostig 1	-0.10	0.04	7	-2.30	0.0552	-0.34				
							PHOS	0.84	0.40	7	2.11	0.0726	0.22				
							NETPEROX	-0.50	0.31	7	-1.63	0.1464	-0.15				
						Volunteer Rye	Oribatid 2-S	0.08	0.04	11	2.01	0.0691	0.47	Volunteer Rye	0.21	0.21	
						Other Broadleaf Weeds	Prostig 2	0.65	-	16	3.05	0.0046	0.65				
						Mesostig 1	Oribatid 2-S	0.35	-	16	1.34	0.1018	0.35				
						Volunteer Rye	Other Broadleaf Weeds	0.64	-	16	3.04	0.0048	0.64				

Table C.3. June 2020

		Model Indicators					Coefficients							Individual R-squared		
Management System	**Microarthropod Grouping**	**AIC**	**BIC**	**Fisher's C**	**P-value**	**DF**	**Response**	**Predictor**	**Estimate**	**Std. Error**	**DF**	**Crit. Value**	**P-value**	**Std. Estimate**	**Response**	**Marginal**	**Conditional**
No Rye - Plowed	Total	29.05	39.87	1.054	0.591	2	Total Berry Weight	BG	-1.62	0.47	9	-3.46	0.0072	-1.15	Total Berry Weight	0.48	0.49
								LAP	0.58	0.28	9	2.06	0.0699	0.75			
								Total Microarthropods	0.03	0.01	9	2.19	0.0562	0.61			
							Total Microarthropods	NAG	-25.01	11.65	9	-2.15	0.0604	-1.14	Total Microarthropods	0.58	0.58
								BG	63.01	19.47	9	3.24	0.0102	1.88			
								LAP	-19.03	4.36	9	-4.37	0.0018	-1.03			
	Order	57.98	76.52	9.981	0.764	14	Total Berry Weight	Collembola	0.05	0.01	5	6.65	0.0012	0.41	Total Berry Weight	0.53	0.99
								Astigmatid Mites	0.02	0.00	5	5.26	0.0033	0.26			
								Prostigmatid Mites	-0.05	0.01	5	-6.27	0.0015	-0.33			
								Mesostigmatid Mites	0.14	0.01	5	12.29	0.0001	0.89			
								Microbial Biomass C:N	1.42	0.10	5	13.5702	0.00001	1.02			
								BG	-3.15	0.19	5	-17.00	0.00001	-2.24			
								LAP	0.71	0.10	5	7.41	0.0007	0.91			
							Prostigmatid Mites	NAG	-10.30	4.24	10	-2.43	0.0354	-1.55	Prostigmatid Mites	0.25	0.43
								BG	13.38	6.56	10	2.04	0.0687	1.33			
							Mesostigmatid Mites	NAG	-7.64	3.26	9	-2.35	0.0436	-1.31	Mesostigmatid Mites	0.52	0.59
								BG	18.43	5.64	9	3.26	0.0098	2.08			
								LAP	-4.73	1.45	9	-3.25	0.0099	-0.96			
							Mesostigmatid Mites	Oribatid Mites	0.45	-	16	1.81	0.0468	0.45			
							Collembola	Oribatid Mites	0.77	-	14	4.55	0.0005	0.77			
							Mesostigmatid Mites	Microbial Biomass C:N	-0.36	-	16	-1.40	0.0924	-0.36			
							Prostigmatid Mites	LAP	-0.28	-	16	-1.06	0.1536	-0.28			
	Family	82.59	112.71	4.578	0.599	6	Total Berry Weight	Microbial Biomass C:N	1.26	0.05	4	26.50	0.00001	0.91	Total Berry Weight	0.54	1
								NAG	1.41	0.08	4	17.26	0.0001	1.52			
								BG	-5.43	0.17	4	-31.42	0.00001	-3.86			
								LAP	1.00	0.05	4	19.86	0.00001	1.29			
								PHOS	0.12	0.04	4	3.35	0.0287	0.12			
								Onychuridae	0.08	0.00	4	20.07	0.00001	0.49			
								Oribatid 2-T	0.10	0.01	4	8.44	0.0011	0.23			
								Mesostig 1	0.19	0.01	4	33.89	0.00001	1.23			
							Onychuridae	Microbial Biomass C:N	2.51	3.04	7	0.82	0.4367	0.30	Onychuridae	0.31	0.31
								NAG	-5.45	4.31	7	-1.27	0.2462	-0.97			
								BG	13.45	7.99	7	1.68	0.1363	1.57			
								LAP	-3.02	2.38	7	-1.27	0.2448	-0.64			

								PHOS	-2.73	2.56	7	-1.07	0. 3218	-0.44			
							Oribatid 2-T	Microbial Biomass C:N	0.91	1.21	7	0.75	0.4781	0.28	Oribatid 2-T	0.27	0.41
								NAG	-3.69	1.65	7	-2.23	0.0606	-1.69			
								BG	2.89	3.16	7	0.91	0.3908	0.87			
								LAP	0.69	0.97		0.71	0.499	0.37			
								PHOS	0.54	1.02	7	0.53	0.6149	0.23			
							Mesostig 1	Microbial Biomass C:N	-4.02	2.16	7	-1.86	0.1046	-0.46	Mesostig 1	0.61	0.68
								NAG	-7.96	2.95	7	-2.70	0.0306	-1.37			
								BG	19.99	5.62	7	3.56	0.0093	2.26			
								LAP	-5.43	1.72	7	-3.16	0.016	-1.11			
								PHOS	1.78	1.82	7	0.98	0. 3585	0.28			
Rye - Plowed	Total	42.76	56.67	6.759	0.873	12	Total Berry Weight	NAG	-1.93	0.79	8	-2.45	0.0399	-1.47	Total Berry Weight	0.37	0.37
								BG	3.32	1.32	8	2.52	0.0358	1.33			
								LAP	-1.10	0.58	8	-1.91	0.0926	-0.63			
								Total Microarthropods	-0.30	0.01	8	-2.19	0.0606	-0.54			
							Total Microarthropods	LAP	-8.62	8.09	11	-1.07	0.3092	-0.27	Total Microarthropods	0.07	0.07
							PHOS	Total Microarthropods	-0.02	0.01	11	-2.26	0.0453	-0.33	PHOS	0.09	0.75
	Order	35.37	46.19	7.374	0.832	12	Total Berry Weight	Oribatid Mites	-0.04	0.02	7	-2.43	0.0453	-0.71	Total Berry Weight	0.35	0.43
								Mesostigmatid Mites	0.06	0.05	7	1.23	0.2574	0.38			
								NAG	-1.23	0.80	7	-1.54	0.1676	-0.93			
								BG	1.69	1.42	7	1.19	0.2741	0.68			
								LAP	-0.71	0.59	7	-1.21	0.265	-0.41			
							PHOS	Prostigmatid Mites	-0.05	0.02	11	3.17	0.009	-0.45	PHOS	0.22	0.72
							PHOS	LAP	0.17	-	16	0.62	0.2725	0.17			
							Mesostigmatid Mites	Oribatid Mites	0.57	-	14	2.58	0.0217	0.57			
	Family	38.69	51.05	6.688	0.153	4	Total Berry Weight	NAG	-2.89	1.22	6	-2.37	0.0552	-2.19	Total Berry Weight	0.36	0.36
								BG	5.46	2.20	6	2.48	0.0477	2.19			
								LAP	-1.26	0.86	6	-1.46	0.1944	-0.72			
								Onychuridae	-0.18	0.11	6	-1.62	0.1572	-0.58			
								Oribatid 2-T	-0.50	0.38	6	-1.34	0.2293	-0.56			
								Hypopi	-0.13	0.08	6	-1.66	0.1479	-0.50			
							Oribatid 2-T	NAG	-1.40	0.74	10	-1.90	0. 0865	-0.95	Oribatid 2-T	0.27	0.61
								BG	3.57	1.44	10	2.49	0. 0321	1.28			
							Oribatid 2-T	Onychuridae	-0.49	-	16	2.00	0.0332	-0.49			
Rye - No Till	Total	29.89	39.16	5.888	0.825	10	Total Berry Weight	BG	-3.83	1.15	9	-3.33	0.0088	-0.86	Total Berry Weight	0.46	0.46
								LAP	0.74	0.54	9	1.37	0.2028	0.32			
								PHOS	0.85	0.58	9	1.46	0.1788	0.42			
							Total Microarthropods	Microbial Biomass C:N	-12.66	4.54	11	-2.79	0.0176	-0.61	Total Microarthropods	0.34	0.41
	Order	70.63	91.49	16.633	0.995	34	Total Berry Weight	Oribatid Mites	0.03	0.02	8	1.01	0. 3421	0.30	Total Berry Weight	0.45	0.49
								Prostigmatid Mites	-0.05	0.03	8	-1.45	0.1859	-0.47			
								BG	-4.22	1.50	8	-2.82	0.0224	-0.94			
								PHOS	1.00	0.67	8	1.50	0.171	0.50			
							Oribatid Mites	Microbial Biomass C:N	-11.58	3.36	11	-3.45	0.005	-0.68	Oribatid Mites	0.44	0.44
							Prostigmatid	Microbial	-6.91	1.79	8	-3.86	0.0048	-0.49	Prostigmatid	0.78	0.78

						Mites	Biomass C:N							Mites				
							NAG	-21.23	5.12	8	-4.15	0.0032	-0.70					
							LAP	-15.92	3.26	8	-4.89	0.0012	-0.71					
							PHOS	7.04	3.39	8	2.08	0.0714	0.36					
						NAG	Collembola	-0.02	0.01	10	-3.78	0.0036	-0.29	NAG	0.12	0.94		
							Astigmatid Mites	0.01	0.00	10	4.05	0.0023	0.34					
						Prostigmatid Mites	Oribatid Mites	0.59	-	16	2.62	0.0106	0.59					
						Oribatid Mites	Collembola	0.43	-	16	1.70	0.0562	0.43					
Family	48.3	62.98	10.302	0.414	10	Total Berry Weight	NAG	1.48	0.62	4	2.36	0.0773	0.48	Total Berry Weight	0.85	0.87		
							BG	-5.76	0.99	4	-5.81	0.0044	-1.29					
							LAP	2.43	0.44	4	5.51	0.0053	1.06					
							PHOS	1.31	0.35	4	3.76	0.0198	0.65					
							Onychuridae	-0.11	0.03	4	-3.29	0.0302	-0.39					
							Oribatid 2-T	-0.32	0.11	4	-2.83	0.0475	-0.46					
							Hypopi	0.09	0.02	4	4.14	0.0143	0.46					
							Oribatid 6-OA	0.20	0.04	4	4.75	0.009	0.72					
						Oribatid 6-OA	Microbial Biomass C:N	-2.86	0.94	9	-3.05	0.0139	-0.56	Oribatid 6-OA	0.55	0.55		
							LAP	-4.33	1.66	9	-2.60	0.0288	-0.54					
							PHOS	-4.72	1.47	9	-3.20	0.0108	-0.67					
						Oribatid 6-OA	Oribatid 2-T	0.08	-	16	0.29	0.3869	0.08					

Table C.4. July 2020

Management System	Microarthropod Grouping	Model Indicators					Coefficients								Individual R-squared		
		AIC	BIC	Fisher's C	P-value	DF	Response	Predictor	Estimate	Std. Error	DF	Crit. Value	P-value	Std. Estimate	Response	Marginal	Conditional
No Rye - Plowed	Total	30.18	40.99	2.182	0.902	6	Total Berry Weight	Microbial Biomass C:N	-0.75	0.42	8	-1.78	0.1134	-0.52	Total Berry Weight	0.51	0.51
								Soil N	54.02	19.96	8	2.71	0.0268	2.23			
								Soil C	-8.67	3.59	8	-2.41	0.0425	-1.92			
								Total Microarthropods	0.03	0.01	8	2.60	0.0315	0.64			
							Total Microarthropods	Microbial Biomass C	-27.03	11.57	10	-2.34	0.0416	-0.51	Total Microarthropods	0.48	0.48
								Microbial Biomass C:N	28.62	7.77	10	3.68	0.0042	0.80			
							Soil C	Soil N	0.97	-	14	14.26	0.00001	0.97			
	Order	59.11	79.2	7.114	0.715	10	Total Berry Weight	Collembola	0.05	0.01	5	8.03	0.0005	1.03	Total Berry Weight	0.92	0.92
								Oribatid Mites	0.06	0.02	5	3.78	0.0129	0.53			
								Prostigmatid Mites	-0.02	0.01	5	-3.03	0.029	-0.31			
								Microbial Biomass C:N	-0.77	0.17	5	-4.47	0.0066	-0.54			
								LAP	1.22	0.22	5	5.48	0.0028	0.67			
								Soil N	106.38	10.79	5	9.86	0.0002	4.39			
								Soil C	-19.76	2.18	5	-9.05	0.0003	-4.39			
							Collembola	Microbial Biomass C	-31.99	7.77	8	-4.12	0.0034	-0.65	Collembola	0.73	0.73
								Microbial Biomass C:N	27.83	6.87	8	4.05	0.0037	0.85			
								Soil N	-775.50	312.81	8	-2.48	0.0382	-1.40			
								Soil C	135.86	56.93	8	2.39	0.0441	1.32			
							Oribatid Mites	LAP	-10.01	4.32	9	-2.31	0.0459	-0.60	Oribatid Mites	0.45	0.49
								Soil N	-512.71	199.91	9	-2.56	0.0305	-2.33			
								Soil C	118.31	38.47	9	3.08	0.0132	2.89			
							Prostigmatid Mites	Oribatid Mites	0.61	-	16	2.76	0.0081	0.61			
							Collembola	Oribatid Mites	0.57	-	16	2.49	0.0136	0.57			
	Family	140.01	178.64	40.01	0.922	54	Total Berry Weight	Microbial Biomass C	0.88	0.03	1	30.85	0.0206	0.41	Total Berry Weight	0.52	1
								Microbial Biomass C:N	-2.86	0.02	1	-169.12	0.0038	-1.99			
								LAP	1.95	0.03	1	71.69	0.0089	1.06			
								NETPEROX	2.43	0.03	1	85.63	0.0074	1.04			
								Soil N	94.30	2.05	1	46.07	0.0138	3.89			
								Soil C	-6.64	0.21	1	-32.04	0.0199	-1.48			
								Entomobryidae	0.15	0.00	1	94.73	0.0067	1.09			
								Oribatid 3	0.18	0.00	1	183.59	0.0035	1.55			
								Prostig 2	-0.26	0.00	1	-133.98	0.0048	-2.08			
								Astig 3	0.47	0.00	1	217.10	0.0029	2.07			
								Mesostig 1	0.03	0.00	1	41.81	0.0152	0.30			
							Entomobryidae	Microbial	-7.66	2.46	10	-3.11	0.011	-0.50	Entomobryidae	0.71	0.71

								Biomass C										
								Microbial Biomass C:N	9.96	1.65	10	6.02	0.0001	0.97				
							Prostig 2	Microbial Biomass C:N	5.86	2.70	11	2.18	0.0523	0.51	Prostig 2	0.26	0.54
							Mesostig 1	Microbial Biomass C	-6.32	2.66	8	-2.37	0.0451	-0.33	Mesostig 1	0.78	0.78
								Microbial Biomass C:N	7.41	2.37	8	3.12	0.0142	0.58			
								NETPEROX	-14.88	5.08	8	-2.93	0.019	-0.72			
								Soil N	-225.03	58.30	8	-3.86	0.0048	-1.05			
							Microbial Biomass C:N	Astig 3	0.09	0.03	11	3.24	0.0079	0.59	Microbial Biomass C:N	0.39	0.63
							Soil N	Astig 3	0.00	0.00	11	-2.74	0.0192	-0.22	Soil N	0.05	0.95
							Soil C	Prostig 2	0.01	0.00	10	2.37	0.0393	0.32	Soil C	0.08	0.91
								Astig 3	-0.02	0.01	10	-3.20	0.0096	-0.37			
							Prostig 2	Entomobryidae	0.51	-	16	2.14	0.0257	0.51			
							Soil C	NETPEROX	-0.28	-	16	-1.06	0.155	-0.28			
							Prostig 2	Oribatid 3	0.51	-	16	2.13	0.0264	0.51			
							Soil C	Soil N	0.67	-	16	3.23	0.0033	0.67			
							Soil C	LAP	0.38	-	16	1.48	0.0817	0.38			
							Microbial Biomass C:N	Oribatid 3	0.43	-	16	1.70	0.0565	0.43			
							Microbial Biomass C:N	Microbial Biomass C	0.34	-	16	1.30	0.1084	0.34			
Rye - Plowed	Total	51.37	69.14	5.368	0.252	4	Total Berry Weight	LAP	0.95	0.25	8	3.87	0.0048	0.46	Total Berry Weight	0.42	0.99
								Soil N	138.09	15.36	8	8.99	0.00001	4.23			
								Soil C	-14.62	2.63	8	-5.56	0.0005	-2.24			
								Total Microarthropods	0.01	0.01	8	0.93	0. 3810	0.10			
							Total Microarthropods	Soil C	-55.34	21.96	11	-2.52	0.0285	-0.56	Total Microarthropods	0.3	0.3
							LAP	Total Microarthropods	-0.01	0.01	11	-1.76	0.1056	-0.41	LAP	0.16	0.33
							Soil N	Total Microarthropods	0.00	0.00	11	-2.29	0.0426	-0.15	Soil N	0.02	0.95
							Soil N	Soil C	0.19	-	16	0.71	0.2452	0.19			
	Order	80.3	107.34	10.297	0.59	12	Total Berry Weight	Oribatid Mites	-0.06	0.02	7	-2.48	0.042	-0.32	Total Berry Weight	0.43	1
								Prostigmatid Mites	0.03	0.01	7	2.07	0.0768	0.35			
								LAP	0.79	0.23	7	3.43	0.0109	0.38			
								Soil N	137.79	12.50	7	11.02	0.00001	4.22			
								Soil C	-13.02	2.33	7	-5.58	0.0008	-2.00			
							Oribatid Mites	LAP	-6.07	3.06	11	-1.98	0.073	-0.51	Oribatid Mites	0.2	0.41
							Prostigmatid Mites	LAP	-16.01	5.86	11	-2.73	0.0195	-0.62	Prostigmatid Mites	0.3	0.56
							Mesostigmatid Mites	LAP	11.75	2.87	10	4.10	0.0021	0.88	Mesostigmatid Mites	0.31	0.95
								Soil C	-63.42	22.41	10	-2.83	0.0179	-1.50			
							Soil N	Prostigmatid Mites	0.00	0.00	11	-2.50	0.0296	-0.17	Soil N	0.03	0.95
							Soil C	Prostigmatid Mites	0.00	0. 001	11	-3.09	0.0103	-0.24	Soil C	0.06	0.93
							Prostigmatid Mites	Oribatid Mites	0.69	-	16	3.47	0.0021	0.69			
							Soil N	Soil C	0.54	-	16	2.30	0.0193	0.54			

							Soil C	Oribatid Mites	0.37	-	16	1.44	0.0865	0.37			
							Mesostigmatid Mites	Soil N	0.30	-	16	1.12	0.1415	0.30			
	Family	51.44	70.75	1.439	0.837	4	Total Berry Weight	LAP	1.13	0.26	7	4.38	0.0032	0.55	Total Berry Weight	0.41	0.99
								Soil N	148.74	18.01	7	8.26	0.0001	4.56			
								Soil C	-19.93	3.92	7	-5.09	0.0014	-3.05			
								Entomobryidae	0.04	0.02	7	1.82	0.1114	0.24			
								Astig 3	-0.07	0.05	7	-1.34	0.223	-0.23			
							Soil C	Entomobryidae	0.00	0.00	10	1.48	0.1700	0.14	Soil C	0.03	0.94
								Astig 3	-0.01	0.01	10	-2.15	0.0571	-0.24			
							Entomobryidae	LAP	-2.32	2.94	11	-0.79	0.4482	-0.21	Entomobryidae	0.04	0.04
							Astig 3	LAP	-1.71	1.87	11	-0.92	0. 3796	-0.24	Astig 3	0.05	0.16
							Astig 3	Entomobryidae	0.57	-	16	2.48	0.0139	0.57			
							Soil C	LAP	0.53	-	16	2.25	0.0213	0.53			
							Soil C	Soil N	0.26	-	16	0.97	0.1752	0.26			
Rye - No Till	Total	28.43	38.47	2.428	0.658	4	Total Berry Weight	LAP	1.42	0.35	8	4.04	0.0038	0.40	Total Berry Weight	0.71	0.95
								NETPEROX	-7.59	1.05	8	-7.23	0.0001	-1.08			
								Soil C	-0.83	0.16	8	-5.34	0.0007	-0.48			
								Total Microarthropods	-0.01	0.01	8	-1.81	0.1074	-0.17			
							Total Microarthropods	NETPEROX	36.66	19.48	11	1.88	0.0866	0.46	Total Microarthropods	0.2	0.21
	Order	47.1	63.33	5.102	0.954	12	Total Berry Weight	Astigmatid Mites	-0.09	0.03	7	-2.93	0.0221	-0.44	Total Berry Weight	0.72	0.72
								Prostigmatid Mites	-0.05	0.03	7	-1.92	0.0965	-0.32			
								Microbial Biomass C	-1.74	0.61	7	-2.86	0.0243	-0.50			
								Soil N	-28.53	6.28	7	-4.54	0.0027	-7.06			
								Soil C	11.91	2.70	7	4.42	0.0031	6.87			
							Astigmatid Mites	LAP	-10.73	4.66	9	-2.30	0.0469	-0.59	Astigmatid Mites	0.34	0.95
								Soil N	-349.24	89.01	9	-3.92	0.0035	-16.81			
								Soil C	154.25	39.46	9	3.91	0.0036	17.29			
							Microbial Biomass C	Prostigmatid Mites	-0.02	0.01	11	-1.94	0.0788	-0.37	Microbial Biomass C	0.13	0.52
							Soil C	Soil N	0.99	-	14	36.52	0.00001	0.99			
	Family	60.44	79.76	10.443	0.577	12	Total Berry Weight	Microbial Biomass C:N	-1.35	0.30	5	-4.52	0.0063	-0.42	Total Berry Weight	0.88	0.97
								NETPEROX	-4.19	0.71	5	-5.92	0.002	-0.60			
								Soil N	1.00	3.73	5	0.27	0.7986	0.25			
								Soil C	-1.43	1.65	5	-0.86	0.4278	-0.82			
								Prostig 2	-0.07	0.02	5	-3.26	0.0226	-0.27			
								Entomobryidae	-0.07	0.01	5	-5.15	0.0036	-0.36			
								Carabid Beetle Larvae	0.09	0.03	5	2.91	0.0336	0.22			
							Entomobryidae	Microbial Biomass C	18.11	7.68	8	2.36	0.046	0.97	Entomobryidae	0.51	0.51
								Microbial Biomass C:N	-23.74	7.66	8	-3.10	0.0147	-1.38			
								Soil N	125.83	44.46	8	2.83	0.0222	5.82			
								Soil C	-59.39	19.39	8	-3.06	0.0155	-6.40			
							Soil C	Prostig 2	0.08	0.04	10	1.91	0.0858	0.53	Soil C	0.25	0.35
								Carabid Beetle Larvae	0.11	0.06	10	1.80	0.1021	0.47			
							Carabid Beetle	Prostig 2	-0.41	-	14	-1.70	0.1114	-0.41			

Larvae							
Soil C	Soil N	0.85	-	16	5.81	0.00001	0.85
Soil C	NETPEROX	-0.29	-	16	-1.10	0.1453	-0.29

Table C.5. September 2020

Piecewise SEM Model Results - September 2020

		Model Indicators					Coefficients							Individual R-squared		
Management System	**Microarthropod Grouping**	**AIC**	**BIC**	**Fisher's C**	**P-value**	**DF**	**Response**	**Predictor**	**Estimate**	**Std. Error**	**DF**	**Crit. Value**	**P-value**	**Std. Estimate**	**Response**	**Marginal**	**Conditional**
No Rye - Plowed	Total	68.24	91.42	8.237	0.766	12	Total Berry Weight	Total Microarthropod	0.05	0.01	3	9.48	0.0025	1.09	Total Berry Weight	0.72	1
								Microbial Biomass C	2.36	0.27	3	8.66	0.0032	1.13			
								Microbial Biomass N	-0.74	0.25	3	-2.90	0.0624	-0.39			
								Soil C	7.18	0.79	3	9.11	0.0028	1.47			
								Aggregate Stability	1.67	0.12	3	13.38	0.0009	1.00			
								Soil Protein	-12.33	0.83	3	-14.78	0.0007	-2.10			
								PHOS	2.44	0.17	3	14.23	0.0008	2.87			
								Other Broadleaf Weeds	0.22	0.03	3	6.85	0.0064	0.40			
								Root Rot Rating	-0.69	0.09	3	-7.86	0.0043	-1.02			
							Total Microarthropods	Microbial Biomass C	-45.06	4.04	6	-11.15	0.00001	-1.06	Total Microarthropods	0.89	0.94
								Microbial Biomass N	8.05	4.08	6	1.97	0.0958	0.21			
								Soil C	-51.11	20.68	6	-2.47	0.0484	-0.51			
								Aggregate Stability	-12.95	4.44	6	-2.92	0.0268	-0.38			
								Soil Protein	139.24	16.84	6	8.27	0.0002	1.16			
								PHOS	-22.83	4.78	6	-4.77	0.0031	-1.31			
							Other Broadleaf Weeds	Microbial Biomass C	-2.43	0.79	9	-3.06	0.0136	-0.65	Other Broadleaf Weeds	0.48	0.48
								Microbial Biomass N	1.79	0.67	9	2.65	0.0265	0.53			
								Soil Protein	3.08	2.22	9	1.39	0.1973	0.30			
	Order	100.37	131.28	20.371	0.774	26	Total Berry Weight	Collembola	-0.02	0.01	4	-1.98	0.1187	-0.18	Total Berry Weight	0.95	0.95
								Prostigmatid Mites	0.02	0.01	4	2.73	0.0526	0.36			
								Mesostigmatid Mites	-0.06	0.02	4	-4.28	0.0128	-0.56			
								Microbial Biomass C	-0.73	0.23	4	-3.19	0.0334	-0.35			
								Microbial Biomass N	-1.25	0.28	4	-4.42	0.0115	-0.67			
								Soil N	21.13	4.67	4	4.52	0.0106	0.67			
								Volunteer Rye	0.76	0.21	4	3.67	0.0214	0.36			
								Root Rot Rating	-0.28	0.11	4	-2.45	0.0706	-0.42			
							Collembola	Microbial Biomass C	-11.44	4.41	10	-2.59	0.0268	-0.54	Collembola	0.41	0.41
								Microbial Biomass N	9.13	3.98	10	2.30	0.0446	0.48			

							Prostigmatid Mites	Microbial Biomass C	-18.60	8.84	10	-2.10	0.0617	-0.52	Prostigmatid Mites	0.35	0.35
								Soil N	361.23	134.24	10	2.69	0.0227	0.67			
							Mesostigmatid Mites	Microbial Biomass C	-11.50	3.66	11	-3.14	0.0094	-0.64	Mesostigmatid Mites	0.4	0.4
							Volunteer Rye	Prostigmatid Mites	-0.01	0.01	10	-2.06	0.0662	-0.48	Volunteer Rye	0.41	0.41
								Mesostigmatid Mites	0.04	0.01	10	3.18	0.0098	0.74			
							Soil N	Mesostigmatid Mites	0.00	4 e - 04	11	-2.59	0.0253	-0.30	Soil N	0.08	0.84
							Mesostigmatid Mites	Prostigmatid Mites	0.71	-	16	3.66	0.0014	0.71			
							Volunteer Rye	Root Rot Rating	0.43	-	16	1.70	0.0565	0.43			
							Prostigmatid Mites	Collembola	0.37	-	16	1.42	0.0902	0.37			
							Volunteer Rye	Microbial Biomass N	0.34	-	16	1.32	0.1047	0.34			
	Family	100.34	131.24	20.341	0.992	38	Total Berry Weight	Entomobryidae	-0.03	0.00	4	-6.99	0.0022	-0.25	Total Berry Weight	0.9	0.99
								Oribatid 2-T	0.12	0.02	4	7.12	0.0021	0.56			
								Oribatid 7-OA	-0.08	0.01	4	-10.21	0.0005	-0.50			
								Hypopi	-0.07	0.01	4	-7.10	0.0021	-0.33			
								Mesostig 1	-0.02	0.00	4	-5.27	0.0062	-0.20			
								Microbial Biomass C	-1.11	0.10	4	-11.19	0.0004	-0.53			
								Microbial Biomass N	-1.54	0.07	4	-22.86	0.00001	-0.82			
								Soil N	49.09	2.35	4	20.93	0.00001	1.55			
							Entomobryidae	Microbial Biomass C	-9.55	3.53	10	-2.71	0.0221	-0.55	Entomobryidae	0.45	0.45
								Microbial Biomass N	8.19	3.18	10	2.58	0.0276	0.52			
							Oribatid 2-T	Microbial Biomass C	-3.04	0.91	10	-3.34	0.0075	-0.32	Oribatid 2-T	0.11	0.9
								Microbial Biomass N	1.83	0.95	10	1.93	0.0825	0.22			
							Oribatid 7-OA	Microbial Biomass C	-7.58	3.52	10	-2.15	0.0571	-0.55	Oribatid 7-OA	0.28	0.28
								Soil C	16.10	8.29	10	1.94	0.0807	0.50			
							Mesostig 1	Microbial Biomass C	-11.40	3.64	11	-3.13	0.0095	-0.64	Mesostig 1	0.4	0.4
							Soil N	Mesostig 1	0.00	0.00	11	-2.57	0.0259	-0.30	Soil N	0.08	0.84
							Mesostig 1	Oribatid 7-OA	0.47	-	16	1.93	0.038	0.47			
							Hypopi	Oribatid 7-OA	-0.60	-	16	-2.68	0.0094	-0.60			
							Soil N	Soil C	0.43	-	16	1.73	0.0537	0.43			
							Soil N	Microbial Biomass C	0.32	-	16	1.21	0.1241	0.32			
Rye - Plowed	Total	33.99	46.36	1.994	0.92	6	Total Berry Weight	Total Microarthropod	-0.03	0.00	6	-6.27	0.0008	-0.52	Total Berry Weight	0.72	0.95
								Soil N	24.08	7.56	6	3.18	0.019	0.56			
								Soil Protein	-2.52	0.90	6	-2.79	0.0315	-0.35			
								BG	-1.27	0.25	6	-4.99	0.0025	-0.50			
								PHOS	0.72	0.18	6	4.06	0.0067	0.62			
								Other	-0.22	0.05	6	-4.10	0.0064	-0.35			

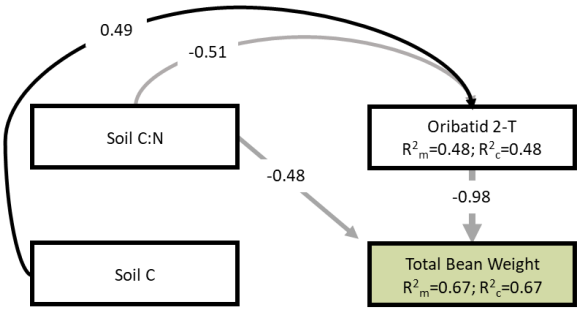
							Broadleaf Weeds									
						Other Broadleaf Weeds	Soil N	-30.15	15.41	10	-1.96	0.079	-0.43	Other Broadleaf Weeds	0.35	0.35
							Total Microarthropod	0.05	0.02	10	2.23	0.0496	0.49			
Order	44.8	60.25	4.8	0.779	8	Total Berry Weight	Collembola	-0.04	0.01	8	-4.35	0.0024	-0.50	Total Berry Weight	0.69	0.9
							Oribatid Mites	-0.03	0.01	8	-3.28	0.0112	-0.36			
							Microbial Biomass N	-0.44	0.23	8	-1.88	0.0966	-0.25			
							Soil N	16.82	8.23	8	2.05	0.0751	0.39			
						Collembola	Microbial Biomass C	-25.80	12.63	10	-2.04	0.0684	-0.51	Collembola	0.28	0.28
							Microbial Biomass N	12.22	6.21	10	1.97	0.0773	0.49			
						Oribatid Mites	Microbial Biomass C	-19.37	10.69	10	-1.81	0.1	-0.42	Oribatid Mites	0.37	0.37
							Microbial Biomass N	15.08	5.25	10	2.87	0.0166	0.67			
Family	131.56	168.64	35.558	0.908	48	Total Berry Weight	Astig 5-OO	-0.04	0.00	1	-1200.06	0.0005	-0.36	Total Berry Weight	0.8	1
							Oribatid 2-T	0.04	0.00	1	1714.20	0.0004	0.30			
							Oribatid 5	0.35	0.00	1	3119.84	0.0002	0.93			
							Oribatid 7-OA	-0.10	0.00	1	-2739.34	0.0002	-0.58			
							Hypopi	0.01	0.00	1	221.22	0.0029	0.13			
							Microbial Biomass N	0.03	0.00	1	21.25	0.0299	0.01			
							Soil N	128.64	0.14	1	938.85	0.0007	2.99			
							Soil C	-15.03	0.02	1	-640.36	0.001	-2.29			
							Volunteer Rye	1.35	0.00	1	2867.88	0.0002	1.05			
							Other Broadleaf Weeds	0.07	0.00	1	329.63	0.0019	0.12			
							Root Rot Rating	-0.44	0.00	1	-1210.72	0.0005	-0.69			
						Oribatid 5	Soil N	-334.73	165.55	10	-2.02	0.0708	-2.93	Oribatid 5	0.29	0.29
							Soil C	44.86	25.32	10	1.77	0.1069	2.57			
						Oribatid 7-OA	Microbial Biomass N	4. 5240	2.32	11	1.95	0.0769	0.42	Oribatid 7-OA	0.15	0.53
						Hypopi	Microbial Biomass N	16.65	4.56	9	3.65	0.0053	0.77	Hypopi	0.45	0.79
							Soil N	2378.13	650.60	9	3.66	0.0053	4.53			
							Soil C	-417.72	97.48	9	-4.29	0.002	-5.21			
						Volunteer Rye	Soil N	-178.56	42.13	7	-4.24	0.0038	-5.36	Volunteer Rye	0.63	0.66
							Soil C	25.52	6.26	7	4.07	0.0047	5.01			
							Astig 5-OO	0.05	0.02	7	2.60	0.0354	0.49			
							Oribatid 2-T	-0.06	0.02	7	-3.34	0.0124	-0.56			
							Oribatid 5	-0.24	0.06	7	-3.77	0.007	-0.82			
						Other Broadleaf Weeds	Microbial Biomass N	1.83	0.71	10	2.57	0.0279	0.63	Other Broadleaf Weeds	0.4	0.4
							Soil C	-7.53	2.63	10	-2.86	0.0169	-0.70			
						Hypopi	Astig 5-OO	-0.63	-	16	-2.92	0.0059	-0.63			
						Other Broadleaf Weeds	Volunteer Rye	-0.53	-	16	-2.23	0.0221	-0.53			
						Other Broadleaf	Root Rot	-0.24	-	16	-0.88	0.1974	-0.24			

							Weeds	Rating								
Rye - No Till	Total	34.16	44.97	6.157	0.406	6	Total Berry Weight	Soil Protein	2.27	1.20	8	1.89	0.0947	0.23	Total Berry Weight	0.59	0.87
								BG	3.91	0.71	8	5.49	0.0006	0.85			
								Aggregate Stability	-1.34	0.54	8	-2.48	0. 0380	-0.58			
								Volunteer Rye	-1.07	0.24	8	-4.47	0.0021	-0.67			
							Volunteer Rye	Soil C	-4.09	1.35	10	-3.04	0.0124	-0.77	Volunteer Rye	0.43	0.65
								Aggregate Stability	-1.07	0.36	10	-3.00	0.0133	-0.74			
	Order	93.33	123.46	15.327	0.975	28	Total Berry Weight	Collembola	0.09	0.02	3	4.02	0.0277	0.54	Total Berry Weight	0.37	0.98
								Oribatid Mites	-0.02	0.01	3	-2.48	0.0889	-0.25			
								Prostigmatid Mites	0.07	0.02	3	4.46	0.0209	0.54			
								Mesostigmatid Mites	-0.13	0.03	3	-3.76	0.0329	-0.52			
								Microbial Biomass C	2.06	0.47	3	4.37	0.0221	0.48			
								Microbial Biomass N	-3.03	0.54	3	-5.65	0.011	-0.94			
								Soil N	-37.63	12.15	3	-3.10	0.0534	-0.57			
								Volunteer Rye	-1.04	0.19	3	-5.61	0.0112	-0.65			
								Other Broadleaf Weeds	0.34	0.13	3	2.62	0.079	0.35			
							Collembola	Microbial Biomass C	-11.95	6.09	10	-1.96	0.0783	-0.45	Collembola	0.39	0.44
								Microbial Biomass N	14.34	4.59	10	3.12	0.0108	0.73			
							Oribatid Mites	Microbial Biomass C	-14.88	11.45	10	-1.30	0.2231	-0.34	Oribatid Mites	0.26	0.26
								Microbial Biomass N	19.27	8.55	10	2.25	0.0479	0.59			
							Volunteer Rye	Collembola	0.06	0.02	9	3.10	0.0128	0.63	Volunteer Rye	0.52	0.56
								Mesostigmatid Mites	-0.07	0.03	9	-2.30	0.047	-0.49			
								Soil N	-28.58	9.07	9	-3.15	0.0117	-0.70			
							Other Broadleaf Weeds	Prostigmatid Mites	-0.05	0.03	9	-1.85	0.0967	-0.36	Other Broadleaf Weeds	0.55	0.6
								Microbial Biomass C	-2.33	0.89	9	-2.63	0.0273	-0.52			
								Microbial Biomass N	2.71	0.68	9	3.99	0.0032	0.81			
							Mesostigmatid Mites	Prostigmatid Mites	0.71	-	14	3.75	0.0021	0.71			
							Oribatid Mites	Prostigmatid Mites	0.50	-	16	2.10	0.0278	0.50			
							Oribatid Mites	Mesostigmatid Mites	0.47	-	16	1.94	0.037	0.47			
	Family	105.82	135.95	27.82	0.888	38	Total Berry Weight	Entomobryidae	-0.28	0.03	4	-10.07	0.0005	-1.20	Total Berry Weight	0.64	0.98
								Oribatid 2-T	0.30	0.03	4	9.55	0.0007	1.56			
								Oribatid 5	-0.23	0.02	4	-12.15	0.0003	-1.54			
								Oribatid 7-OA	-0.23	0.02	4	-11.21	0.0004	-1.30			
								Hypopi	0.18	0.02	4	9.53	0.0007	0.89			
								Soil C	5.51	1.05	4	5.24	0.0063	0.65			
								Volunteer Rye	-1.53	0.14	4	-11.19	0.0004	-0.95			

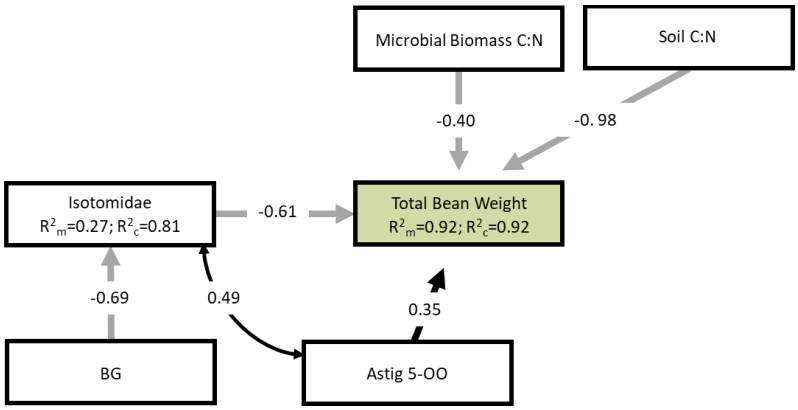
	Other Broadleaf Weeds	0.88	0.12	4	7.59	0.0016	0.92			
Oribatid 2-T	Microbial Biomass N	9.81	3.71	10	2.64	0.0246	0.58	Oribatid 2-T	0.36	0.36
	Soil C	-17.03	9.81	10	-1.74	0.1133	-0.38			
Oribatid 7-OA	Microbial Biomass N	8.72	4.29	11	2.03	0.0667	0.48	Oribatid 7-OA	0.22	0.22
Volunteer Rye	Oribatid 2-T	0.15	0.04	8	4.11	0.0034	1.28	Volunteer Rye	0.53	0.58
	Oribatid 5	-0.08	0.02	8	-3.36	0.01	-0.81			
	Oribatid 7-OA	-0.08	0.03	8	-2.73	0.0257	-0.73			
	Hypopi	0.05	0.03	8	2.06	0.0739	0.43			
Other Broadleaf Weeds	Microbial Biomass N	1.02	0.51	8	2.01	0.0791	0.30	Other Broadleaf Weeds	0.6	0.81
	Soil N	50.22	22.04	8	2.28	0.0522	0.73			
	Soil C	-8.59	2. 672	8	-3.22	0.0123	-0.97			
	Entomobryidae	0.09	0.03	8	2.69	0.0275	0.37			
Oribatid 7-OA	Oribatid 2-T	0.63	-	16	2.90	0.0062	0.63			
Oribatid 7-OA	Entomobryidae	-0.35	-	16	-1.36	0.0981	-0.35			
Other Broadleaf Weeds	Entomobryidae	0.62	-	16	2.85	0.0068	0.62			

Appendix D. Piecewise structural equation models (SEM) for family level microarthropod groupings for all sampling dates. Black arrows represent positive relationships, and grey arrows represent negative relationships. Arrow thickness indicates p-values; thick arrows are for p-values <0.01, thin arrow are for p-values <0.05. Standardized path coefficients are shown for significant relationships. Marginal (R^2_m) and conditional (R^2_c) coefficients of determination are shown for each component model, which describes the proportion of response variance associated with the fixed effects (marginal) and the fixed effects with random effects included (conditional).

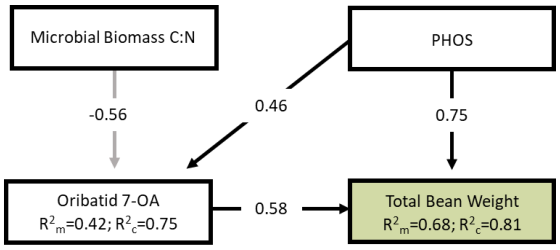
D.1. June 2019 – Family Level SEMs



No Rye – Plowed

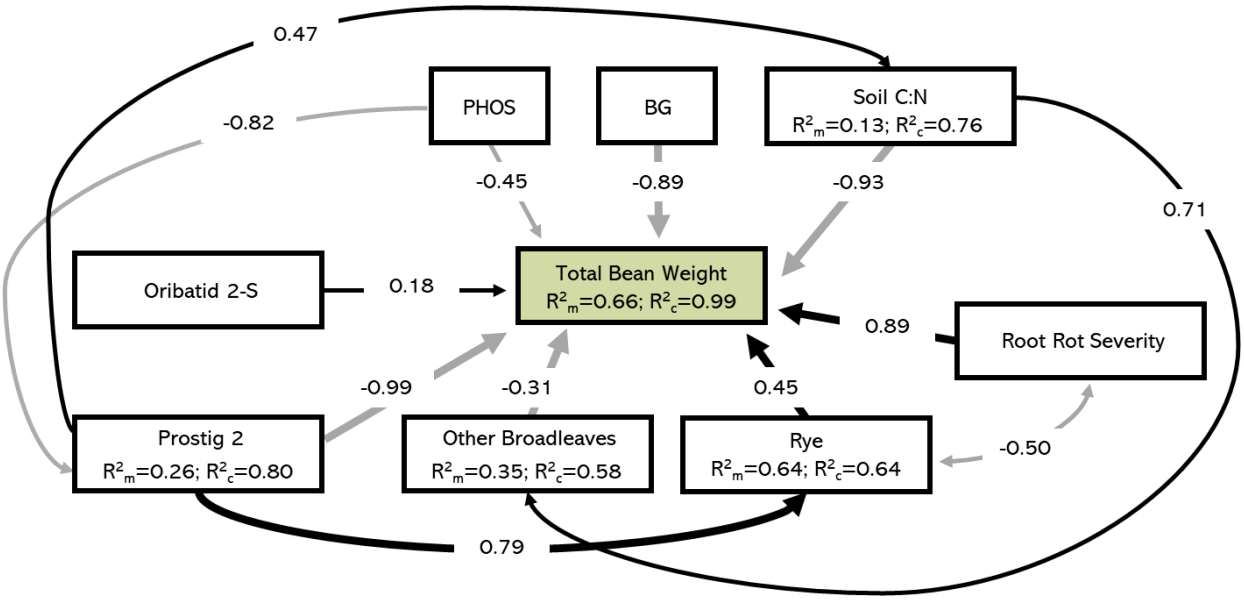


Rye – Plowed

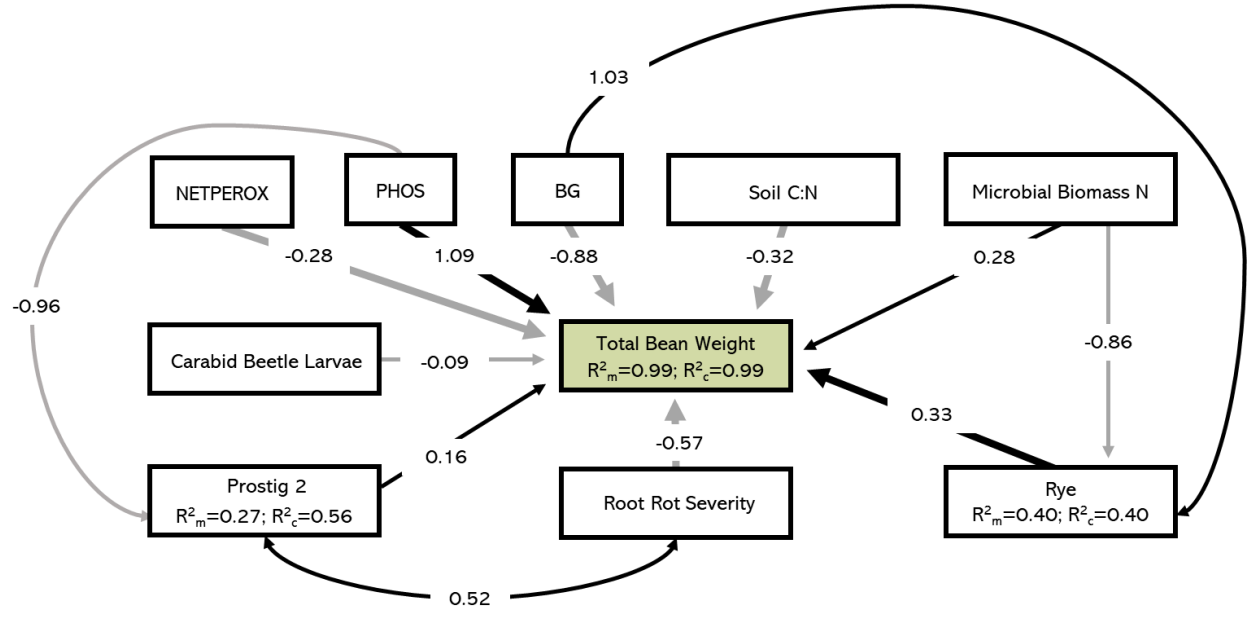


Rye – No Till

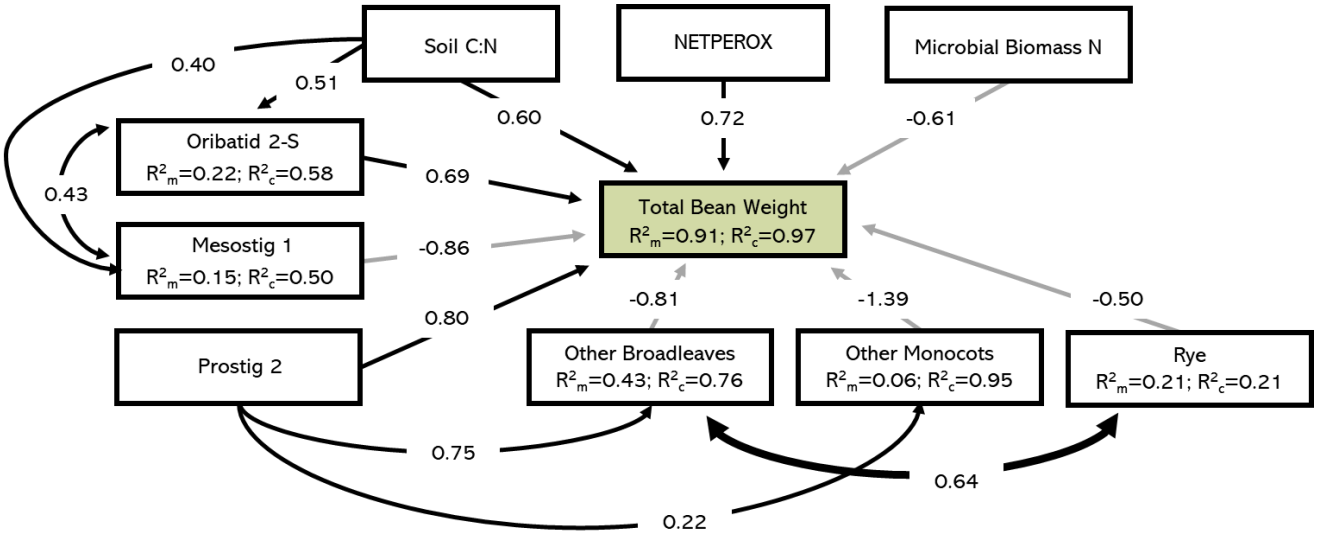
D.2. September 2019 – Family Level SEMs



No Rye – Plowed

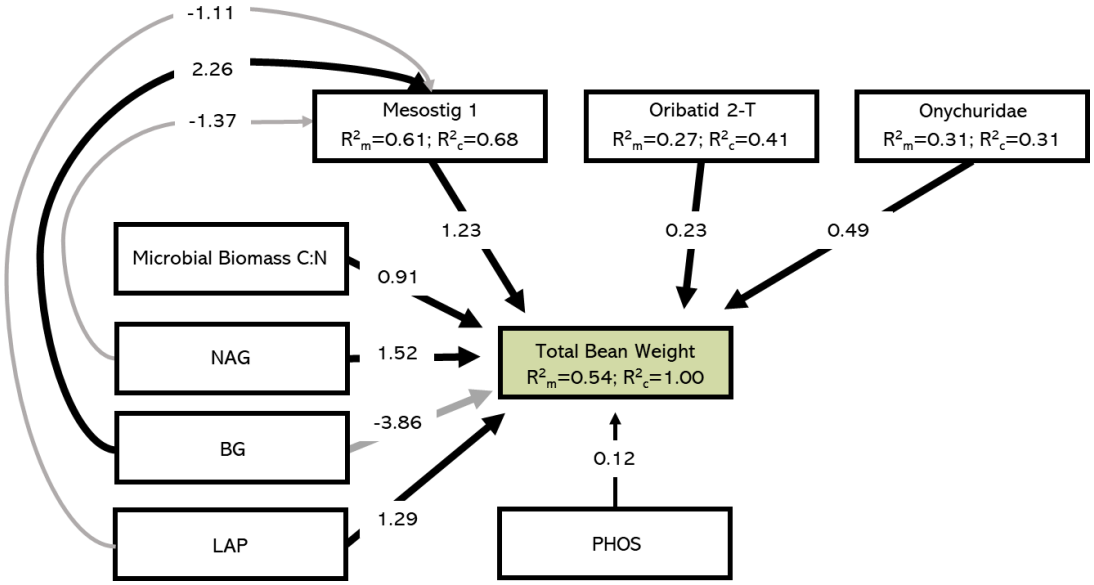


Rye – Plowed

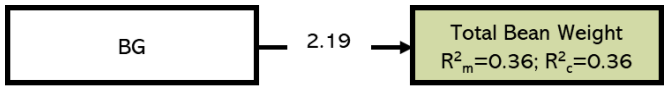

Soil C:N
NETPEROX
Microbial Biomass N
0.40
0.51
0.60
0.72
-0.61
Oribatid 2-S
R^2_m=0.22; R^2_c=0.58
0.43
0.69
Total Bean Weight
R^2_m=0.91; R^2_c=0.97
Mesostig 1
R^2_m=0.15; R^2_c=0.50
-0.86
-0.81
-1.39
-0.50
0.80
Prostig 2
Other Broadleaves
R^2_m=0.43; R^2_c=0.76
Other Monocots
R^2_m=0.06; R^2_c=0.95
Rye
R^2_m=0.21; R^2_c=0.21
0.75
0.64
0.22

Rye – No Till

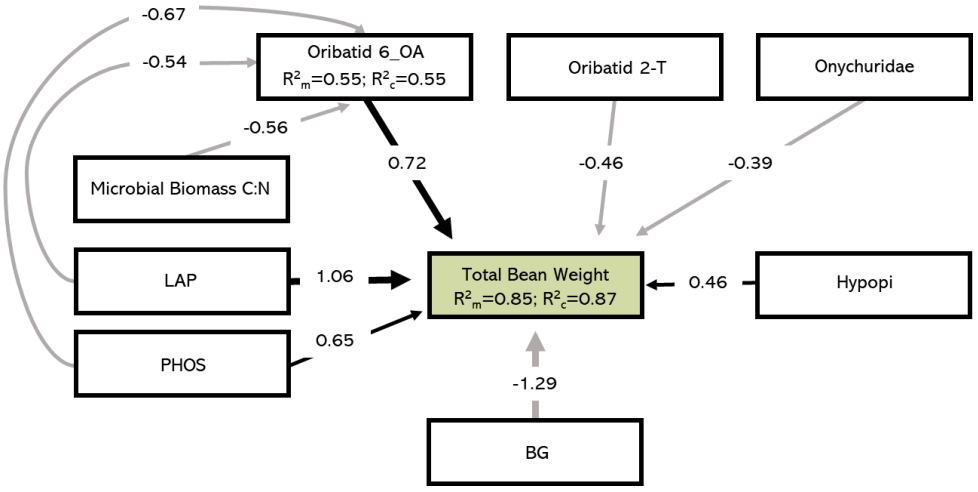
D.3. June 2020 – Family Level SEMs



No Rye – Plowed

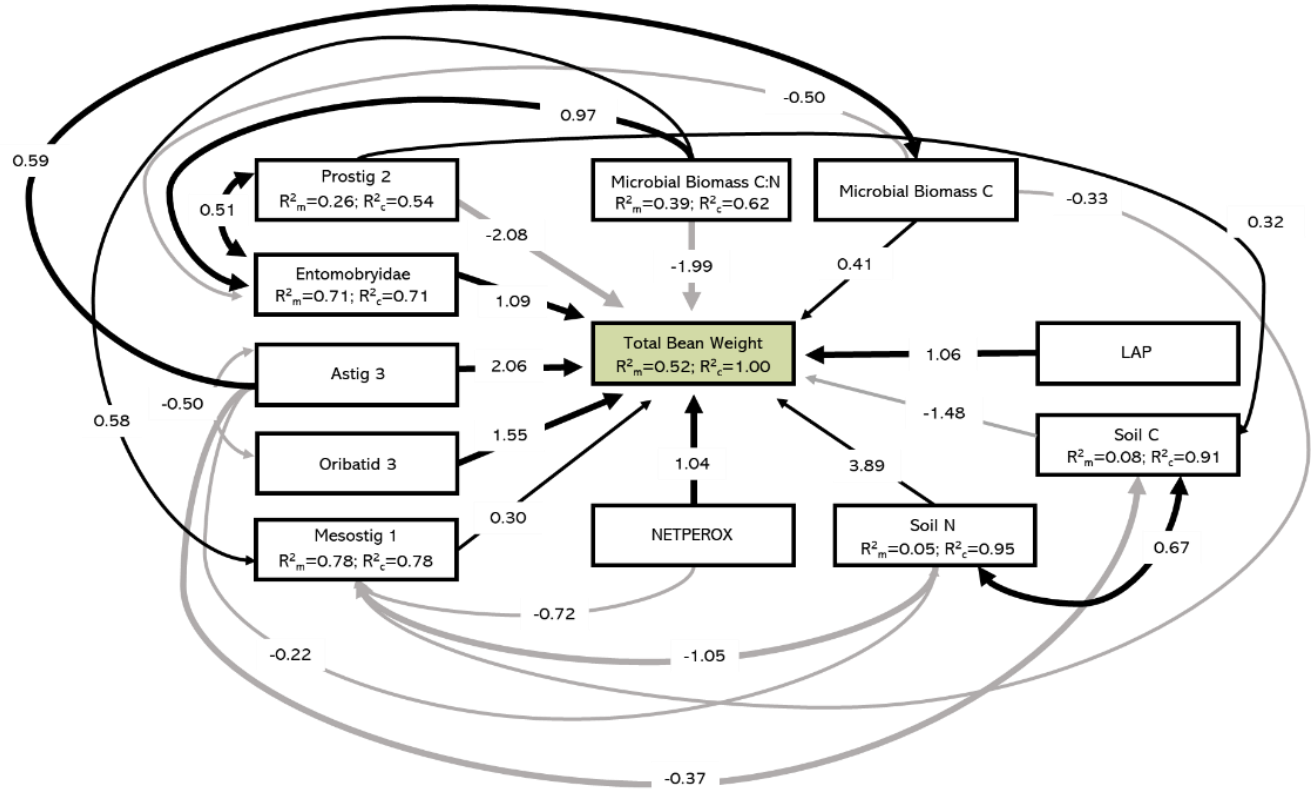


Rye – Plowed

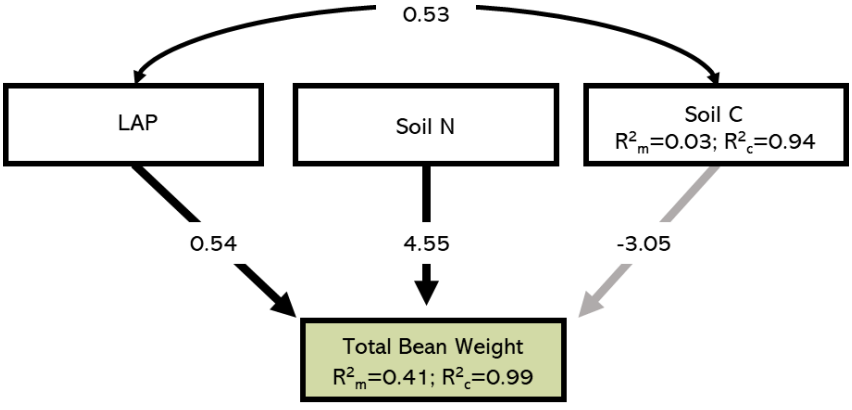


Rye – No Till

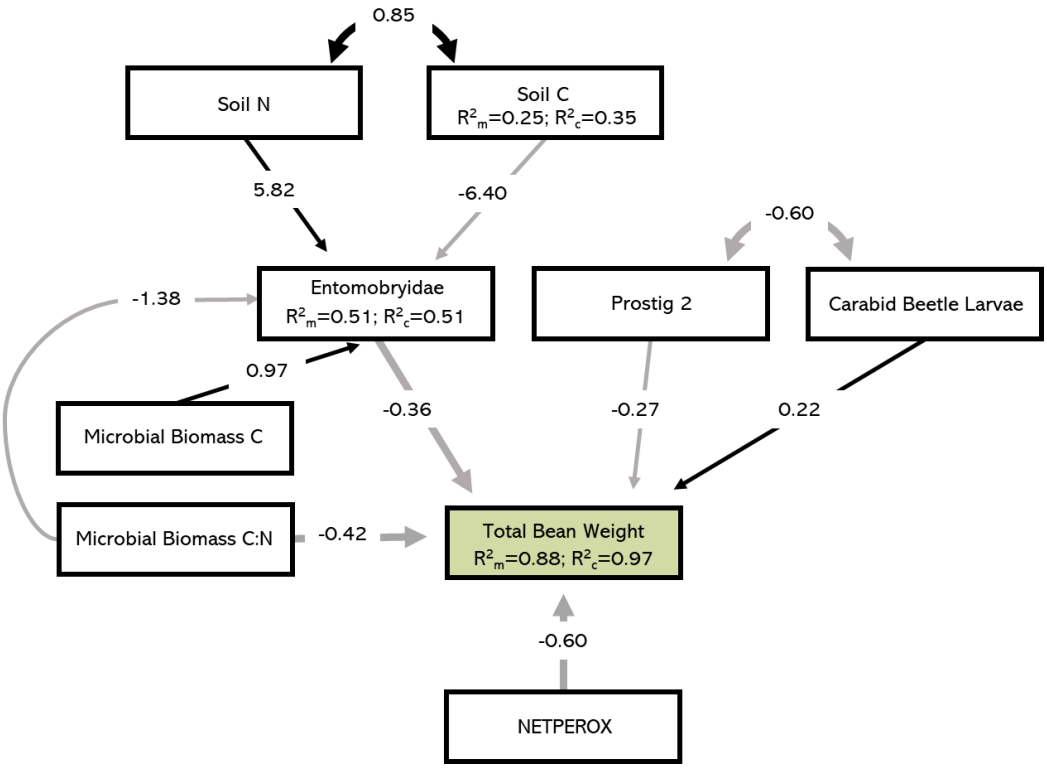
D.4. July 2020 – Family Level SEMs



No Rye – Plowed

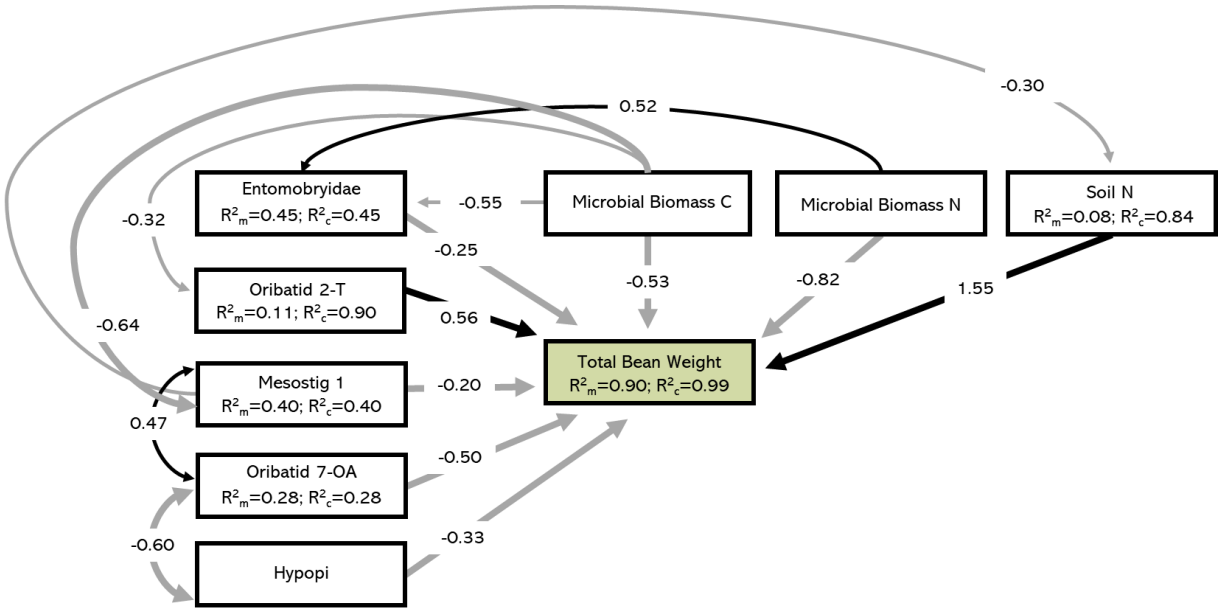


Rye – Plowed

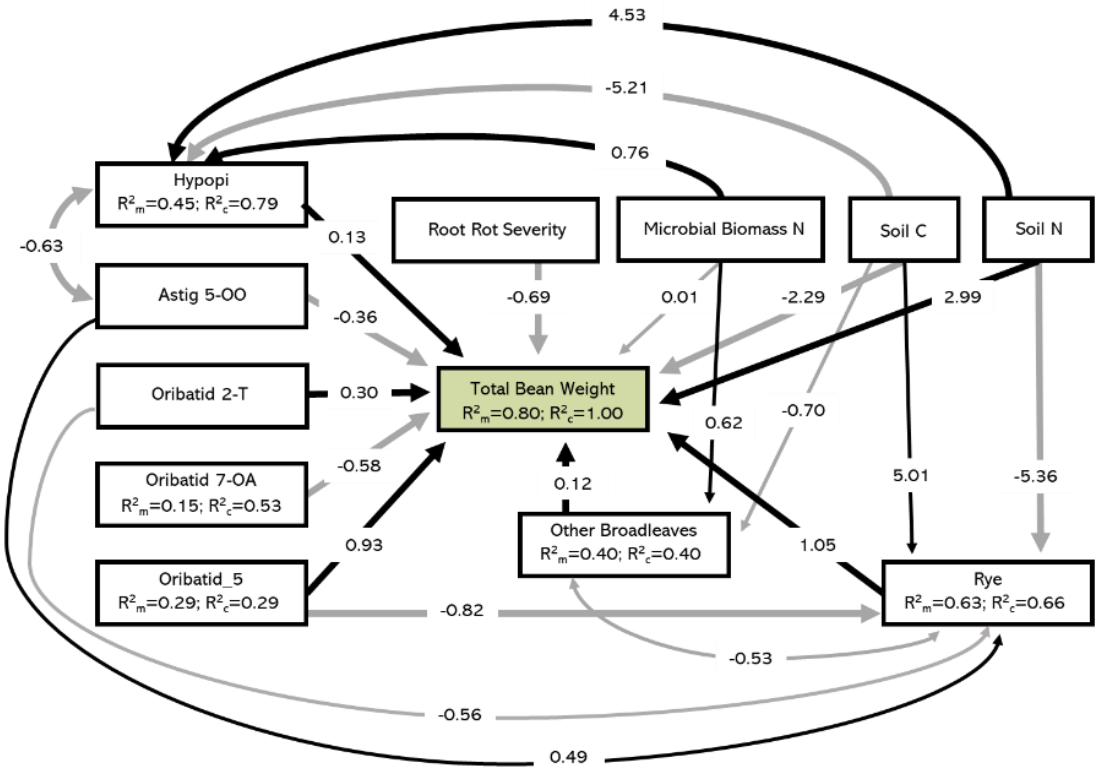

0.85
Soil N
Soil C
R^2_m=0.25; R^2_c=0.35
5.82
-6.40
-0.60
-1.38
Entomobryidae
R^2_m=0.51; R^2_c=0.51
Prostig 2
Carabid Beetle Larvae
0.97
-0.36
-0.27
0.22
Microbial Biomass C
Microbial Biomass C:N
-0.42
Total Bean Weight
R^2_m=0.88; R^2_c=0.97
-0.60
NETPEROX

Rye – No Till

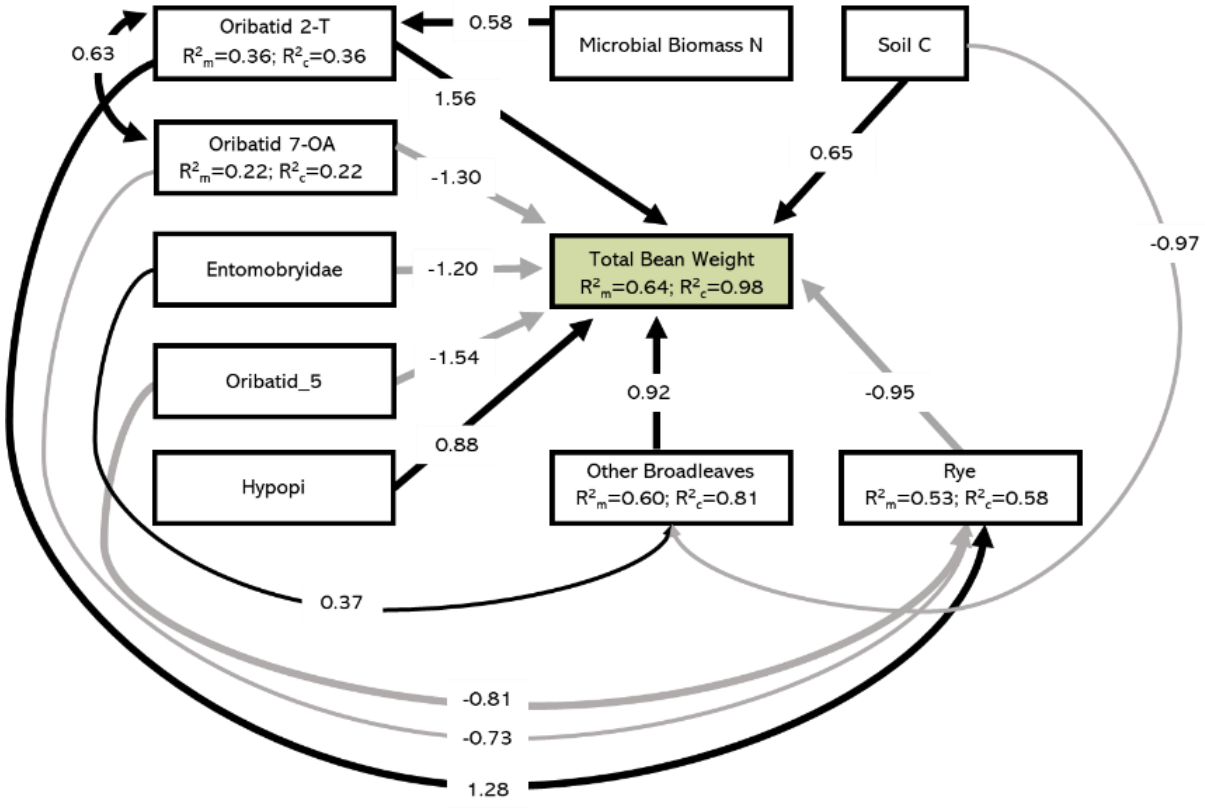
D.5. September 2020 – Family Level SEMs



No Rye - Plowed



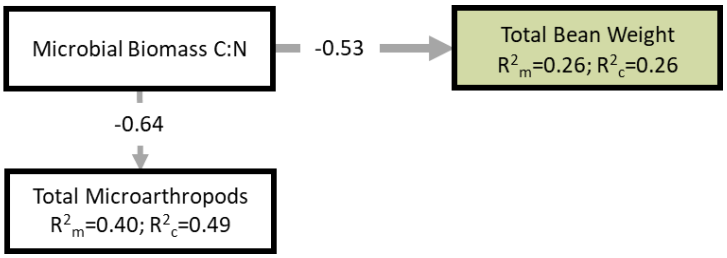
Rye - Plowed


Oribatid 2-T
R^2_m=0.36; R^2_c=0.36
Microbial Biomass N
Soil C
Oribatid 7-OA
R^2_m=0.22; R^2_c=0.22
Entomobryidae
Oribatid_5
Hypopi
Total Bean Weight
R^2_m=0.64; R^2_c=0.98
Other Broadleaves
R^2_m=0.60; R^2_c=0.81
Rye
R^2_m=0.53; R^2_c=0.58
0.58
0.63
1.56
0.65
-1.30
-1.20
-1.54
0.88
0.92
-0.95
-0.97
0.37
-0.81
-0.73
1.28

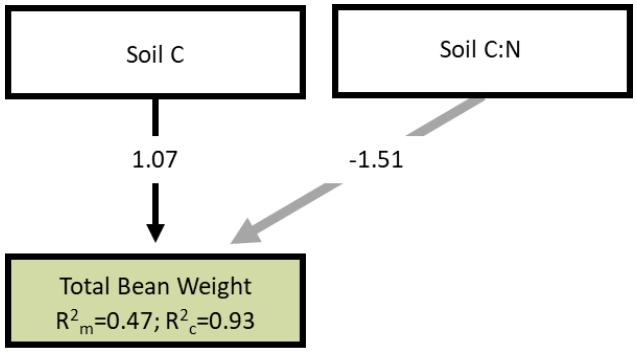
Rye – No Till

Appendix E. Piecewise structural equation models (SEM) for total microarthropod grouping for all sampling dates. Black arrows represent positive relationships, and grey arrows represent negative relationships. Arrow thickness indicates p-values; thick arrows are for p-values <0.01, thin arrow are for p-values <0.05. Standardized path coefficients are shown for significant relationships. Marginal (R^2_m) and conditional (R^2_c) coefficients of determination are shown for each component model, which describes the proportion of response variance associated with the fixed effects (marginal) and the fixed effects with random effects included (conditional).

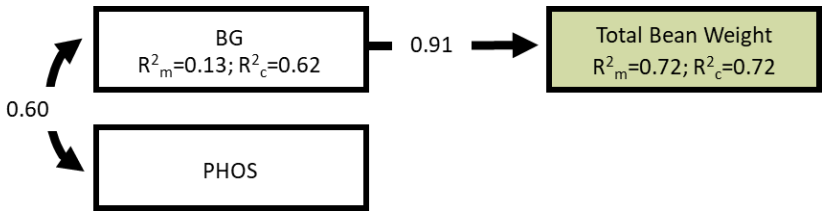
E.1. June 2019 – Total Microarthropod Group SEMs



No Rye – Plowed

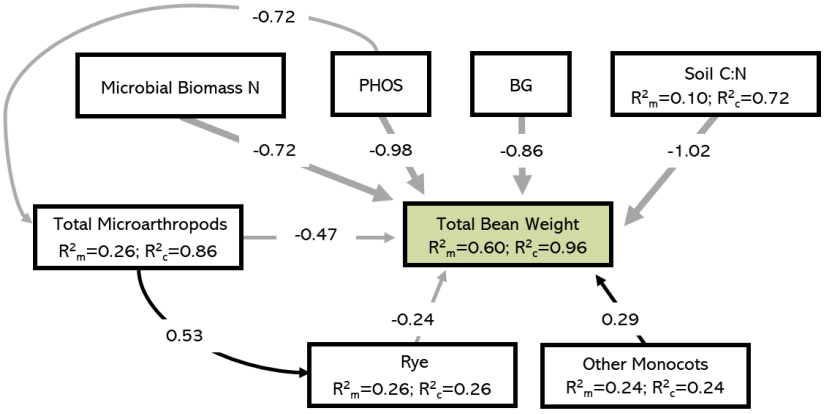


Rye – Plowed

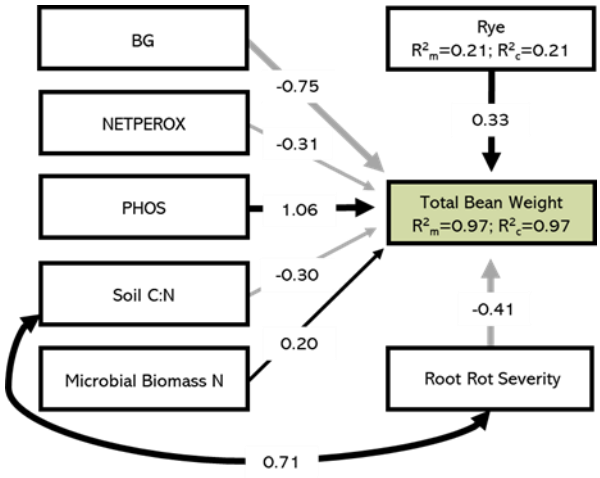


Rye – No Till

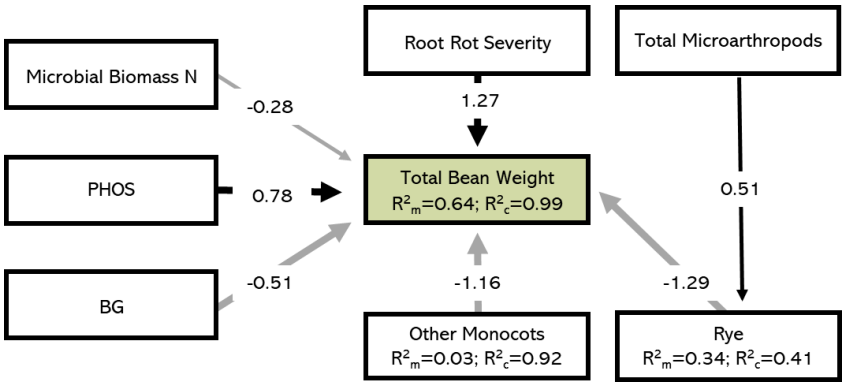
E.2. September 2019 – Total Microarthropod Group SEMs



No Rye – Plowed

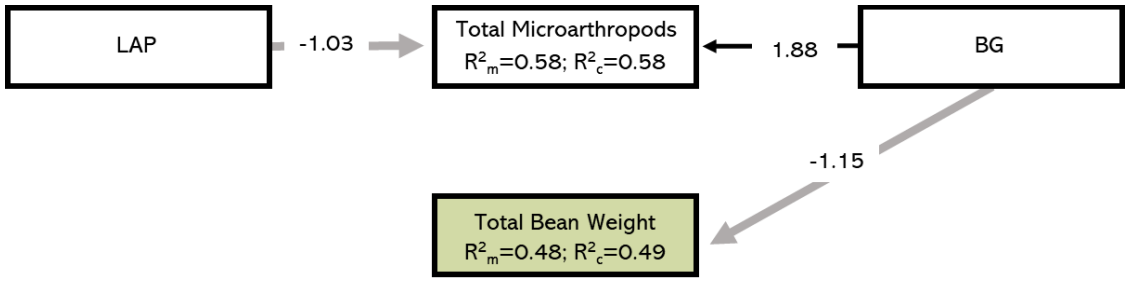


Rye- Plowed

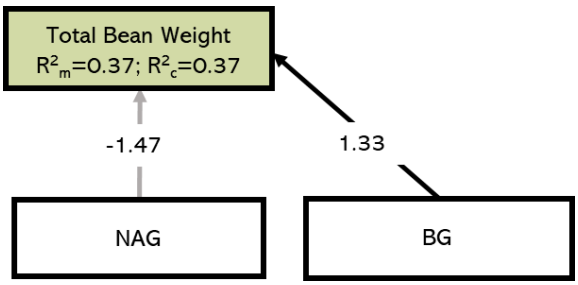


Rye – No Till

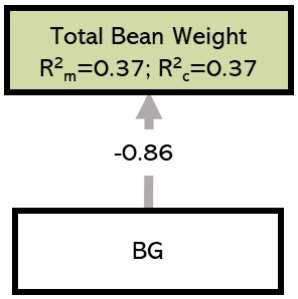
E.3. June 2020 – Total Microarthropod Group SEMs



No Rye – Plowed

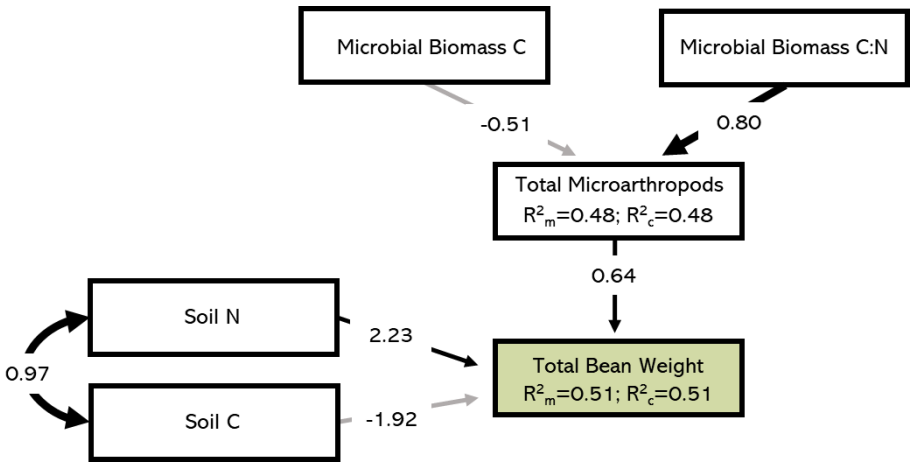


Rye – Plowed

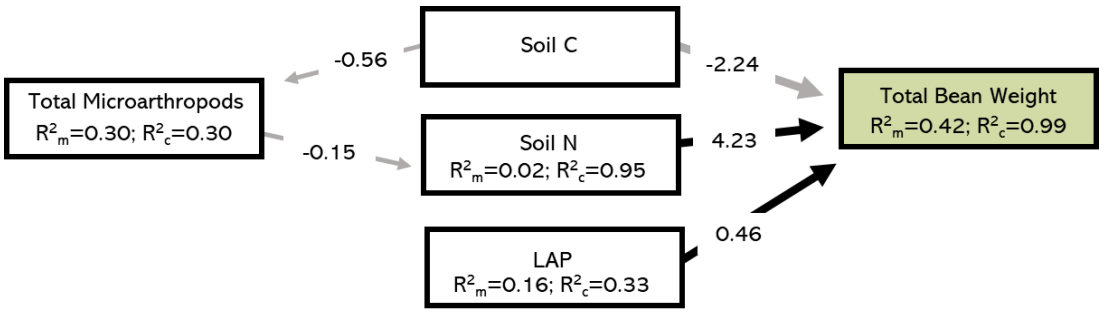


Rye – No Till

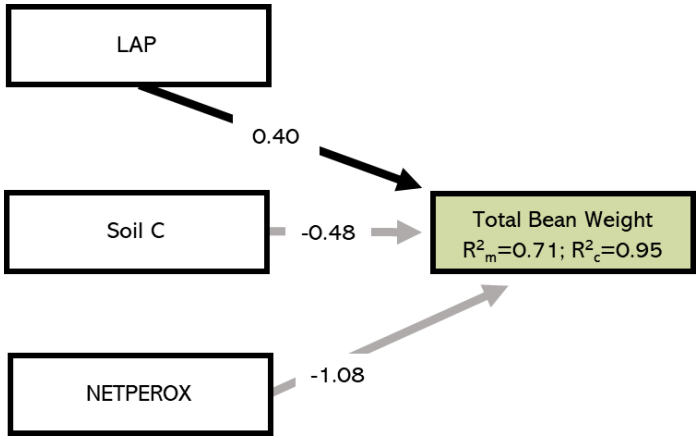
E.4. July 2020 – Total Microarthropod Group SEMs



No Rye – Plowed

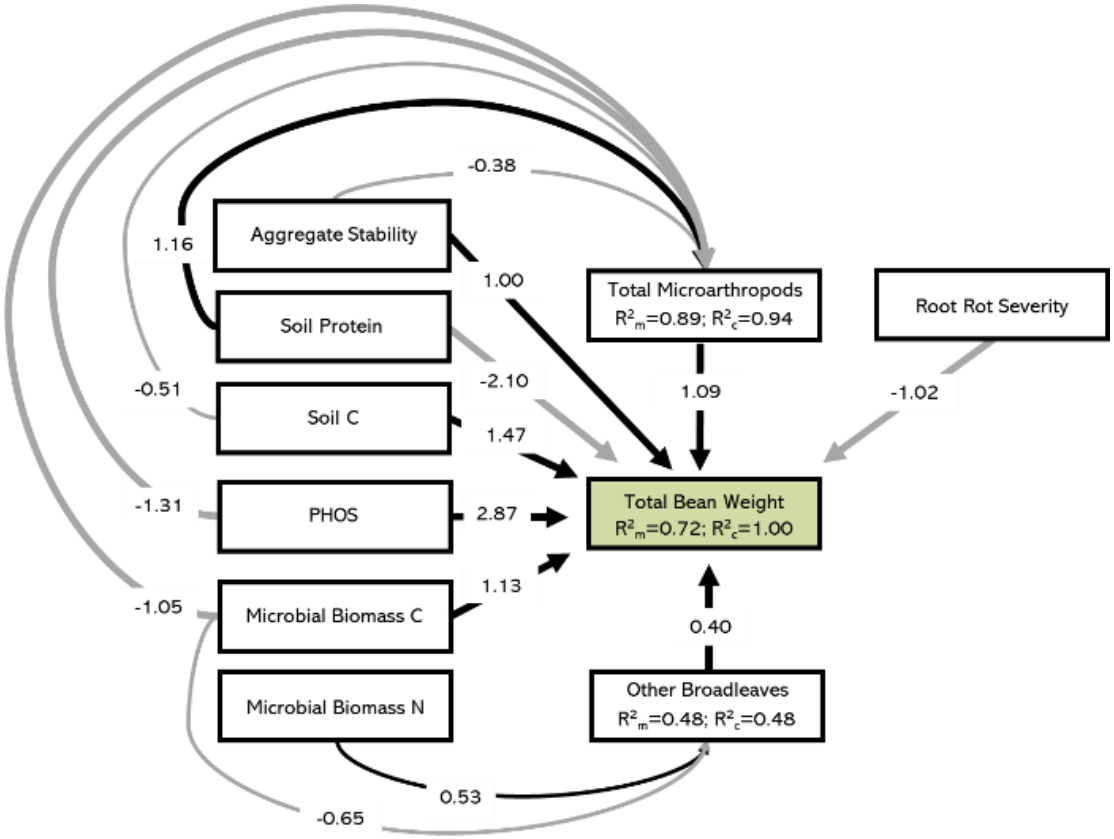


Rye – Plowed

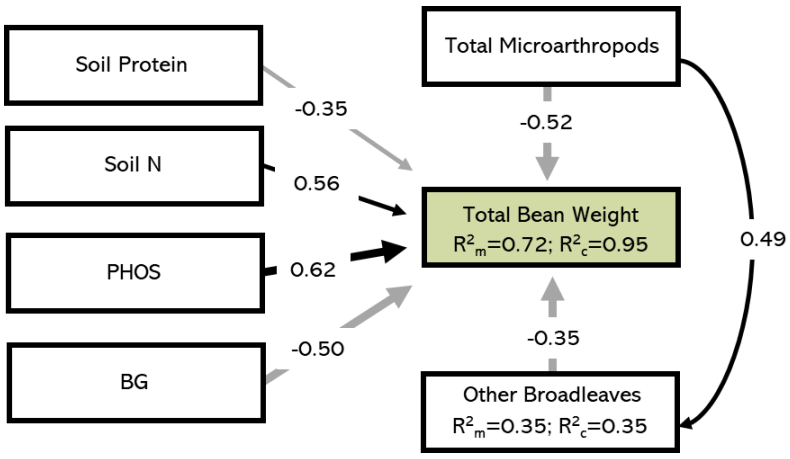


Rye – No Till

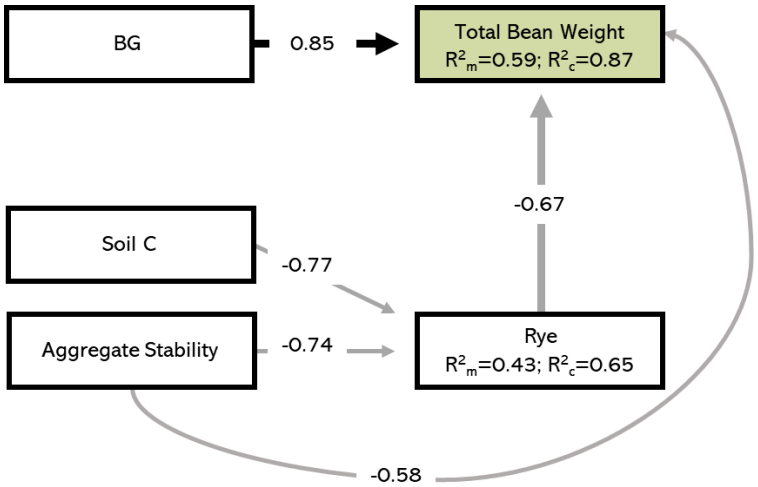
E.5. September 2020 – Total Microarthropod Group SEMs



No Rye – Plowed



Rye – Plowed


BG
0.85
Total Bean Weight
R^2_m=0.59; R^2_c=0.87
-0.67
Soil C
-0.77
Aggregate Stability
-0.74
Rye
R^2_m=0.43; R^2_c=0.65
-0.58

Rye – No Till

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CHAPTER 3

SOIL MICROARTHROPODS IMPROVE OAT NUTRITIONAL QUALITY AND MEDIATE THE EFFECTS OF FERTILIZERS ON SOIL BIOLOGICAL ACTIVITY

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 collembolan 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 (microarthropods, microbial biomass, microbial enzymes, 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 a greater number of effects on soil microbial activity. These effects enhanced 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 outcomes primarily through their effects on soil biological processes.

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 hectares, between 2011 and 2019 (USDA ERS, 2020). Many other farms utilize organic management practices beyond those that seek official certification. 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 it often relies on the long-term accumulation and release of nutrients over multiple growing seasons from complex organic matter sources. Organic fertilizer options vary from mineral to complex organic 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 soil biota play 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 fauna moderate these processes through both direct and indirect pathways (Jernigan *et al.*, 2022). One group of fauna, the 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 and Nielsen, 2016; Zhang *et al.*, 2021). Proposed mechanisms underlying this relationship involve the liberation of carbon 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 alter soil nitrogen composition and cycling rates, which translates to changes in soil fertility.

Microarthropod effects on nutrient cycling are dependent on their density and diversity (Seastedt, 1984; Sjursen, et al., 2005; Verhoef and Brussaard, 1990). The impacts that changes in microarthropod communities have on nutrient cycling can manifest in crop growth and nutrient acquisition (Bardgett and 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.) (Cole *et al.*, 2004). This study additionally showed that increasing species richness in microarthropod communities led to greater shoot biomass production. Further research confirms that increasing microarthropod community abundance and diversity generally increases crop biomass production and nutrient acquisition (Eisenhauer *et al.*, 2018; Forey, Coulibaly and Chauvat, 2015; Thakur and Eisenhauer, 2015).

Previous work suggests the importance of microarthropods for soil nitrogen cycling and plant nutrient acquisition can vary based on nutrient input type (Cole and Bardgett, 2002). Researchers found that the role of fauna on nitrogen dynamics was more important for faster decomposing litters including clover (*Trifolium* spp.) and false indigo bush (*Amorpha fruticose*) compared to slower decomposing 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). Until this area of research is explored further, recommendations to farmers on soil biological fertility management will remain limited. To that end, this research aimed to clarify the role microarthropod communities play 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, USA between June and November 2019. The greenhouse was maintained at 24°C during the day and 21°F at night, with no supplemental lighting. Both experiments followed a randomized complete-factorial design and included microarthropod and fertilizer treatments (Appendix A). The first experiment's microarthropod treatment consisted of a single Collembola species (*Isotomiella minor*, Schaffer 1896) applied at three different abundance levels (none [NC], low [LC], high [HC]). The second experiment's fauna treatment consisted of native microarthropod communities also applied at three different abundance levels (none [NC], low [LC], high [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 collected on microarthropod abundances in agricultural fields across New York State (A. Jernigan, unpublished data).

Each experiment incorporated identical fertilizer treatments. Three organic fertilizers were chosen as treatments in addition to the no fertilizer control treatment, (1) Alfalfa green manure, (2) Kreher's Poultry Litter Compost 5-4-3 (Organic Materials Review Institute), and (3)

Chilean Nitrate. 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 for plants (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 per hectare, which converted to 0.057 g N per pot (SARE, 2007). The amount of fertilizer added to each pot was standardized to the rate of 0.057 g N (alfalfa green manure = 0.915 g [6.15% N], poultry litter compost = 0.896 g [6.38% N], Chilean nitrate = 0.381 g [13.65% N]).

Soil (Arkport Series – coarse-loamy, mixed, active, mesic Lamellic Hapludalfs) was collected and then 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 is effective at eliminating 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. After mixing, the soil was remoistened with deionized water to approximately one third of the soils' water holding capacity and was 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 cm^2) for each experiment. Each pot was filled almost completely, leaving about 2.5 cm of space at the top. The average weight of soil in each pot was 324 g (wet weight at 35% moisture).

Each pot was placed in an individual PVC tube that was capped with thrips netting (no-thrips insect screen, hole opening size: 192 microns, BioQuip Products, Inc.) on the top and bottom to prevent cross contamination of fauna treatments (Appendix A).

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 near 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 approximately the higher end of the recommended rate of 135-202 kg per hectare, 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, low abundance treatments received approximately 100 Collembola, and high abundance 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 hour to ensure all collembolans moved from the specimen cups into the soil. Roughly the same amount of water was added to the control pots as was added to the low and high abundance treatment pots when completing the Collembola transfer.

2.3 Experiment 2 (Diverse Community)

A preliminary fauna extraction was completed on soil cores collected from a research field in Geneva, NY (42.887264, -77.009832) 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). Each sample was then placed on Berlese funnels. Over the course of the 3-day extraction, temperature was gradually increased from 30°C to 50°C. Invertebrates were extracted into 70% ethanol, then were topped off with 95% ethanol and stored until the samples were processed. In this study soil fauna include mites, Collembola, and other taxa within the Arthropoda. Extracted fauna were identified to family using published taxonomic keys (Borror and DeLong, 1964; Dindal, 1990; Krantz and Walter, 2009). After the soil samples were removed from the Berlese funnels, soil dry mass was determined. All arthropod abundances are reported as the number of individuals kg^{-1} dry soil. The fauna data were used to determine the amount of soil needed to extract sufficient animal numbers for the experiment.

On September 10th, 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 abundance treatments in successive layers of bulk soil each inoculated with a deli cup of microarthropods then mixed by hand. This process was repeated until all the soil was combined. 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 the no community, low community, and high community abundance treatments. 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 (# 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 other 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.

A weekly check was conducted every 7 days during which the number of oat plants germinated, the height of the tallest and shortest oat plant, and the approximate oat growth stage were recorded for each pot. The height of oat plants was chosen as a non-destructive proxy for plant biomass during the weekly checks and Zadok's growth scale was used to determine oat growth stages (Zadoks, et al., 1974). Qualitative plant health observations were also recorded, including signs of nutrient deficiencies or disease.

2.5 Harvest Metrics

During each experiment two destructive harvests were conducted at which time half (n=48) of the pots were randomly selected to be harvested. The first harvest was completed 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 separated from the soil, 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 and Powlson, 1976). Half of all samples were fumigated

by adding 3 ml of chloroform to 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 carbon and nitrogen on a Shimadzu TOC-TN analyzer (Shimadzu Scientific Instruments, INC., Columbia, MD). Microbial biomass carbon was determined by subtracting non-fumigated from fumigated carbon values and by applying a k_{EC} value of 0.45 (Joergensen, 1996). Microbial biomass nitrogen was derived using the same calculations and applying a k_{EC} value of 0.54. Biomass carbon and nitrogen is presented as μg 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, Sinsabaugh and Zak, 2002; Wickings and 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 (POX) 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 phenol oxidase or L-DOPA plus hydrogen

peroxide (0.3%) for peroxidase. 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, Winooski, VT, United States). Potential enzyme activity for each substrate was calculated as nmol of substrate h^{-1} 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, Metuchen, NJ, USA), weighed into tin capsules, and combusted to determine carbon (C) and nitrogen (N) concentration. Soil C and N was measured by elemental analysis (Costech EA 4010 CHNS-O Analyzer, Costech Analytical Technologies, Valencia CA, USA) using acetanilide, organic rye flour, and certified soil reference material (Elemental Microanalysis, Ltd, UK) 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 LSD method, with Tukey adjustment and significance was declared for $P \leq 0.05$.

A redundancy analysis was performed on the corresponding soil and plant variable

datasets collected at each harvest in both experiments using the *rda* function in the 'vegan' package (Oksanen *et al.*, 2010). All variables were standardized using the *decostand* 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 Results – Experiment 1 (Single-Species)

3.1.1 Weekly Plant Growth Metrics

Seedling emergence was significantly affected by the fertilizer treatments at weeks one and two (Appendix B). Seedling emergence was lower in pots receiving green manure compared to the other fertilizer treatments, with an average of 13.4 plants per pot compared to 15 plants per pot in the other treatments after thinning.

The growth stages of the oats were affected by the interaction of the Collembola and fertilizer treatments at weeks two and three (Appendix B). Within the no Collembola treatment, oats developed faster in pots receiving compost and green manure than when receiving other fertilizers (week 2 = 11.4 vs. 11.0; week 3 = 12.5 vs. 12.0). After week 3, there were no longer any significant differences in plant growth and development between the treatments.

3.1.2 Harvest Metrics

Collembola Abundances

At harvest 1, Collembola abundances had decreased relative to the start of the experiment in both the low and high abundance 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) indicating that between the harvests

the vast majority of Collembola died (Figure 1).

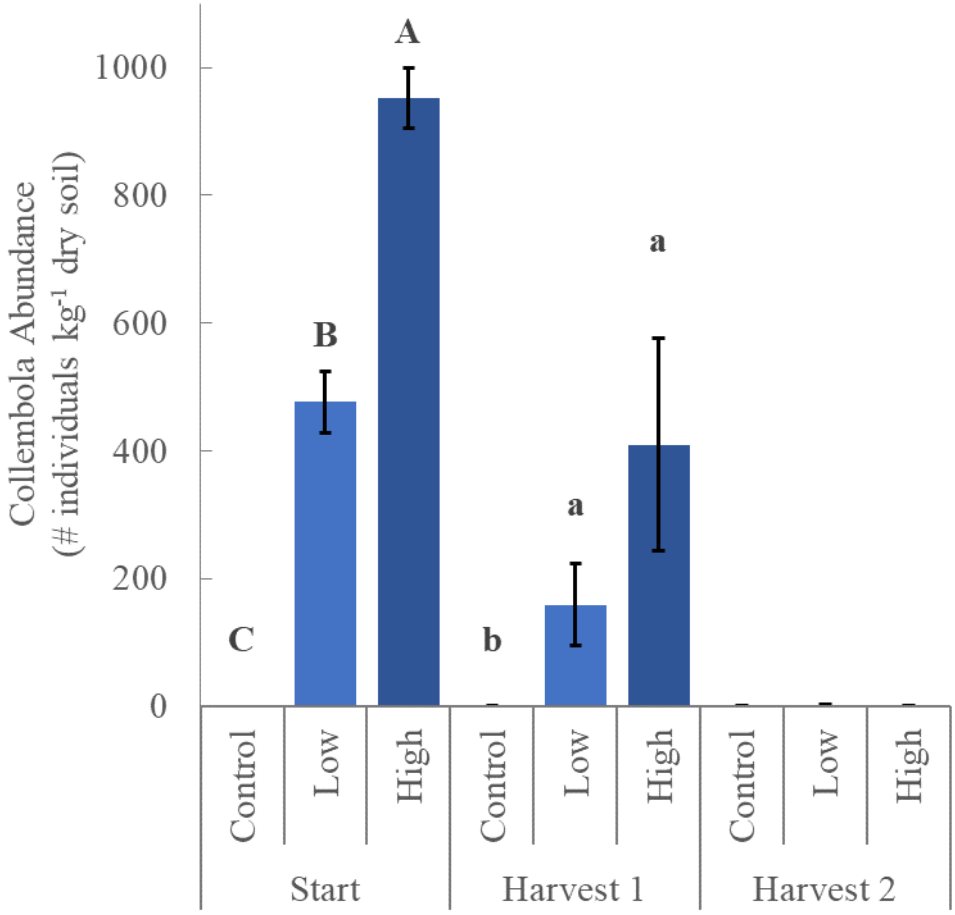

Figure 1. Collembola treatment effects on collembolan abundances (# individuals kg^{-1} dry soil) in the single species experiment. Separate mean comparisons were conducted for each time point. Bars with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

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 tissue carbon and nitrogen, as well as the C:N ratio, of both the roots and shoots, excluding the percent of carbon in oat shoots (Table 1). Generally, the presence of the Collembola increased the magnitude of the effect of fertilizers on nitrogen content of the roots and had mixed effects on root carbon content. For the most part the C:N ratio of the roots decreased as the fertilizer source became more plant available (no fertilizer<green manure<compost<Chilean nitrate). As with the roots, the presence of the Collembola increased the effect of the fertilizers on nitrogen content of the shoots. The C:N ratio of the shoots also tended to decrease as the fertilizer source was more plant available as with the roots, however for the shoots, this effect was not exacerbated when Collembola were present.

By harvest 2, the nitrogen content of the oat root and shoots were primarily affected by the Collembola and fertilizer treatments independently, however the root C:N ratio and the seed composition was affected by treatment interactions. The nitrogen content in the roots increased as the fertilizer plant availability increased (Table 1).

At harvest 2, in the absence of Collembola root C:N was lower in pots receiving compost compared to nonamended controls, and at low Collembola abundances the C:N ratio was greater in the absence of fertilizer. Generally, the nitrogen content of the shoots was greater when Collembola were present and greater as the fertilizer source was more plant available. The C:N ratio of the shoots decreased as Collembola abundances increased and as the fertilizer source was more plant available. The nitrogen content of the seeds tended to increase as the fertilizer source was more plant available (no fertilizer<green manure<compost<Chilean nitrate), however the

presence of the Collembola exacerbated this effect. The C:N ratio of the seeds generally decreased as the fertilizer source was more plant available, however again the presence of the Collembola magnified this effect.

Table 1. The effect of Collembola abundance and fertilizer treatments on the nutrient composition of soils and plant tissues for the single species experiment. Significance levels from the ANOVAs performed the metrics with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

			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
Harvest 1	**P-Value**	Collembola	0.3723	0.0372	**0.0071**	0.1413	0.4260	0.0447	0.2351	0.2420	0.3435			
		Fertilizer	0.3972	0.0433	**0.0317**	3.16E-11	0.0007	1.29E-14	2.20E-16	**8.50E-12**	2.20E-16			
		Collembola x Fertilizer	0.4311	**0.0411**	0.0563	**0.0086**	**0.0001**	**0.0502**	**0.0092**	0.1092	**0.0011**			
	Main Effects													
	Collembola	control			23.9 b					40.1				
		low density			23.1 ab					40.0				
		high density			25.3 a					40.3				
	Fertilizer	no fertilizer			25.1 a					41.0 a				
		green manure			23.2 b					39.9 b				
		compost			24.9 ab					40.4 ab				
		Chilean nitrate			23.3 ab					39.2 c				
	Interaction Effects													
	No collembola	no fertilizer		4.9 ab		1.2 c	36.7 a	30.2 ab	2.0 c		21.0 ab			
		green manure		4.4 b		1.3 c	34.1 b	26.0 bc	3.0 b		13.3 bc			
		compost		4.8 ab		1.5 abc	37.4 a	26.6 bc	2.3 c		18.1 b			
		Chilean nitrate		4.95 ab		1.5 abc	33.9 b	23.4 c	3.8 a		10.3 c			
	Low collembola	no fertilizer		4.6 ab		1.1 c	36.0 a	33.2 ab	1.8 c		22.4 ab			
		green manure		4.6 ab		1.3 bc	35.6 ab	28.0 bc	3.0 bc		13.8 bc			
		compost		4.7 ab		1.2 c	36.0 a	31.6 ab	2.3 c		18.2 b			
		Chilean nitrate		4.7 ab		1.6 ab	33.9 b	21.6 cd	3.8 a		10.3 c			
	High collembola	no fertilizer		5.5 a		1.1 c	37.1 a	33.9 a	1.7 c		24.4 a			
		green manure		4.8 ab		1.4 bc	33.1 b	24.5 bc	3.4 ab		11.9 bc			
		compost		5.3 a		1.2 c	33.1 b	27.2 bc	2.9 bc		14.4 bc			

		Chilean nitrate		4.5 b		1.7 a	36.3 a	21.3 cd	3.7 a		10.8 c			
	P-Value	Collembola	0.3723	0.1878	0.1558	0.2484	0.2135	0.0586	**0.0001**	**0.0009**	**0.0008**	0.0070	0.0018	0.0137
		Fertilizer	0.3972	1.04E-05	**0.0004**	**0.0009**	0.1354	1.90E-05	**2.20E-16**	**0.0092**	**2.20E-16**	1.99E-11	1.30E-05	1.42E-09
		Collembola x Fertilizer	0.4311	**0.0293**	0.0984	0.1286	0.1290	**0.0217**	0.4369	0.1597	0.1439	**0.0107**	**0.0024**	**0.0139**
	Main Effects													
	Collembola	control			24.7	1.2			1.3 b	42.8 a	37.9 a			
		low density			25.0	1.2			1.6 a	42.0 b	32.3 ab			
		high density			25.9	1.3			1.7 a	42.6 a	28.6 b			
	Fertilizer	no fertilizer			27.3 a	1.1 c			0.8 d	42.7 a	55.9 a			
		green manure			24.5 b	1.2 bc			1.7 bc	42.7 a	26.3 bc			
		compost			25.0 b	1.3 ab			1.4 c	42.4 ab	32.3 b			
		Chilean nitrate			24.2 b	1.4 a			2.5 a	42.0 b	17.5 d			
	Interaction Effects													
Harvest 2	No collembola	no fertilizer		5.5 a				36.3 a				2.8 cd	43.3 ab	15.8 ab
		green manure		5.1 ab				29.1 ab				2.9 cd	44.2 a	15.1 ab
		compost		4.8 ab				27.1 ab				2.8 cd	43.8 ab	15.9 ab
		Chilean nitrate		4.5 b				28.5 ab				3.4 bc	43.4 ab	13.4 bcd
	Low collembola	no fertilizer		5.5 a				37.3 a				2.6 d	43.1 b	17.1 ab
		green manure		4.5 b				22.4 b				3.3 bc	43.6 ab	14.0 bc
		compost		5.2 ab				27.8 ab				3.1 cd	43.7 ab	14.4 bc
		Chilean nitrate		4.8 ab				23.4 b				4.2 a	42.1 c	10.1 cd
	High collembola	no fertilizer		5.5 ab				27.7 ab				2.8 cd	43.2 ab	15.6 ab
		green manure		5.0 ab				27.8 ab				3.7 ab	43.5 ab	11.8 cd
		compost		4.9 ab				29.1 ab				3.1 bcd	44.0 ab	14.5 bc
		Chilean nitrate		5.2 ab				21.0 b				3.6 ab	43.7 ab	12.3 d

Microbial Biomass Carbon and Nitrogen

At harvest 1, there was greater microbial biomass carbon in the absence of Collembola compared to high Collembola abundances, and nonamended pots had greater microbial biomass carbon than the pots that received green manure and Chilean nitrate (Table 2). The microbial biomass nitrogen was also significantly affected by the fertilizer treatments with the green manure and Chilean nitrate pots having greater microbial biomass nitrogen than the no fertilizer and compost pots (Table 2). Within the no Collembola treatment, the microbial biomass C:N ratio was higher in the absence of fertilizer than the other fertilizer treatments and the pots with compost had a higher microbial biomass C:N ratio than the pots with Chilean nitrate (Table 2).

At harvest 2, microbial biomass carbon, microbial biomass nitrogen, and their ratio were all impacted by both the Collembola and fertilizer treatments (Table 2). The microbial biomass carbon was greater when there were no Collembola and low Collembola abundances present compared to when high Collembola abundances were present (Table 2). The microbial biomass carbon differed significantly between each fertilizer treatment (Chilean nitrate< green manure<compost< no fertilizer). The microbial biomass nitrogen was greater when there were low Collembola abundances compared to when no 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 than when low and high Collembola abundances were present (Table 2). The microbial C:N ratio increased significantly between each fertilizer treatment, in increasing order from the Chilean nitrate to green manure to compost to no fertilizer (Table 2).

Table 2. The effect of Collembola abundance and fertilizer treatments on the microbial metrics for the single species experiment. Significance levels from the ANOVAs performed the metrics with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

			Microbial C	Microbial N	Microbial C:N	NAG	LAP	PHOS	PHENOX	Peroxidase
Harvest 1	**P-Value**	Collembola	**0.0438**	0.9005	0.8882	**0.0367**	**0.0273**	0.2904	**0.0221**	0.1046
		Fertilizer	**1.06E-06**	**1.21E-08**	**4.01E-16**	0.0642	**1.48E-06**	0.1216	**0.0251**	0.6373
		Collembola x Fertilizer	0.3373	0.2866	**0.0031**	0.1150	**0.0030**	**0.0011**	0.5414	**0.0114**
	Main Effects									
	Collembola	control	131 a	14.2		21.5 b			1.52 a	
		low density	123 ab	14.2		26.7 ab			1.25 ab	
		high density	118 b	13.6		30.4 a			0.82 b	
	Fertilizer	no fertilizer	147 a	8.8 b		15.9			2.00 a	
		green manure	120 b	16.9 a		34.3			1.07 b	
		compost	135 ab	11.3 b		23.5			1.15 b	
		Chilean nitrate	93 c	22.8 a		31.2			0.56 b	
	Interaction Effects									
	No collembola	no fertilizer			18.6 a		70.3 b	346 b		0.39 ab
		green manure			7.9 b		520.6 a	113 b		0.51 ab
		compost			9.0 b		59.7 b	575 a		0.38 ab
		Chilean nitrate			4.5 b		48.6 b	223 b		0.57 ab
	Low collembola	no fertilizer			16.9 a		83.8 b	453 b		0.54 ab
		green manure			5.7 b		141.8 b	114 b		0.79 ab
		compost			14.4 a		70.7 b	140 b		0.39 b
		Chilean nitrate			4.0 b		62.3 b	205 b		0.48 ab
	High collembola	no fertilizer			15.1 a		63.0 b	647 a		0.46 ab
		green manure			8.9 b		78.8 b	229 b		0.57 ab
		compost			13.4 a		77.8 b	121 b		1.04 a
		Chilean nitrate			4.0 b		41.0 b	199 b		0.52 ab
Harvest 2	**P-Value**	Collembola	**0.0005**	**0.0104**	**0.0001**	0.7870	0.8138	0.3567	0.3896	0.2190
		Fertilizer	**1.53E-14**	**2.00E-16**	**2.20E-16**	0.1003	**0.0145**	0.1023	**0.0024**	**0.0182**
		Collembola x Fertilizer	0.5856	0.0509	0.4645	0.7070	0.7418	0.6413	0.3077	0.5134
	Main Effects									
	Collembola	control	207 a	10.1 b	20.0 a		99.1		0.74	0.59
		low density	197 a	12.8 a	14.9 b		94.5		0.64	0.45
		high density	163 b	12.1 ab	12.7 b		94.1		0.62	0.52
	Fertilizer	no fertilizer	271 a	2.7 b	101.0 a		102.5 a		0.96 a	0.72 a
		green manure	166 c	20.6 a	7.9 c		105.0 a		0.59 b	0.44 b
		compost	209 b	17.0 a	12.1 b		101.8 ab		0.60 b	0.49 ab
		Chilean nitrate	109 d	19.4 a	5.4 d		77.1 b		0.55 b	0.45 b

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 presence of high Collembola abundances compared to the absence of Collembola. The pots that revied compost with high Collembola abundances had greater peroxidase activity than the pots that received compost with low Collembola abundances. In the absence of Collembola, the green manure pots had greater LAP activity than the other fertilizer treatments and the compost pots had greater PHOS activity than the nonamended soil. The nonamended soil had the greatest PHENOX activity compared to the soils with fertilizers added (Table 2).

At harvest 2, there was greater LAP activity in the nonamended and green manure pots compared to the Chilean nitrate pots. The nonamended pots had the greatest PHENOX activity. There was 39% greater peroxidase activity when there was no fertilizer compared to the pots that received green manure and Chilean nitrate (Table 2).

Soil Carbon and Nitrogen

At harvest 1, in the high Collembola treatment soils receiving no fertilizer or compost had greater soil carbon than those receiving Chilean nitrate (Table 1). At harvest 2, in the no Collembola treatment, the nonamended soil had greater soil carbon than the soil that received compost and Chilean nitrate. However, in the low Collembola treatment the nonamended soil had greater soil carbon than the green manure and Chilean nitrate, and the compost had greater soil carbon than the green manure (Table 1).

The soil C:N ratio was affected by the Collembola at harvest 1, with soils with high Collembola abundances having greater ratios than the soils with low Collembola abundances (Table 1). In contrast, the soil C:N ratios were affected by the fertilizer treatments at harvest 2,

with the nonamended soil having a greater ratio than the soils that received each of the other fertilizer treatments (Table 1).

3.1.3 Redundancy Analysis and Metric Correlations

The results of the redundancy analysis aligned well with those from the univariate ANOVA. 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 (Appendix C). At harvest 1, microbial biomass nitrogen and carbon and the microbial enzymes LAP and BG were significantly correlated to the plant metrics (Figure 2; Appendix C). At harvest 2, microbial biomass nitrogen and carbon and the microbial enzyme BG were significantly correlated to the plant metrics (Figure 2; Appendix C).

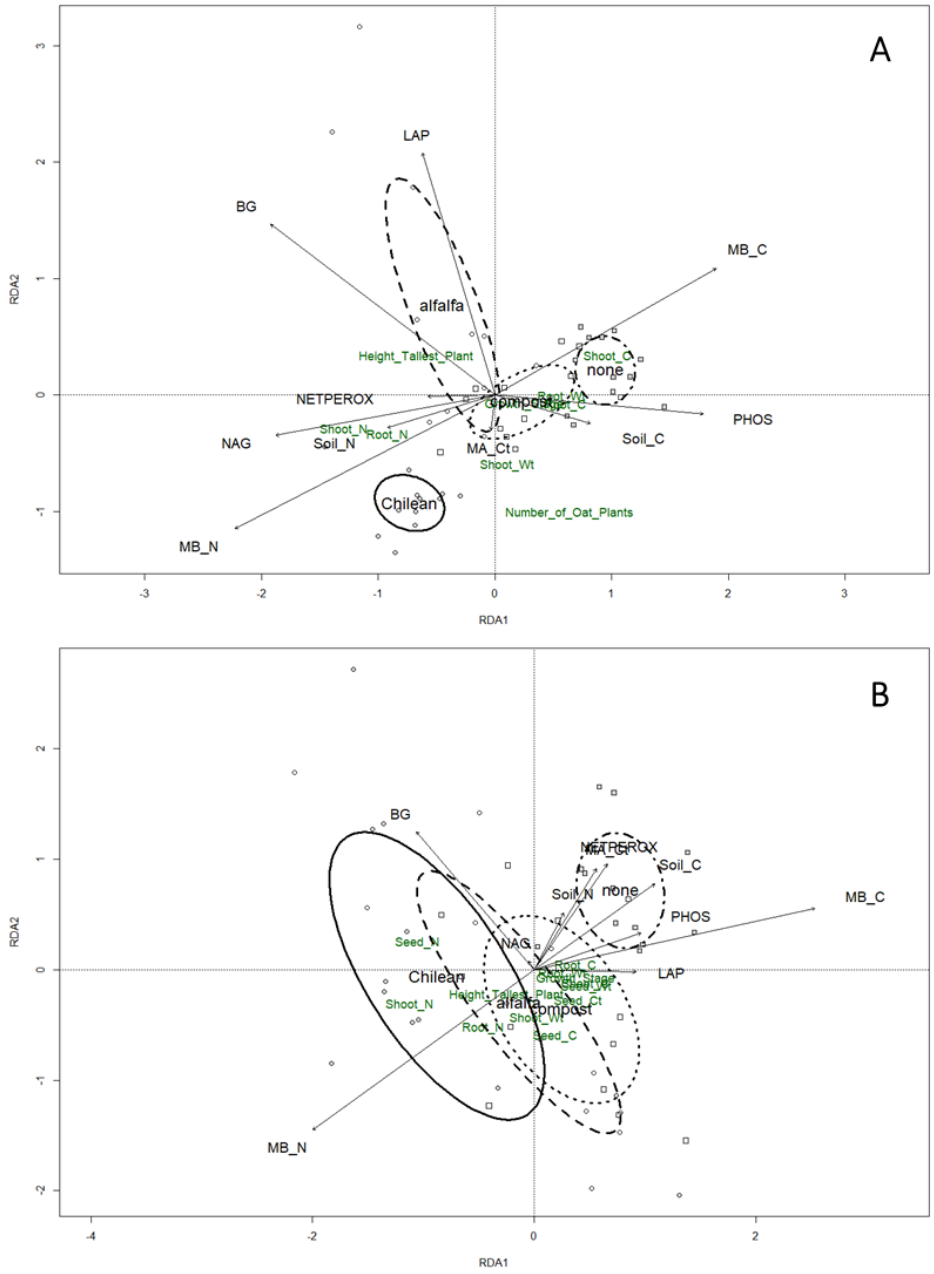

Figure 2. Ordinations of the redundancy analysis indicating the relationships between the soil and plant metrics at harvest 1 (A) and harvest 2 (B) in the single species experiment to evaluate the effect of the soil metrics on plant growth. Arrows represent soil metrics and green text indicates plant metrics. Ellipse lines indicate fertilizer treatment: none = dashes and dots, alfalfa = all dashes, compost = all dots, Chilean nitrate = solid line.

3.2 Results – 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 ($P<0.0001$; # individual per pot: control = 0 ±0, low = 42.7 ±3, high 130.9 ±5).

3.2.2 Weekly Plant Growth Metrics

Seedling emergence was significantly affected by the fertilizer treatments at weeks one and two (Appendix D). Seedling emergence was lower in pots receiving green manure 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. Generally, oats that received green manure were developmentally behind the other fertilizer treatments (Appendix D).

3.2.3. Harvest Metrics

Microarthropod Abundances

At harvest 1, within the low fauna treatment, the green manure pots had more microarthropods than the other fertilizer treatments, and within the high fauna treatment the green manure pots had more microarthropods than the Chilean nitrate (Figure 3). At harvest 2, fauna-free controls had fewer microarthropods than the low and high fauna treatments, and the green manure had more microarthropods than the three other fertilizer treatments (Figure 3). The initial microarthropod communities added to the pots ($P=0.99$) and the community composition at both harvests did not differ between the fauna or fertilizer treatments.

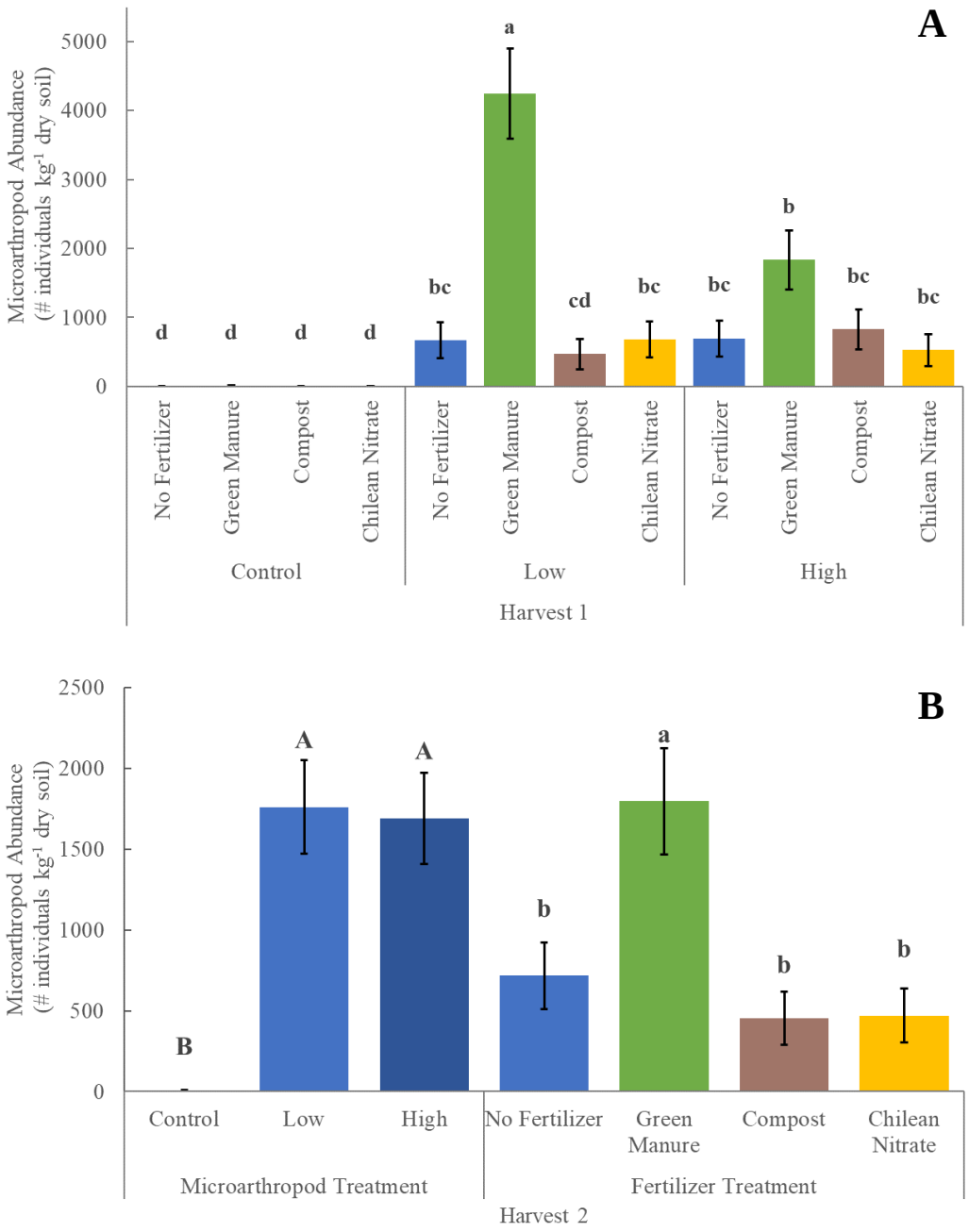

Figure 3. Fauna abundance and fertilizer effects on microarthropod abundances (# individuals kg^{-1} dry soil) in the diverse community experiment at harvest 1 (A) and harvest 2 (B). Separate mean comparisons were conducted for each treatment main effect at harvest 2. Bars with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

The initial microarthropod communities added to the pots (P=0.99) and the community composition at both harvests did not differ between the fauna or fertilizer treatments. However, microarthropod species richness was affected by the fauna treatment at both harvests, at each time point taxon diversity increased as fauna abundance increased (P= 2.00E-16 and P= 2.78E-16).

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 Chilean nitrate and compost produced more shoot biomass than those that received no fertilizer and green manure, and the oats that received green manure produced less root biomass than those that received the other three fertilizer treatments (Figure 4). However, when the lower germination in the green manure pots is accounted for, the shoot biomass differences were not significantly different between the three fertilizers (P>0.05). At harvest 2, the oats that received Chilean nitrate produced more shoot biomass than all other treatments and the nonamended soil produced less oat shoot biomass than the other treatments (Figure 4). However, at harvest 2, the absence of fertilizer led to greater oat root biomass than the other treatments except for the Chilean nitrate. Also at harvest 2, oat seed numbers and biomass were significantly higher in pots receiving Chilean nitrate and compost than those receiving no fertilizer and green manure (Figures 4 & 5), but the oats grown in green manure were developmentally delayed by up to 10 growth stages (Appendix D).

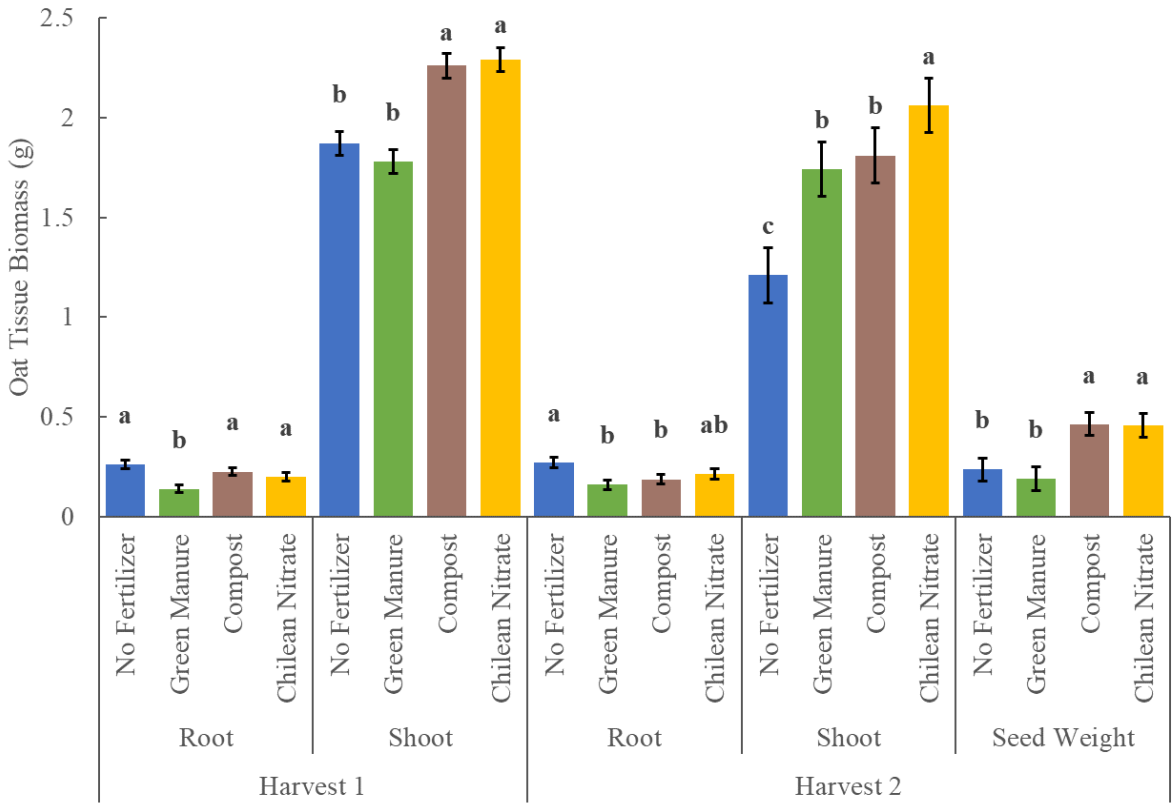

Figure 4. Fertilizer effect on oat tissue biomass in the diverse community experiment to evaluate oat growth. Separate mean comparisons were conducted for each oat tissue type within each harvest time point. Bars with the same letters are not significantly different (Fisher's LSD, P > 0.05).

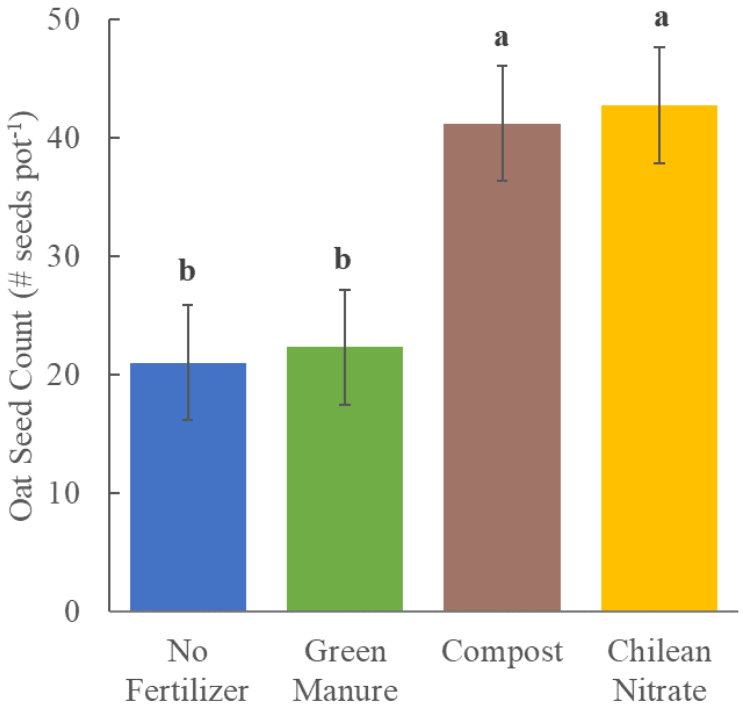

Figure 5. Fertilizer treatment effects on oat seed count at harvest 2 in the diverse community experiment to evaluate grain production. Bars with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

Oat Tissue Carbon and Nitrogen

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

By harvest 2, we observed similar effects on the oat root and shoot carbon and nitrogen content as at harvest 1. At harvest 2, the seeds also showed very similar effects of the fertilizer treatment with the nitrogen and carbon content generally increasing as the fertilizer source was

more plant available and the C:N ratio decreasing as the fertilizer source was more plant available, however there were no effects of the microarthropods on the carbon and nitrogen content of the seeds (Table 3). Oat seed carbon and nitrogen content were significantly affected by the application of green manure since the oats in that treatment matured slower than the other treatments and were less developed (Table 3; Appendix D).

Table 3. The effect of fauna abundance and fertilizer treatments on the nutrient composition of soils and plant tissues for the diverse community experiment. Significance levels from the ANOVAs performed the metrics with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

			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
Harvest 1	**P-Value**	Fauna	2.34E-05	1.36E-06	3.16E-06	0.1363	**0.0351**	**0.0087**	**1.63E-06**	**0.0245**	1.02E-07			
		Fertilizer	0.0017	0.8454	0.1649	**2.00E-16**	**0.0500**	**2.20E-16**	**2.20E-16**	**0.0004**	2.20E-16			
		Fauna x Fertilizer	**0.0164**	**0.0007**	**0.0008**	0.1250	0.3773	0.0541	0.4093	0.5559	**0.0002**			
	Main Effects													
	Fauna	control				1.1	35.1 ab	33.3 a	2.4 b	41.6 b				
		low density				1.2	35.6 a	31.0 ab	2.5 b	41.9 ab				
		high density				1.2	33.9 b	30.0 b	2.8 a	42.3 a				
	Fertilizer	no fertilizer				0.8 b	34.6 ab	43.6 a	1.4 c	41.6 bc				
		green manure				1.4 ab	33.8 b	24.7 c	3.7 a	41.4 c				
		compost				1.1 b	36.0 a	33.0 b	2.2 b	42.5 a				
		Chilean nitrate				1.5 a	35.0 ab	24.5 c	3.7 a	42.2 ab				
	Interaction Effects													
	No fauna	no fertilizer	0.177 ab	6.9 a	39.4 a						31.5 a			
		green manure	0.176 abc	5.4 b	31.2 c						11.9 e			
		compost	0.186 a	6.7 ab	36.2 ab						22.3 bc			
		Chilean nitrate	0.172 bc	5.8 b	33.9 bc						12.1 e			
	Low fauna	no fertilizer	0.167 c	5.2 b	31.1 c						33.0 a			
		green manure	0.181 ab	5.8 b	32.2 bc						11.6 e			
		compost	0.176 a	5.4 b	30.9 c						20.3 cd			
		Chilean nitrate	0.172 bc	5.8 b	33.5 bc						11.7 e			
	High fauna	no fertilizer	0.165 c	4.9 b	29.5 c						25.8 b			
		green manure	0.176 a	5.4 b	30.6 c						11.1 e			
		compost	0.165 c	5.1 b	31.1 c						17.6 d			
		Chilean nitrate	0.165 c	5.3 b	31.9 bc						10.9 e			
Harvest 2	**P-Value**	Fauna	**0.0022**	1.98E-11	4.16E-12	**0.0057**	**0.0066**	**0.0003**	**2.66E-05**	0.2076	**7.82E-07**	0.6625	0.5023	0.3680
		Fertilizer	**5.17E-12**	0.0147	9.30E-11	**2.20E-16**	**0.0026**	**6.86E-16**	**2.20E-16**	0.0619	**2.20E-16**	**7.95E-08**	**0.0017**	**1.86E-06**
		Fauna x Fertilizer	0.0865	**0.0044**	**0.0031**	0.2730	0.3597	0.8887	0.3620	0.4008	0.1535	0.7846	0.6749	0.4917
	Main Effects													
	Fauna	control	0.195 a			0.86 b	37.2 ab	45.2 a	1.2 b		38.6 a	1.8	28.0	18.4
		low density	0.182 b			0.89 ab	37.9 a	44.1 ab	1.3 b		36.0 b	1.9	36.0	20.3
		high density	0.190 ab			0.96 a	36.0 b	39.1 c	1.5 a		32.4 c	1.9	36.1	20.4
	Fertilizer	no fertilizer	0.167 b			0.67 c	35.5 b	53.9 a	0.8 d		54.4 a	1.4 b	32.8 ab	25.6 a

	green manure	0.192 a			0.99 b	37.1 ab	39.0 bc	1.7 b		25.3 c	1.4 b	17.0 b	15.3 c
	compost	0.196 a			0.89 b	37.4 a	42.6 b	1.0 c		42.3 b	2.3 a	46.4 a	20.5 b
	Chilean nitrate	0.200 a			1.09 a	38.1 a	35.8 c	2.1 a		20.8 d	2.7 a	46.3 a	17.4 bc
Interaction Effects													
No fauna	no fertilizer		7.0 a	40.2 a									
	green manure		5.7 bc	29.0 d									
	compost		6.5 ab	33.5 bc									
	Chilean nitrate		7.1 a	33.8 bc									
Low fauna	no fertilizer		5.5 c	34.3 b									
	green manure		5.8 bc	30.2 cd									
	compost		5.6 bc	29.2 d									
	Chilean nitrate		5.6 bc	30.3 cd									
High fauna	no fertilizer		5.0 c	30.2 cd									
	green manure		5.1 c	26.9 d									
	compost		5.4 c	27.0 d									
	Chilean nitrate		5.7 b	28.6 d									

Microbial Biomass Carbon and Nitrogen

At harvest 1, within the high fauna treatment soil that received the Chilean nitrate had up to 72% less microbial carbon than the soil that received the other fertilizer treatments (Table 4). The pots with no fauna had 19% less microbial biomass nitrogen than the pots with low and high fauna abundances, and the nonamended soils had up to 33% less microbial biomass nitrogen than the soils that received the other three fertilizer treatments. The pots with high fauna abundances had lower microbial biomass C:N ratio than those with no fauna, and the soils that received Chilean nitrate had a lower ratio than the soils with no fertilizer and compost (Table 4).

At harvest 2, the soils that received compost had 29% greater microbial biomass carbon than the soils that received Chilean nitrate (Table 4). The pots with high fauna abundances had 14% greater microbial biomass nitrogen than those with no fauna, and the soils that received compost had greater microbial biomass nitrogen than the soils that received no fertilizer and Chilean nitrate. The soils that received Chilean nitrate had less microbial biomass nitrogen than those that received all the other fertilizer treatments (Table 4).

Table 4. The effect of fauna abundance and fertilizer treatments on the microbial metrics for the diverse community experiment. Significance levels from the ANOVAs performed the metrics with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

			Microbial C	Microbial N	Microbial C:N	NAG	BG	LAP	PHOS	PHENOX	Peroxidase
Harvest 1		Fauna	0.1247	**0.0006**	**0.0021**	0.1505	0.9104	0.0088	0.6092	0.4339	0.2162
	P-Value	Fertilizer	0.0022	**3.25E-06**	**1.06E-05**	0.0001	0.3051	0.0000	0.7697	0.7988	0.6501
		Fauna x Fertilizer	**0.0321**	0.1729	0.0538	**0.0005**	**0.0057**	**3.32E-05**	**0.0141**	**0.0007**	0.4397
	Main Effects										
	Fauna	control		20.8 b	9.2 a						
		low density		25.6 a	7.3 ab						
		high density		25.4 a	6.3 b						
	Fertilizer	no fertilizer		18.5 b	10.4 a						
		green manure		27.5 a	6.1 bc						
		compost		23.7 a	8.3 ab						
		Chilean nitrate		26.0 a	5.6 c						
	Interaction Effects										
	No fauna	no fertilizer	174.8 a			16.7 a	16.8 a	10.0 b	51.8 a	0.13 ab	
		green manure	167.7 a			10.8 b	13.0 ab	5.1 d	36.4 a	0.22 ab	
		compost	194.9 a			13.1 ab	15.2 ab	17.6 ab	40.2 a	0.63 a	
		Chilean nitrate	188.6 a			8.4 b	10.1 b	4.3 d	41.2 a	0.30 ab	
	Low fauna	no fertilizer	192.9 a			12.1 a	14.7 ab	7.9 c	43.7 a	0.20 ab	
		green manure	176.5 a			13.6 a	12.5 ab	6.3 cd	46.0 a	0.25 ab	
		compost	195.4 a			12.1 a	14.2 ab	7.8 c	44.9 a	0.27 ab	
		Chilean nitrate	137.3 a			8.6 b	13.1 ab	4.1 d	39.0 a	0.21 ab	
	High fauna	no fertilizer	206.9 a			9.5 b	12.6 ab	19.2 a	32.6 b	0.67 a	
		green manure	148.4 a			13.3 a	13.6 ab	10.3 bc	48.1 a	0.29 ab	
		compost	190.3 a			10.7 b	11.5 ab	6.7 cd	41.6 a	0.02 b	
		Chilean nitrate	58.4 b			9.9 b	15.9 ab	4.9 d	40.9 a	0.49 ab	
Harvest 2		Fauna	0.7117	**0.0396**	0.6590	0.0033	0.2401	0.0760	0.3015	**0.0351**	0.0913
	P-Value	Fertilizer	**0.0356**	**4.17E-06**	0.7016	1.10E-09	0.2326	**4.13E-07**	3.78E-66	0.0649	**0.0001**
		Fauna x Fertilizer	0.1283	0.1692	0.8841	**4.97E-08**	0.0605	0.1536	**0.0002**	0.5985	0.0907
	Main Effects										
	Fauna	control	140	10.8 b				6.57		0.31 b	0.36
		low density	152	11.4 ab				8.1		0.44 a	0.34
		high density	148	12.5 a				7.74		0.43 ab	0.40

Fertilizer	no fertilizer	151 ab	11.2 b			9.07 ab	0.32	0.46 ab
	green manure	154 ab	12.1 ab			6.80 b	0.43	0.23 c
	compost	164 a	13.9 a			10.02 a	0.36	0.34 bc
	Chilean nitrate	117 b	9.1 c			4.89 c	0.47	0.50 a
Interaction Effects								
No fauna	no fertilizer			15.1 a		55.3 a		
	green manure			8.3 b		31.3 b		
	compost			8.4 b		37.5 b		
	Chilean nitrate			6.0 c		30.4 b		
Low fauna	no fertilizer			7.7 bc		35.4 b		
	green manure			9.1 b		35.0 b		
	compost			9.6 b		46.8 a		
	Chilean nitrate			5.9 c		26.7 b		
High fauna	no fertilizer			8.2 bc		33.2 b		
	green manure			7.5 c		38.4 b		
	compost			10.7 b		43.2 a		
	Chilean nitrate			5.8 c		26.9 b		

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 treatment. Within the no fauna treatment, 40% more BG was produced in the soils that received no fertilizer compared to the soils that received Chilean nitrate. The lowest PHOS activity was in the high fauna treatment when there was no fertilizer added. The compost fertilizer affected PHENOX activity variability the most, with the greatest activity in the absence of fauna and the least activity when high fauna abundances were present.

At harvest 2, NAG and PHOS were also impacted by the fauna and fertilizer interactions (Table 4). LAP and peroxidase were only impacted by the fertilizer treatments (Table 4). There was greater LAP activity in the pots that received compost compared to those that recieved green manure and Chilean nitrate, and in the nonamended and green manure pots compared to the Chilean nitrate pots. There was greater net peroxidase activity in the soils that received Chilean nitrate compared to those that received the compost and green manure, and in the nonamended soil compared to the soil that received green manure (Table 4). Collembola 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 green manure had the greatest nitrogen content, however when fauna were not present, the soils that received compost had the greatest nitrogen content (Table 3). At harvest 2, the soil nitrogen content was slightly greater in the no and high fauna treatments and in the absence of fertilizer soil nitrogen was reduced by up to 16% (Table 3). At both harvests, the soil carbon tended to decrease as

microarthropod abundance increased with soil carbon increasing as the fertilizer source was more plant available, however this effect was more pronounced when there were no microarthropods present.

At harvest 1, the soil C:N ratio generally decreased as microarthropod abundances increased, and in the absence of fauna the fertilizer source affected the C:N ratio (Table 3). A similar trend was also observed at harvest 2, however the effect of the fertilizer was observed in all fauna treatments, though the fertilizer had less of an impact on the C:N ratio as microarthropod abundance increased (Table 3).

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 (Appendix C). At harvest 1, microarthropod abundance, microbial biomass nitrogen, and the microbial enzymes NAG and LAP were significantly correlated to the plant metrics (Figure 6; Appendix C). At harvest 2, the microbial enzymes NAG and BG, and soil carbon and nitrogen content were all significantly correlated to the plant metrics (Figure 6; Appendix C).

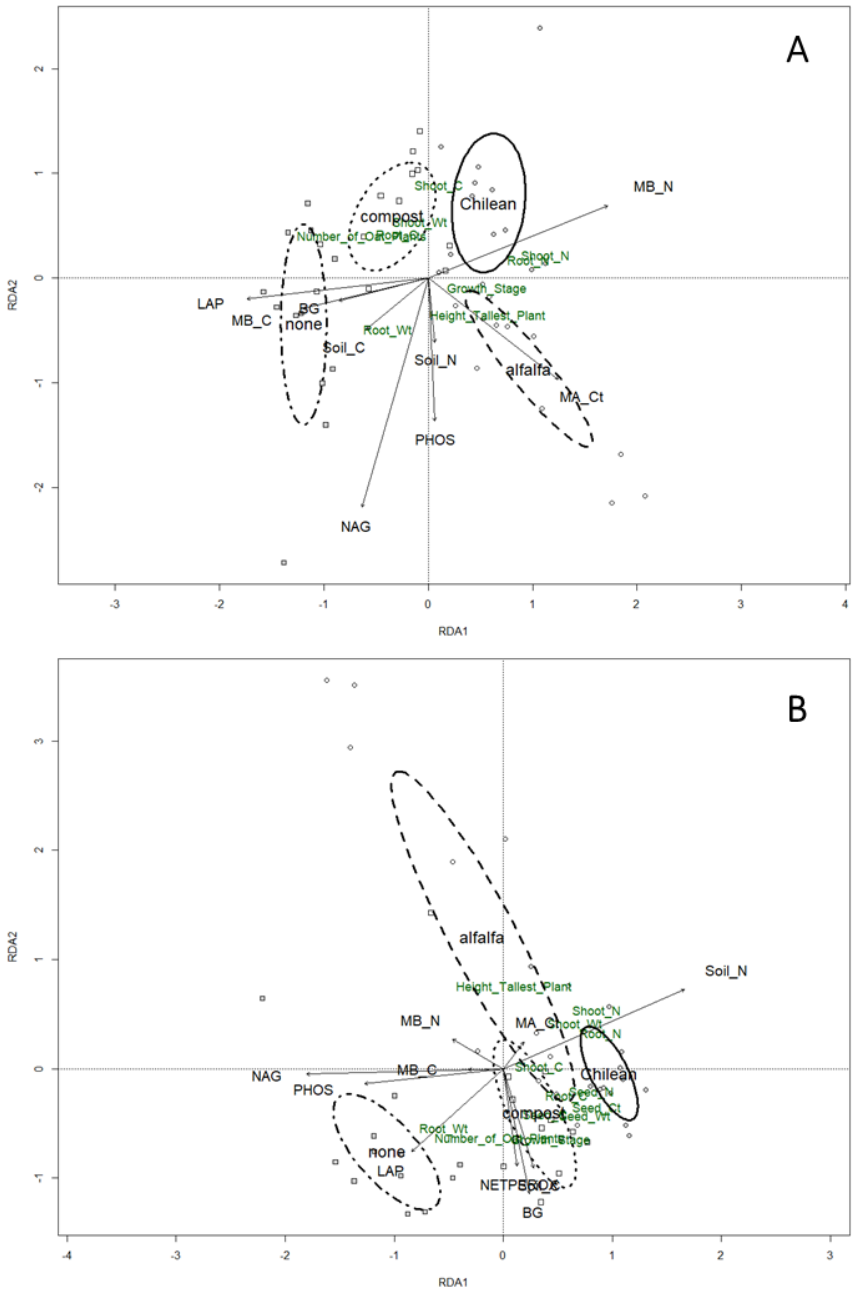

Figure 6. Ordinations of the redundancy analysis indicating the relationships between the soil and plant metrics at harvest 1 (A) and harvest 2 (B) in the diverse community experiment to evaluate the effect of the soil metrics on plant growth. Arrows with corresponding text represent soil metrics and green text indicates plant metrics. Ellipse lines indicate fertilizer treatment: none = dashes and dots, alfalfa = all dashes, compost = all dots, Chilean nitrate = solid line.

4. DISCUSSION

4.1. Drivers of Oat Production Outcomes

4.1.1. Microarthropods

The addition of microarthropods, either single species or diverse communities, improved the nutritional quality of the oats by stimulating nitrogen uptake. Given the important role that microarthropods play in nitrogen availability in soils (Filser, 2002; Verhoef and Brussaard, 1990) this positive effect on nitrogen uptake was expected. The presence of Collembola has been found to increase the uptake of nitrogen in annual bluegrass (*Poa annua* L.), perennial ryegrass (*Lolium perenne* L.), and white clover (*Trifolium repens* L.) (Forey, Coulibaly and Chauvat, 2015; Scheu, Theenhaus and Jones, 1999; Winck *et al.*, 2020). Interestingly, in our study the magnitude of the effect of microarthropods on oat tissue nitrogen content varied between the forage and grain harvest dates. 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, reproduction (seeds)), despite many other studies finding microarthropods to affect the growth of annual grass species (Chauvat and Forey, 2021; Eisenhauer *et al.*, 2018; Forey, Coulibaly and Chauvat, 2015; Kuťáková *et al.*, 2018). Other studies using diverse microarthropod assemblages found positive effects of microarthropods on plant reproductive measurements (Eisenhauer *et al.*, 2018; Forey, Coulibaly and Chauvat, 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 nitrogen 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, Bonkowski and Scheu, 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.

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, LAP) to soil nutrient content and microbial enzyme activity (soil N, soil C, NAG, BG). This shift in the soil metrics relationships with the plant growth metrics suggests 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, Haberkorn and Ortiz, 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 nitrogen 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 nitrogen 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 alfalfa green manure had unique effects on oat growth. The alfalfa green manure 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 and Beauchamp, 2002; Swift, Heal and Anderson, 1979; Thambirajah, Zulkali and Hashim, 1995).

The primary and secondary metabolites in the alfalfa green manure may be driving specific oat growth and development outcomes. In both experiments oat germination was negatively impacted by the application of alfalfa green manure. Despite their many benefits, there is evidence that some green manures contain allelochemicals that inhibit the germination of monocotyledonous plant species (Rugare, Pieterse and Mabasa, 2021; Singh, Batish and Kohli, 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. 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 carbon (Kallenbach and 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 carbon. This may be due to the nitrogen 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 and Ladd, 1981; McGill *et al.*, 1982). The effects of the microarthropods on the ratio of C:N in the microbial biomass was greater in the single-species experiment compared to the microarthropod community experiment. In both experiments, the overall trend was 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 and Sinsabaugh, 2006; Saqib and John Whitney, 2006). These results align with previous findings of microarthropod presence having mixed effects on microbial enzyme activity (Crowther, Boddy and Hefin Jones, 2012; Wickings and 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. At the same time, BG was rarely affected by the microarthropod and fertilizer treatments imposed, aside from the minor treatment effects observed at the second harvest in the diverse community experiment. 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 because it is not strongly affected by external factors such as other soil biota or fertilizer amendments in this study.

4.3. Conclusions

Our study illustrated that microarthropods, both single species and diverse communities, stimulated nitrogen 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 soils 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.

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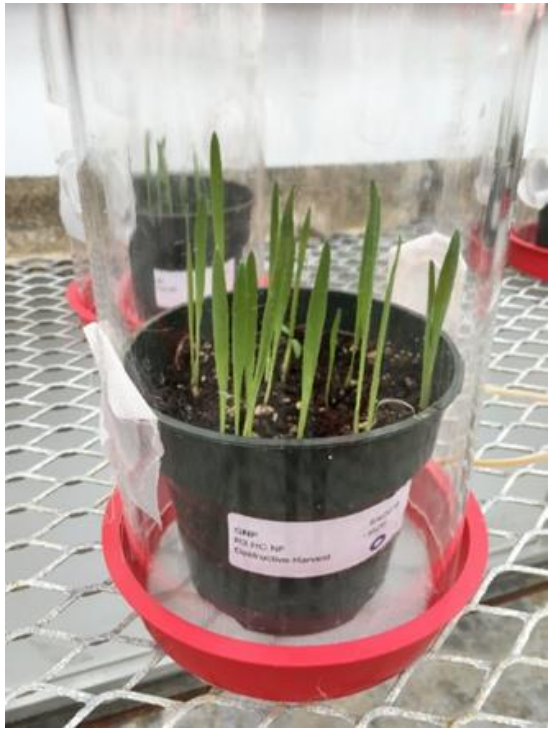
Appendices

Appendix A. Experimental set up photos.



Appendix B. The effect of Collembola abundance and fertilizer treatments on oat growth from the single species experiment weekly checks. Significance levels from the ANOVAs performed the metrics with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

		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 Shortest	Height of Tallest	Height of Tallest	Height of Tallest	Height of Tallest
P-Value	Collembola	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
	Fertilizer	**0.0259**	**0.0005**	**1.20E-14**	0.0649	**0.0049**	**1.79E-06**	0.0014	**1.35E-08**	**0.0002**	**0.0079**	**0.0001**	**0.0004**	**0.0004**	**0.0010**
	Collembola x Fertilizer	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
Main Effects															
Collembola	control	14.6	2.1	18.5 a	11.1	30.4	14.3	12.1	39.6	41.5	26.9	57.0	50.2	50.6 a	50.1
	low density	14.8	2.6	20.0 a	11.1	30.4	14.8	12.1	40.2	44.8	27.1	53.1	47.0	46.3 b	46.6
	high density	14.8	2.9	20.2 a	11.0	29.8	14.7	12.0	38.3	41.6	28.0	53.4	46.6	45.8 b	45.7
Fertilizer	no fertilizer	14.2 b	3.1 a	21.2 a	11.0	28.3 b	15.6 a	12.0	35.6 c	37.3 b	26.3 ab	49.0 c	43.1 c	42.9 c	43.0 c
	green manure	14.4 ab	1.3 b	14.5 b	11.1	31.2 a	13.4 b	12.2	43.0 a	46.3 a	25.2 b	60.2 a	53.7 a	53.4 a	53.1 a
	compost	15.1 ab	2.8 a	21.8 a	11.1	31.2 a	15.6 a	12.0	40.4 ab	43.4 a	28.4 ab	52.5 bc	45.6 bc	45.1 bc	45.2 bc
	Chilean nitrate	15.2 a	3.5 a	20.8 a	11.0	30.0 ab	15.0 a	12.0	38.5 b	43.5 a	29.4 a	56.2 ab	49.4 ab	48.8 ab	48.6 ab
Interaction Effects															
No collembola	no fertilizer				11.0 b			12.0 b							
	green manure				11.0 b			12.5 a							
	compost				11.4 a			12.0 b							
	Chilean nitrate				11.0 b			12.0 b							
Low collembola	no fertilizer				11.0 b			12.0 b							
	green manure				11.2 ab			12.1 b							
	compost				11.0 b			12.1 b							

	Chilean nitrate	11.0 b	12.0 b
High collembola	no fertilizer	11.0 b	12.0 b
	green manure	11.1 b	12.0 b
	compost	11.0 b	12.0 b
	Chilean nitrate	11.0 b	12.0 b

Appendix C. Redundancy analysis (RDA) results data for both the single species and diverse community experiments at both harvests. Significant P-values (<0.05) are bolded.

	Single-Species Experiment						Diverse Community Experiment					
PerMANOVA model	**Forage Harvest**			**Grain Harvest**			**Forage Harvest**			**Grain Harvest**		
Degrees of freedom	10			10			9			10		
F-value	2.79			1.43			1.97			2.41		
P-value	0.001			0.042			0.003			0.001		
Soil Variable	**Variance**	**F-Value**	**P-Value**	**Variance**	**F-Value**	**P-Value**	**Variance**	**F-Value**	**P-Value**	**Variance**	**F-Value**	**P-Value**
Microarthropod Abundance	0.1648	1.18	0.304	0.2578	1.10	0.288	0.5074	3.14	**0.024**	0.1883	0.88	0.456
Microbial Biomass N	1.5422	11.12	**0.002**	1.0471	4.48	**0.002**	0.6558	4.06	**0.002**	0.2706	1.27	0.244
Microbial Biomass C	0.3785	2.73	**0.016**	0.6484	2.77	**0.016**	0.2479	1.53	0.176	0.1166	0.54	0.764
NAG	0.1652	1.19	0.328	0.161	0.68	0.656	0.4956	3.07	**0.014**	1.3403	6.30	**0.004**
LAP	0.5903	4.25	**0.002**	0.1157	0.49	0.838	0.370	2.29	**0.04**	0.3383	1.59	0.164
BG	0.4061	2.92	**0.012**	0.5701	2.44	**0.048**	0.259	1.60	0.166	0.9791	4.60	**0.004**
PHOS	0.159	1.14	0.316	0.1395	0.59	0.634	0.0226	0.13	0.994	0.0615	0.28	0.96
NETPEROX	0.108	0.77	0.576	0.1977	0.84	0.522	0.000	0.01	1.00	0.2637	1.24	0.274
Soil N	0.1692	1.22	0.274	0.1185	0.50	0.768	0.1406	0.87	0.468	0.7753	3.64	**0.006**
Soil C	0.1869	1.34	0.204	0.1007	0.43	0.892	0.1738	1.07	0.36	0.7993	3.75	**0.01**

Appendix D. The effect of fauna abundance and fertilizer treatments on oat growth from the diverse community experiment weekly checks. Significance levels from the ANOVAs performed the metrics with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

		Week 1			Week 2		Week 3		Week 4			Week 5		Week 6		Week 7		Week 8	
		Growth Stage	Height of Tallest	Number of Plants	Height of Tallest	Number of Plants	Growth Stage	Height of Tallest	Growth Stage	Height of Tallest	Number of Plants	Growth Stage	Height of Tallest	Growth Stage	Height of Tallest	Growth Stage	Height of Tallest	Growth Stage	Height of Tallest
P-Value	Fauna	0.5938	0.9188	0.3400	0.8667	0.3109	0.7083	0.4702	0.8705	0.2315	0.2223	**0.0081**	0.5008	0.6935	0.4128	0.4656	0.7912	0.6897	0.6390
	Fertilizer	**2.78E-15**	**2.60E-14**	**2.00E-16**	**0.0013**	**2.00E-16**	**4.40E-09**	**0.0003**	**4.19E-09**	**2.05E-06**	**1.79E-14**	**2.66E-12**	**8.62E-15**	**2.35E-05**	**2.00E-16**	**1.73E-05**	**1.96E-07**	**0.0019**	**3.12E-06**
	Fauna x Fertilizer	0.2561	0.0945	0.3473	0.5448	0.9660	0.9530	0.6136	0.2314	0.6071	0.1436	0.4719	0.3410	0.3357	0.2828	0.4025	0.9620	0.6921	0.9822
Main Effects																			
Fauna	control	10.6	6.3	18.5	18.7	19.0	21.4	34.6	31.3	40.8	14.3	32.3 b	43.8	41.5	48.3	58.6	53.9	62.8	58.8
	low density	10.5	6.2	18.1	18.5	18.8	20.3	34.5	31.3	39.8	14.6	32.4 b	42.8	40.8	47.2	58.6	55.6	62.8	60.4
	high density	10.4	6.1	17.5	18.9	18.1	21.5	35.7	31.4	41.8	14.0	32.7 a	44.0	40.7	46.5	56.4	55.4	61.2	61.5
Fertilizer	no fertilizer	11.0 a	6.9 a	21.2 a	18.8 a	21.3 a	21.2 b	32.8 b	31.0 b	36.2 b	15.2 a	31.6 c	36.2 d	40.1 bc	38.3 d	57.7 b	43.0 c	63.0 a	49.5 c
	green manure	9.1 b	4.3 c	11.0 c	16.8 b	12.6 b	13.4 c	33.2 b	30.6 c	42.3 a	11.8 b	32.6 c	49.6 a	38.1 c	57.2 a	49.7 c	66.3 a	56.5 b	71.7 a
	compost	10.9 a	7.4 a	20.2 ab	19.9 a	20.5 a	25.1 a	36.6 a	31.9 a	41.6 a	15.0 a	32.7 ab	42.5 c	44.3 a	45.2 c	61.3 ab	54.8 b	63.5 a	60.8 b
	Chilean nitrate	10.9 a	6.1 b	19.6 b	19.2 a	20.0 a	24.5 ab	37.2 a	31.8 a	43.0 a	15.0 a	33.0 a	46.0 b	41.4 b	48.7 b	62.8 a	55.8 b	66.0 a	58.9 b

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CHAPTER 4

ISOTOMIELLA MINOR REDUCES WEED BIOMASS AND DRIVES OUTCOMES OF WEED COMMUNITY ASSEMBLAGE

ABSTRACT

The goals of building soil health and controlling weeds in organic agricultural systems are often at odds given the limited management strategies available to organic producers. Increasing our understanding of biotic controls on agricultural pests may help bridge this divide. Soil microarthropods are a unique group of fauna in soil ecosystems that may contribute to balancing these two goals in crop production. Soil microarthropod feeding behavior can affect plant growth through multiple mechanisms, although their impacts on agricultural plant communities is largely unknown. A greenhouse experiment was conducted in 2021 to investigate if microarthropods impact weed community assemblage. A model weed seed bank, consisting of seeds from six taxonomically diverse (2 grasses + 4 broadleaves) summer annual weed species, was used. The study included four different treatments: Collembola (*Isotomiella minor*, Schaffer 1896) abundance (none, low, high), soil microbial presence (sterilized/unsterilized), seed starting condition (sterilized/unsterilized), and fertilizer (presence/absence of compost). This setup was meant to create environments with varying levels of resource amount and diversity. Collembola increased weed germination during the first week, but reduced germination after the third week. At harvest the Collembola reduced weed counts more for the broadleaf weeds than the grass weeds. The Collembola had decreased total weed biomass production by up to 23%. Collembola decreased broadleaf weed biomass (up to 45% reduction for certain species) more than the grass weed biomass. A follow-up lab experiment was conducted to understand the potential

mechanisms driving the greenhouse experiment results by examining individual weed species interactions with Collembola. Collembola only affected the germination of yellow foxtail in the lab experiment, indicating that the Collembola were more likely impacting the broadleaf weed growth by feeding on their roots than directly affecting germination in the greenhouse experiment. Our findings indicate that Collembola, and microarthropods in general, likely have the potential to play a role in weed management decisions in agricultural systems.

INTRODUCTION

The theory of community assembly in ecology looks at how communities are assembled over time as they are affected by both biotic and abiotic constraints that act as filters (Booth and Swanton, 2002). This theory has been applied to weed communities in agricultural settings to determine how management filters such as tillage affect weed community structure (Booth and Swanton, 2002). However, weed ecologists have yet to begin exploring soil biota as potential filters in weed community assembly. This connection between soil biota and weed communities remains an unknown axis of soil health.

Organic agriculture faces the challenge of balancing weed control with soil health (Osterholz *et al.*, 2021). These two important factors in crop production are often at odds since soil cultivation is the primary tool organic farmers have for weed control, yet tillage is known to reduce soil health (Pearsons *et al.*, 2023; Rubio, Sawchik and van Es, 2022a). There is a need to improve the balance between soil health and weed control in these agricultural systems.

Soil microarthropods may be the key to balancing these two goals in crop production. Soil microarthropods are a group of small invertebrates (100µm to 2mm) dominated by Collembola and mites that play an important role in multiple soil biological processes.

Microarthropods affect soil microbial communities through their feeding and movement through soils (Anderson, Coleman and Cole, 1981). Most notably, microarthropods affect organic matter decomposition and nutrient cycling through direct consumption of organic matter and indirectly through the grazing of microbial communities (Soong and Nielsen, 2016). The presence of microarthropods has been shown to increase seedling establishment, primary plant productivity, and crop yields by increasing nutrient mineralization (Eisenhauer et al., 2018; Kaneda et al., 2012; Kuťáková et al., 2018; Soong et al., 2016).

While existing literature suggests the effects that microarthropods have on crop plants through feeding on beneficial microbes is generally positive, it is evident that this relationship is taxon dependent and does not always occur (Jernigan *et al.*, 2022; Kuťáková *et al.*, 2018). Similarly, whenever microarthropods feed on pathogenic microbes they generally have positive effects on crop growth and development by decreasing disease infection and severity in the plants (Innocenti and Sabatini, 2018).

Microarthropods, especially Collembola, can affect seedling establishment and plant growth by grazing on beneficial fungi that associate with seed coats and plant roots, such as mycorrhizal fungi (Klironomos and Ursic, 1998; Mitschunas, Wagner and Filser, 2008; Nietschke *et al.*, 2011). Fungal seed coat grazing is also known to positively affect germination by reducing the presence of microbial pathogens (Pollard, 2018). However, seed coats vary between different plant species, therefore any effects microarthropods have on seeds through this mechanism are likely plant species specific (Müller-Stöver *et al.*, 2016).

Research regarding root herbivory remains limited. Some research suggests that when plant roots are present, Collembola switch their diet to almost exclusively plant roots over litter (Endlweber, Ruess and Scheu, 2009). Root herbivory by microarthropods is believed to be a rare

occurrence (Endlweber and Scheu, 2006), however there is evidence that is does occur under certain conditions (Joseph *et al.*, 2015).

Based on the evidence that microarthropods can affect plant growth by grazing on fungal seed coats and through root herbivory, it is likely that they would affect weeds in the same manner despite few studies investigating weed-microarthropod interactions. One field study demonstrated a positive correlation between soil microarthropods and weeds, suggesting a mutual soil feedback (Eo, 2010).

Though it is evident that microarthropods can affect plant growth and development through multiple indirect and direct mechanisms (Jernigan *et al.*, 2022), it remains unclear how exactly these effects manifest in individual plants and plant communities. Given our general understanding of how soil microarthropods affect plant growth and development described previously, it is likely that these fauna may be an important filter for weed community assemblage, enhancing the germination and growth of certain weed species over others in agricultural fields.

The primary objective of this research was to determine if microarthropods could be affecting weed communities. While addressing this objective, we studied these interactions in environments with varying levels of resource amount and diversity in order to better understand how collembolan feeding preferences could influence their impact on weed communities. We hypothesized that *I. minor* would increase the germination of the weeds with textured seeds more than the weeds with smooth seeds due to differences in their microbial seed coats. Furthermore, we predicted that the presence of fungal seed coats would increase germination and that this increase would be magnified in the presence of *I. minor* due to their grazing of the microbial seed coats. Additionally, we hypothesized that the presence of collembolans would decrease root

biomass production and predicted that the magnitude of this effect would diminish in the presence of alternative food resources (microbes and organic matter).

METHODS

Greenhouse Experiment

Experiment Design and Set Up

A greenhouse experiment was conducted in the summer of 2021 at Cornell AgriTech in Geneva, NY. The greenhouse was maintained at 25.5°C during the day and 21.1°C at night, with supplemental lighting to achieve a 12-hour day length period. The experiment followed a randomized factorial design and included Collembola, soil, seed coat, and fertilizer treatments (Figure 1). This setup was designed to create environments with varying levels of resource amount and diversity. Five replicates of this design (n = 90) were established using greenhouse flats (10.5"L x 10.5"W x 2.375"H).

Figure 1. Experimental design illustrating Collembola, microbial community, and fertilizer treatments.

A diverse weed community was set up using yellow foxtail (*Setaria pumila*), giant foxtail (*Setaria faberi*), Powell amaranth (*Amaranthus powellii*), waterhemp (*Amaranthus tuberculatus*), common lambsquarters (*Chenopodium album* L.), and velvetleaf (*Abutilon theophrasti*). These weeds were selected because as summer annuals they will all germinate under the same conditions. Additionally, these weed species are taxonomically and morphologically diverse, producing seeds that vary significantly in size and texture, which could impact how they interact with the Collembola.

In the fall of 2020, all weed seeds were collected from local fields in Geneva, NY. The seeds were cleaned through screening and air separators to remove debris. Weed seed germination rates were determined by putting 50 seeds from each species on germination paper, wetting the paper, and checking the number of seeds germinated after 2 and 4 weeks. The germination rates were used to calculate how many seeds of each species needed to be added to each flat to have 20 seeds germinate. The total number of seeds that were added to each pot were based on naturally occurring weed seed bank densities for our region (Jernigan et al., 2017).

This experiment utilized an organism commonly used in soil microarthropod research, the Collembola *Isotomiella minor*, Schaffer 1896, from existing lab colonies. Three abundance levels of *I. minor* (none, low, and high) were used. The abundance levels were set at 100 individuals per flat and 200 individuals per flat, respectively, based on reported agricultural microarthropod abundances (Coleman, Callaham and Crossley, 2018) and data collected on microarthropod abundances in agricultural fields across New York State (A. Jernigan, unpublished data).

To reduce or eliminate microbes from *I. minor* before their introduction to pots (Anslan, Bahram and Tedersoo, 2016), the specimens were transferred sequentially among sterile

containers daily for a period of five days using a repetitive isolation protocol (Appendix 1). Collembola were plated on potato dextrose agar to determine if the sterilization was successful (Appendix 1). The protocol was successful in removing microbes from *I. minor* with the exception of *Saccharomyces cerevisiae*, which was used as a food source for the *I. minor* cultures and could not be fully eliminated from our study system.

Soil (Lima and Kendaia loam) was collected from an organically managed farm in Geneva, NY and mixed with potting mix at a 1:1 ratio. All flats and soil were autoclaved prior to adding the weed seeds to eliminate any microbes. This sterilization also killed any viable weed seeds present in the original soil and potting mix. For the non-sterile soil treatment, the soil was re-inoculated with a microbial extract created from the original soil collected. To create the soil extract, a 20% (v/v) field soil solution was prepared in sterile 0.85% (w/v) NaCl (aq) in a flask and mixed on a shaker at 180 r.p.m. for 10 min. The mixture was then filtered (11 μm pore size, Whatman #1 filter paper) to remove soil particles (Howard, Bell and Kao-Kniffin, 2017). The filtered extract was then incorporated into the sterilized soil using gentle hand mixing and allowed to incubate for two weeks.

In the treatments with sterile seed coats, the weed seeds were surface sterilized using a series of bleach, ethanol, and water baths to remove any microbes prior to adding the seeds to the flats (Posada *et al.*, 2007). The sterilized seeds were then plated on agar to confirm that the microbes were successfully removed. The seed sterilization process used to remove microbes from the seeds can begin to chemically breakdown the protective seed coats thereby stimulating germination (Davoudpour *et al.*, 2020). While this effect of the sterilization process was not ideal, it was a necessary compromise to be able to remove the microbes.

Fertilizer presence/absence treatments were then imposed. The no fertilizer treatment flats received no fertilizer additions, and the fertilizer treatment flats received Kreher's Poultry Litter Compost 5-4-3 OMRI. The fertilizer was applied at the recommended rate for oats of 50 lbs of nitrogen per acre (SARE, 2007), which calculated to 6.24 g of fertilizer added to each fertilizer treatment flat.

After setting up the treatments the flats were placed in netted cages within the greenhouse to separate the Collembola treatments within each replicate. The flats were watered twice a week throughout the experiment.

Data Collection

After the initial set up, every 7th day the number of individual plants germinated for each species was counted and recorded to determine if there are any effects of the microarthropods on germination over time.

At four weeks we conducted the destructive harvest. This timing was chosen to minimize any potential effects of weed competition that could occur as resources became more limited for the weeds. During the harvest, the number of plants germinated for each species was recorded. The aboveground weed biomass was clipped at ground level and divided by species. After harvesting the aboveground plant biomass, the soil from each pot was divided in half. One half of the soil was processed to remove the root biomass. The root biomass was washed to remove any remaining soil. Both the aboveground and belowground plant biomass was placed in drying ovens, and once dried the biomass weights were recorded.

The other half of the soil was placed on Berlese funnels to extract the Collembola to verify the Collembola treatments and determine any changes in abundance over time. Over the course of a 3-day extraction, the temperature gradually increased from 30°C to 50°C. The

Collembola were extracted into 70% ethanol, then were topped off with 95% ethanol and stored until the samples were processed. After the soil samples were removed from the Berlese funnels, soil mass loss was determined from the air-dried weights of the soil samples. Collembola abundances are reported as the number of individuals kg^{-1} dry soil.

Data 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 variable measured during the weekly checks and the harvest using the *lmer* function in the 'lme4' package. The Collembola, soil, seed coat, 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. The soil treatment was not included in the treatment interaction variables. If the soil treatment had a significant effect, the soil treatments (sterile and not sterile) had separate ANOVAs ran to determine the effects of the other treatments within each soil treatment. The Collembola data was square root transformed to meet the assumptions of normality and homoscedasticity for the ANOVAs. Pairwise mean comparisons were made by using Fisher's LSD method, and significance was declared for $P \leq 0.05$.

A permutation-based multivariate ANOVA (Anderson, 2001) was run on the weed abundance data using the Adonis2 function of the 'Vegan' package (Oksanen et al., 2010) to see if the Collembola treatment affected weed community composition.

Lab Experiment

Experiment Design, Set Up, and Data Collection

A lab assay was conducted to investigate the impacts of *I. minor* on weed seed germination. Twenty seeds each, from the same weed species as were used in the greenhouse

experiment, were placed on moistened germination paper in deli cups. At the same time as seeds were added, *I. minor* was also added to the deli cups at four abundance levels (0, 10, 20, and 30) individuals. Collembola used for the assay were predominately adults.

Each weed species-*I. minor* abundance level combination was replicated 5 times for a total of 120 deli cups. Each replicate was grouped together on carts, with the deli cup placement randomized within each replicate. The carts were placed in front of a window to receive natural sunlight and maintained at ambient temperature.

Data Collection

Germination was measured after 5 and 7 days by counting the germinated seeds in each deli cup.

Data Analysis

Analysis of variance (ANOVA) was used to test for differences in weed germination using the *lmer* function in the 'lme4' package. The Collembola treatment and weed species were included as fixed effects, and a random replicate effect was included to account for potential spatial variability.

RESULTS

Greenhouse Experiment

Collembola Treatments

At the end of the experiment, Collembola abundances in the three abundance level treatments remained significantly different ($p = 8.55E-06$; 0, 8, and 21 individuals per kg soil in the control, low, and high Collembola treatments respectively), despite being greatly reduced from the start of the experiment. Collembola abundances were also affected by the seed coat treatment ($p = 0.0238$) with greater abundances occurring in the flats with the seeds that did not

undergo the sterilization process than those receiving surface-treated seeds (12 and 4 individuals per kg soil).

The Collembola treatment did not affect weed community composition at the end of the experiment ($F_{(2,89)} = 0.72$, $p = 1$).

Weed Counts

Soil sterilization led to significantly lower weed abundance than in non-sterile soil. Weed abundances were almost always affected by the soil treatment (Table 1; Appendix 2). Results were interpreted within each individual soil treatment when there was a significant effect of the soil.

The Collembola treatments affected the total weed, total grass, and total broadleaf counts at the 1-week check (Table 1; Figure 2). The Collembola treatment still affected total broadleaf counts at the 2-week check (Table 1; Figure 2). At the harvest time point after 4 weeks, the Powell amaranth and waterhemp counts were reduced by increasing Collembola abundances (Table 1).

The seed coat treatment affected the total, grass, and broadleaf weed counts at each weekly check (Table 1), with there being consistently more weeds in the sterilized seed coat treatment. The fertilizer treatment consistently affected the total broadleaf counts throughout the experiment (Table 1), having greater abundances in the no fertilizer treatment.

Table 1. Significance levels from the ANOVAs performed on grouped weed counts at each weekly check with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$). Soil Treatments: SS = Sterile Soil, NSS = Not Sterile Soil.

		Total Weed Count			Grass Count			Broadleaf Count		
	soil treatment	(SS+NSS)	(SS)	(NSS)	(SS+NSS)	(SS)	(NSS)	(SS+NSS)	(SS)	(NSS)
Week 1	**P-Value**									
	Soil*	**4.30E-12**			**5.21E-07**			**8.16E-12**		
	Seed Coat	**2.20E-16**	**2.20E-16**		**2.55E-14**	**2.33E-13**		**2.20E-16**	**1.70E-15**	
	Collembola	**5.99E-05**	**0.0029**	**0.0234**	**0.0046**	**0.0220**	0.2363	**0.0001**	**0.0075**	**0.0116**
	Fertilizer	*0.0757*	0.1413	*0.0742*	0.6332	0.8568	0.1994	**0.0304**	*0.0608*	*0.0949*
	Seed:Collembola	0.1164	**0.0131**	0.2341	0.2180	*0.0815*	0.2656	**0.0448**	**0.0085**	0.4210
	Seed:Fertilizer	0.3678	0.5096		0.1460	0.2692		0.7589	0.8412	
	Collembola:Fertilizer	0.9547	0.6035		0.5774	0.9383		0.8450	0.3762	
	Seed:Collembola:Fertilizer	0.5725	0.5514		0.8425	0.9196		0.5126	0.4067	
	Means									
	Seed Coat									
	MSC	80.4 B	58.4		24.9 B	18.2 B		55.4 B	39.9 B	
	SSC	146.8 A	124.8		47.7 A	41.0 A		99.2 A	83.7 A	
	Collembola									
	NC	98.5 b	78.8 b	89.2 b	31.4 b	25.1 b	26.6	66.9 b	53.5 b	62.5 b
	LC	123.4 a	96.8 a	117.1 a	39.8 a	32.2 a	34.5	83.8 a	64.5 a	82.5 a
	HC	118.7 a	99.1 a	101.1 ab	37.6 a	31.6 ab	33.4	81.1 a	67.4 a	67.7 ab
	Fertilizer									
	NF	118.0	95.3	109.6	36.8	29.8	34.1	80.9 A	65.3	75.3
	F	109.0	87.9	95.3	35.8	29.4	28.9	73.6 B	58.3	66.5
	Soil									
	SS	91.6 B			29.6 B			61.8 B		
	NSS	135.7 A			42.9 A			92.8 A		
	Interaction									
	Seed Coat:Collembola									
	MSC									
	NC		54.5 a					51.0 a	39.5 a	
	LC		53.8 a					59.4 a	36.3 a	
	HC		66.8 a					55.9 a	44.0 a	

	SSC									
	NC		103.1 B					82.9 B	67.4 B	
	LC		139.9 A					108.3 A	92.8 A	
	HC		131.4 A					106.3 A	90.8 A	
	P-Value									
	Soil*	**3.86E-06**			0.4282			**6.90E-09**		
	Seed Coat	**2.20E-16**	**2.00E-16**		**2.00E-16**	**2.00E-16**		**2.20E-16**	**2.49E-13**	
	Collembola	*0.0888*	0.3631	0.4010	0.4920	0.5042	0.5813	**0.0324**	0.2341	0.4288
	Fertilizer	**0.0006**	**0.0112**	**0.0054**	0.4951	0.5516	0.4249	**1.90E-05**	**0.0016**	**0.0018**
	Seed:Collembola	0.3412	0.3134	0.8496	0.8628	0.6896	0.9375	0.1922	0.2118	0.7549
	Seed:Fertilizer	0.9737	0.9555		0.7101	0.7206		0.8414	0.7454	
	Collembola:Fertilizer	0.7263	0.8571		0.1905	0.3531		0.9981	0.9002	
	Seed:Collembola:Fertilizer	0.7254	0.6427		0.1530			0.7496	0.6119	
Week 2	**Means**									
	Seed Coat									
	MSC	106.0 B	93.4 B		32.0 B	31.1 B		74.3 B	62.1 B	
	SSC	183.0 A	169.7 A		65.3 A	64.4 A		117.5 A	105.3 A	
	Collembola									
	NC	138.0	126.0	115.0	47.1	46.2	31.4	91.2 B	79.5	83.9
	LC	151.0	136.0	125.0	49.0	47.4	33.9	101.7 A	88.3	90.6
	HC	145.0	133.0	119.0	49.9	49.8	33.4	94.9 AB	83.3	85.3
	Fertilizer									
	NF	153.0 a	139.0 a	128.0 a	49.3	48.5	33.7	103.3 a	90.7 a	94.4 a
	F	137.0 b	124.0 b	111.0 b	48.0	47.0	32.1	88.5 b	76.6 b	78.8 b
	Soil									
	SS	132.0 B			47.8			83.7 B		
	NSS	158.0 A			49.5			108.2 A		
	P-Value									
	Soil*	**9.80E-07**			0.1308			**1.43E-07**		
	Seed Coat	**2.20E-16**	**6.80E-16**		**2.00E-16**	**2.00E-16**		**8.85E-16**	**8.42E-13**	
	Collembola	0.1206	0.3851	0.2967	0.1098	0.1865	0.3557	0.1169	0.2896	0.3456
Week 3	Fertilizer	**0.0064**	**0.0305**	0.1169	0.5289	0.5302	0.9196	**0.0002**	**0.0029**	*0.0743*
	Seed:Collembola	0.9565	0.8871	0.5042	0.7085	0.6204	0.7216	0.9685	0.9831	0.4543
	Seed:Fertilizer	0.8282	0.8997		*0.0943*	0.1230		0.3202	0.3912	
	Collembola:Fertilizer	0.1864	0.3950		0.6572	0.8855		0.1899	0.3201	
	Seed:Collembola:Fertilizer	0.8645	0.8789		0.4081	0.1059		0.8132	0.9581	
	Means									

Seed Coat									
MSC	110.0 B	98.3 B		28.9 B	27.7 B		81.3 B	70.4 B	
SSC	172.0 A	160.0 A		52.6 A	51.3 A		119.5 A	108.7 A	
Collembola									
NC	139.0	127.0	120.0	38.6	37.0	29.2	100.1	89.5	90.7
LC	147.0	134.0	129.0	42.2	40.6	31.5	104.7	93.5	97.5
HC	138.0	127.0	118.0	41.4	40.8	29.9	96.4	85.7	88.3
Fertilizer									
NF	147.0 a	135.0 a	127.0	39.9	38.9	30.1	106.7 a	95.8 a	97.1
F	136.0 b	124.0 b	118.0	41.6	40.1	30.3	94.1 b	83.3 b	87.3
Soil									
SS	129.0 B			39.5			89.5 B		
NSS	153.0 A			42.0			111.3 A		
P-Value									
Soil*	**9.90E-03**			0.5102			**7.10E-04**		
Seed Coat	**2.20E-16**	**4.15E+15**		**2.00E-16**	**2.00E-16**		**2.46E-15**	**2.42E-11**	
Collembola	0.4247	0.8507	0.1634	0.5297	0.6316	0.7930	0.1985	0.6624	0.1271
Fertilizer	*0.0740*	0.1312	0.3132	0.6510	0.6927	0.5457	**0.0048**	**0.0144**	0.3165
Seed:Collembola	0.9491	0.8205		0.7290	0.7827		0.9735	0.8072	
Seed:Fertilizer	0.8834	0.9371		0.3886	0.5640		0.4766	0.8161	
Collembola:Fertilizer	0.7252	0.8895	0.9083	0.8237	0.8839	0.8164	0.4634	0.6346	0.9604
Seed:Collembola:Fertilizer	0.6543	0.6775		0.6888	0.8169		0.4979	0.5423	
Means									
Week 4 Seed Coat									
MSC	138.0 B	125.0 B		40.2 B	38.9 B		97.6 B	85.7 B	
SSC	271.0 A	258.0 A		106.2 A	104.9 A		164.5 A	152.6 A	
Collembola									
NC	206.0	192.0	157.0	70.9	69.0	41.7	135.0	122.0	115.0
LC	210.0	195.0	158.0	75.4	73.8	42.5	134.0	121.0	115.5
HC	197.0	187.0	138.0	73.2	73.0	40.0	124.0	114.0	97.7
Fertilizer									
NF	212.0	200.0	156.0	72.4	71.1	42.3	139.0 A	129.0 A	113.0
F	197.0	183.0	146.0	73.9	72.8	40.5	123.0 B	110.0 B	105.0
Soil									
SS	191.0 b			71.9			119.0 b		
NSS	217.0 a			74.4			143.0 a		

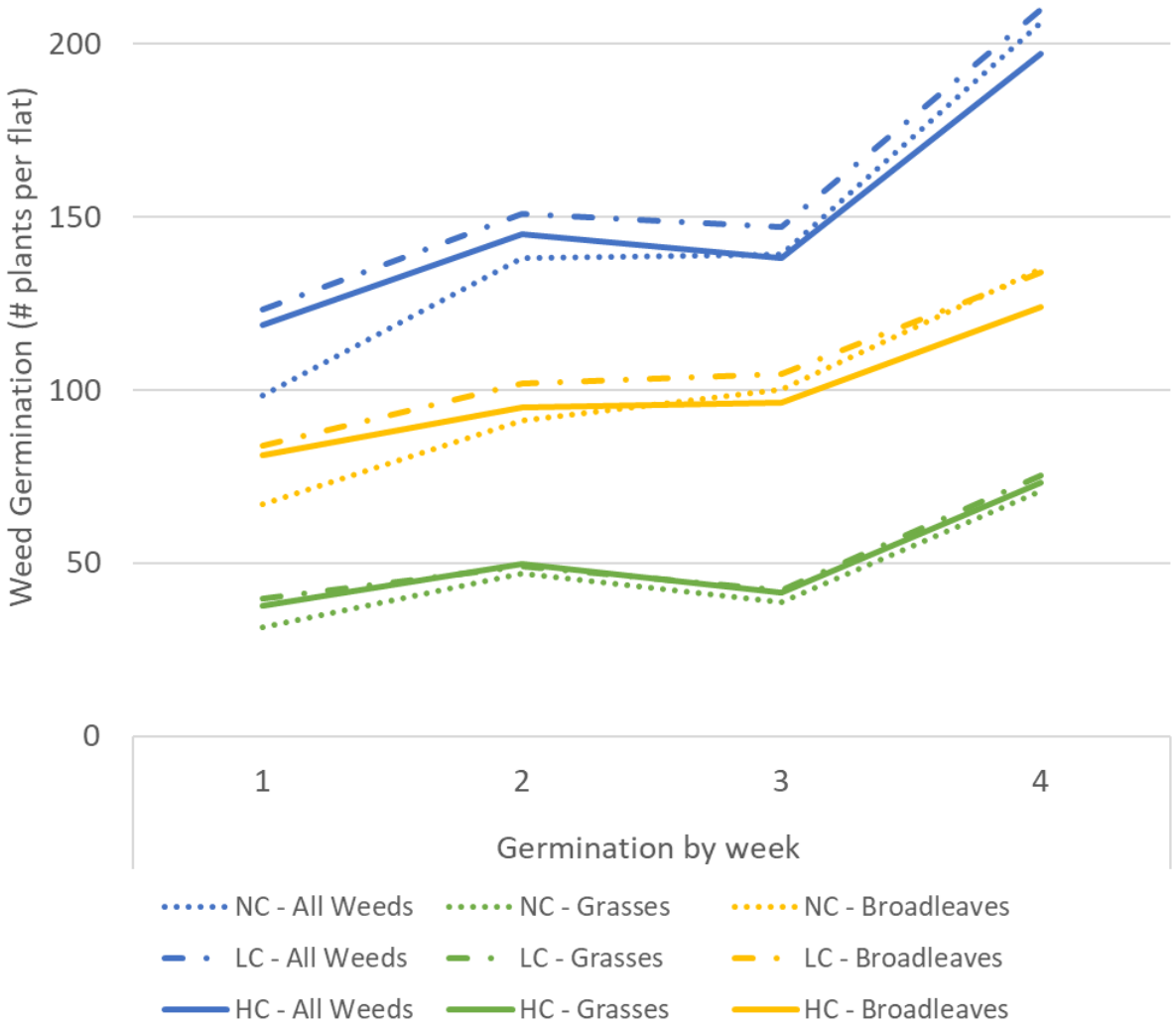

Figure 2**.** Collembola treatment effects on weed germination (average number of individual plants germinated per flat). Line type indicates the Collembola abundance (dotted = no Collembola; dashed = low Collembola; solid = high Collembola). Line color indicates weed category (blue = all weeds; green = all grass weeds; yellow = all broadleaf weeds). Asterisks indicate at which time points the Collembola treatments significantly affected the weed groups.

Weed Biomass

The soil treatment affected total, grass, broadleaf, pigweed and waterhemp biomass (Tables 2 & 3), having consistently greater biomass in the non-sterilized soil. In the non-sterilized soil treatment, the Collembola treatments decreased the total aboveground biomass, which was driven by the Collembola reducing the broadleaf biomass, especially the waterhemp biomass (Tables 2 & 3; Figure 3). The presence of Collembola also reduced the total root biomass in the non-sterilized soil (Table 2; Figure 4).

Table 2. Significance levels from the ANOVAs performed on the grouped weed biomass at harvest with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$). Interaction means not shown.

	Total Weed Biomass			Total Root Biomass			Grass Biomass			Broadleaf Biomass		
soil treatment	(SS+NSS)	(SS)	(NSS)	(SS+NSS)	(SS)	(NSS)	(SS+NSS)	(SS)	(NSS)	(SS+NSS)	(SS)	(NSS)
P-Value												
Soil*	**1.02E-06**			0.1008			**3.01E-05**			**3.61E-05**		
Seed Coat	**3.05E-14**	**2.41E-11**		**1.07E-09**	**4.65E-08**		**2.11E-11**	**5.55E-10**		**7.06E-07**	**4.31E-06**	
Collembola	0.1308	0.8502	**0.0003**	0.1003	0.7110	**0.0097**	0.6258	0.9759	*0.0776*	*0.0623*	0.4874	**0.0067**
Fertilizer	0.8165	0.8588	**0.0056**	0.1009	0.1608	*0.0929*	0.4116	0.2692	0.1665	0.3791	0.6935	**0.0241**
Seed:Collembola	0.2891	0.4868		0.9648	0.4903		0.6929	0.6967		*0.0645*	0.1672	
Seed:Fertilizer	**0.0168**	0.1113		0.3550	0.3870		*0.0532*	0.2015		*0.0501*	0.1928	
Collembola:Fertilizer	0.5054	0.6809	0.1370	0.3415	0.6813	0.1419	0.5556	0.6106	0.7482	0.7193	0.4000	0.1531
Seed:Collembola:Fertilizer	0.5484	0.7828		0.1924	0.2909		0.7744	0.8824		0.4687	0.7494	
Means												
Seed Coat												
MSC	1.08 B	0.94 B		0.143 B	0.132 B		0.530 B	0.447 B		0.410 B	0.356 B	
SSC	1.61 A	1.46 A		0.237 A	0.226 A		0.827 A	0.743 A		0.542 A	0.488 A	
Collembola												
NC	1.41	1.22	1.42 a	0.208	0.187	0.190 a	0.701	0.596	0.693	0.497	0.434	0.535 a
LC	1.34	1.19	1.18 b	0.181	0.172	0.139 b	0.671	0.590	0.583	0.491	0.432	0.459 ab
HC	1.29	1.18	1.09 b	0.182	0.177	0.134 b	0.664	0.600	0.565	0.44	0.401	0.396 b
Fertilizer												
NF	1.35	1.19	1.32 A	0.200	0.189	0.167	0.665	0.574	0.647	0.485	0.427	0.502 A
F	1.34	1.20	1.15 B	0.181	0.169	0.141	0.692	0.616	0.580	0.466	0.417	0.424 B
Soil												
SS	1.20 b						0.595 B			0.422 B		
NSS	1.49 a						0.762 A			0.529 A		

Table 3. Significance levels from the ANOVAs performed on the weed species biomass at harvest with means ($P < 0.05$, bolded).

Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$). Interaction means not shown.

	Velvetleaf Biomass	Giant Foxtail Biomass			Yellow Foxtail Biomass			Lambsquarters Biomass			Pigweed Biomass			Waterhemp Biomass		
soil treatment	(SS+NSS)	(SS+ NSS)	(SS)	(NSS)	(SS+ NSS)	(SS)	(NSS)	(SS+ NSS)	(SS)	(NSS)	(SS+ NSS)	(SS)	(NSS)	(SS+ NSS)	(SS)	(NSS)
P-Value																
Soil*	0.1011	**0.0003**			**0.0095**			**1.11E-06**			**0.0345**			**0.0217**		
Seed Coat	**0.0003**	0.3007	0.2809		**2.20E-16**	**4.87E-13**		**0.0004**	**0.0006**		*0.0729*	*0.0886*		**0.0289**	**0.0238**	
Collembola	0.3461	0.8751	0.7094	*0.0625*	0.5504	0.6286	0.5935	0.1776	0.6113	**0.0044**	**0.0493**	0.1502	*0.0539*	0.6633	0.2319	**0.0121**
Fertilizer	0.2234	0.1873	0.5837	**0.0097**	**0.0059**	**0.0396**	0.2745	**0.0001**	**0.0067**	**4.69E-06**	0.6563	0.5128	0.7780	**0.0061**	**0.0454**	**0.0164**
Seed:Collembola	0.1008	0.7030	0.7502		0.9153	0.8130		0.9828	0.3831		0.6814	0.7488		*0.0584*	0.2180	
Seed:Fertilizer	0.2417	0.1782	0.5664		0.1246	0.2116		*0.0795*	0.3789		0.8567	0.8893		0.8172	0.7667	
Collembola:Fertilizer	0.3768	0.2796	0.3453	0.9204	0.9603	0.9830	0.4869	0.2522	0.4879	0.2459	0.6650	0.9077	0.2929	0.5836	0.3197	0.6972
Seed:Collembola: Fertilizer	0.3193	0.6086	0.6744		0.9274	0.9839		0.6293	0.6403		0.6619	0.7388		0.3981	0.2269	
Means																
Seed Coat																
MSC	0.199 B	0.343	0.291		0.187 B	0.155 B		0.188 B	0.158 B		0.0075	0.0058		0.0154 A	0.0131 A	
SSC	0.291 A	0.372	0.320		0.455 A	0.424 A		0.229 A	0.200 A		0.0104	0.0087		0.0110 B	0.0086 B	
Collembola																
NC	0.255	0.364	0.290	0.456	0.337	0.305	0.237	0.217	0.177	0.245 a	0.0113 a	0.0092	0.0131	0.0139	0.0102	0.0240 a
LC	0.258	0.359	0.316	0.369	0.311	0.274	0.214	0.212	0.186	0.213 ab	0.0085 ab	0.0074	0.0073	0.0121	0.0092	0.0160 ab
HC	0.224	0.349	0.310	0.361	0.315	0.289	0.204	0.196	0.173	0.193 b	0.0071 b	0.0052	0.0073	0.0136	0.0131	0.0132 b
Fertilizer																
NF	0.232	0.373	0.313	0.444 A	0.292 B	0.261 B	0.203	0.228 A	0.195 A	0.252 A	0.0093	0.0067	0.0089	0.0156 A	0.0128 A	0.0213 A
F	0.258	0.342	0.298	0.347 B	0.350 A	0.318 A	0.233	0.189 B	0.163 B	0.182 B	0.0087	0.0078	0.0095	0.0107 B	0.0089 B	0.0141 B
Soil																
SS		0.372 A			0.289 B			0.179 B			0.0073 B			0.0108 B		
NSS		0.343 B			0.352 A			0.238 A			0.0106 A			0.0155 A		

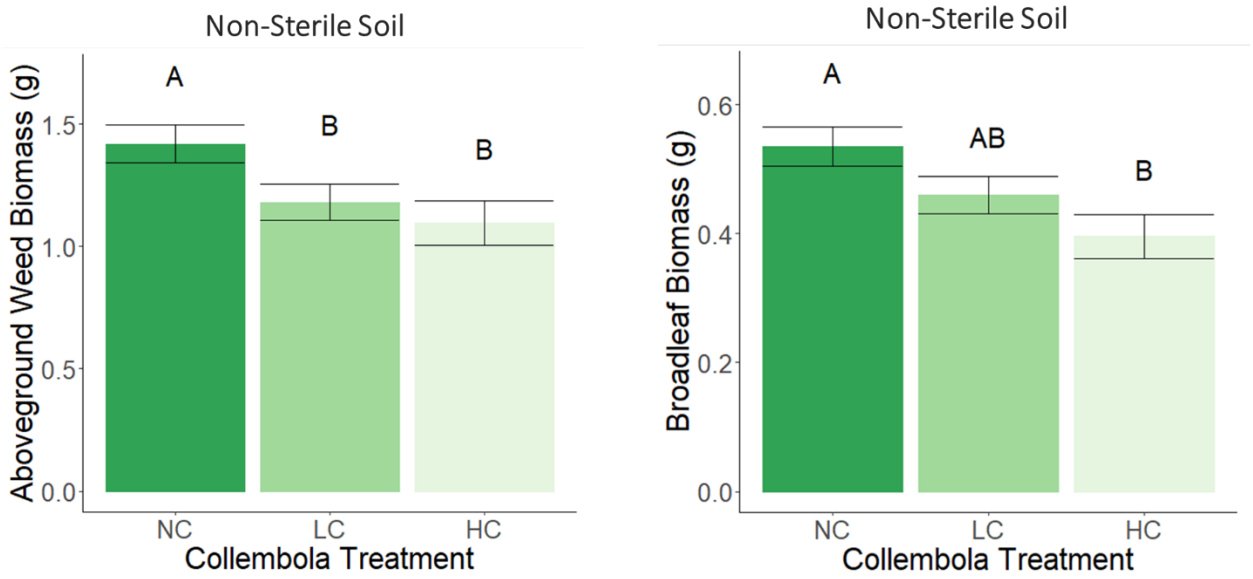

Figure 3. Bar graphs illustrating the effects of the Collembola treatment on aboveground weed biomass of all weed species combined (Left, $F_{(1,73)} = 12.2$, $p = 0.0003$) and aboveground broadleaf weed biomass (Right, $F_{(1,73)} = 6.2$, $p = 0.006$) in the non-sterile soil treatment.

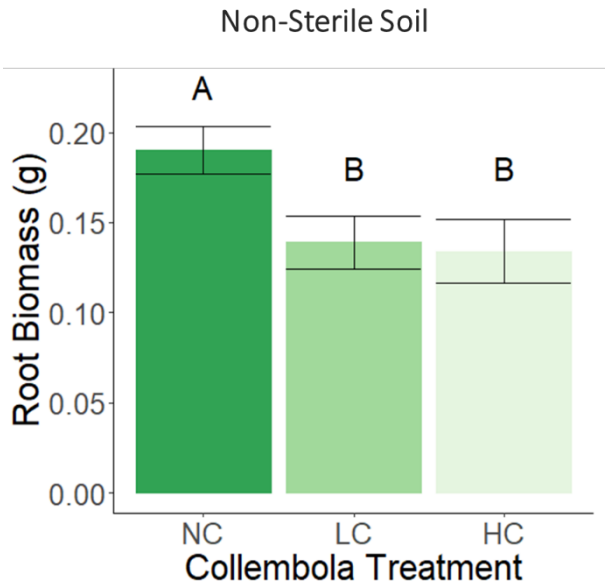

Figure 4. Bar graph illustrating the effects of the Collembola treatment on total root biomass ($F_{(1,73)} = 5.9$, $p = 0.0009$) in the non-sterile soil treatment.

The seed coat treatment affected the total aboveground, total root, grass, and broadleaf weed biomass (Table 2), with there being consistently greater weed biomass in the sterilized seed coat treatment. The waterhemp biomass opposed this trend, having produced greater biomass in the treatment where the seed coat was not sterilized (Table 2).

The fertilizer additions decreased the total aboveground weed biomass in the non-sterilized soil treatment (Table 2), which was driven by the fertilizer decreasing the broadleaf weed biomass.

Lab Experiment

At both the 5- and 7-day germination checks there was an interaction effect between the weed species and Collembola treatments ($p = 0.001$ and $p = 0.0002$, respectively), with the Collembola treatments only affecting the germination of the yellow foxtail. At both time points, the yellow foxtail in the very high Collembola abundance treatment had greater germination than the other Collembola abundance treatments. At the 7-day germination check the very high Collembola abundance treatment had almost double the germination of the other treatments (no Collembola = 9.2, low Collembola = 11.8, high Collembola = 10, and very high Collembola = 17.4; number of seeds germinated out of 20).

DISCUSSION

In flats where the seeds did not undergo the sterilization process there were greater Collembola abundances, likely because the microbes on the seeds were another food source for them (Nietschke *et al.*, 2011). Interestingly, Collembola abundances were not affected by the soil or fertilizer treatments, supporting the assertion that the seed surface wash procedure eliminated an important food source, most likely surface colonizing microbes, for the collembolans.

These findings suggest that the collembolans may have preferred feeding on the microbes on the seeds over the fertilizer and microbes in the soil environment (Buse and Filser, 2014; Ulber, 1980). Ulber (1980) found that the collembolan (*Onychiurus fimatus* Gisin) preference for feeding on plant seedlings was diminished in the presence of fungi and other organic materials in soil. A similar feeding preference response may have been occurring in this experiment since the collembolans appeared to prefer feeding on the microbial seed coats. It was possible for the collembola to be consuming weed roots as they were feeding on the seed coats they were attracted to, which could lead to effects on germination and weed biomass production (Nietschke *et al.*, 2011).

Collembola decreased total aboveground weed biomass production by up to 23%, with the greatest magnitude of this effect in the non-sterilized soil environment. This may be because in the sterilized soil the collembolan effects were dampened by the seed coat effects, since there was significantly lower collembola abundances when the microbial seed coat was not present. The mechanism underlying the reduction of weed biomass by the collembolans may have been root feeding or germination effects caused by their interactions with the weed seeds.

Collembola effects on weed community assemblage remain unclear, likely due to small community size of only 6 species used in this experiment, while naturally occurring weed seedbanks can contain dozens of different species (Jernigan *et al.*, 2017; Mohler *et al.*, 2018). The Collembola do however appear to stimulate germination at the first week more for some species than others and generally had greater impacts on the broadleaf weeds. The Collembola decreased broadleaf weed biomass, up to 45% reduction for certain species, more than the grass weed biomass.

It was unclear if the Collembola effects observed in the greenhouse experiment were driven primarily through effects on germination or through root feeding. The follow-up lab experiment was conducted to understand the effects of collembolans on the germination of these weed species and investigate why the collembolans had more of an effect on the broadleaf weeds compared to the grasses. Since the Collembola only affected the germination of yellow foxtail in the lab experiment, the Collembola were most likely not affecting the germination of the broadleaf weeds in the greenhouse experiment. The Collembola effects on germination for one specific species highlights the differing effects that Collembola can have on broadleaf and grass species. Previous research has also shown that Collembola can affect the germination of plant species differently (Nietschke *et al.*, 2011). While the observations in the greenhouse did not reveal Collembola effects on weed community assemblage, these lab finding illustrate their potential to impact weed community structures and assemblage.

The observed decreases in weed biomass production caused by the Collembola was promising from a weed management perspective. However, to fully understands what drove these observations, it would be necessary to know what was going on within the soil environment. Experimentally there are not great tools for answering these questions within a soil environment. Developing this area of study is important since we cannot directly observe the effects of soil organisms on germination in a soil environment, and many interactions occur before a cotyledon breaks through the soil surface.

Our findings suggest that microarthropods likely have the potential to play a role in weed management decisions in agricultural systems, though their effects on weed management will be highly dependent on the soil environment and the alternative food sources that are available for the microarthropods. With further research, microarthropods could be used to aid in weed

management which would expand weed management options for organic producers that are dependent upon “many little hammers” for weed control (Liebman and Gallandt, 1997). Soil microarthropods have the potential to be an important filer in weed community assemblage, and as such could be a be a key bridge to integrating weed management and soil health in agricultural systems.

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Appendix 1 - Collembola Sterilization Protocol

All steps for the Collembola sterilization protocol are completed in a sterile hood. All materials are sterilized using an autoclave for 20 minutes.

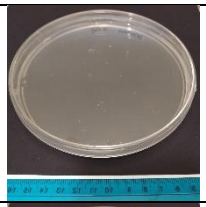
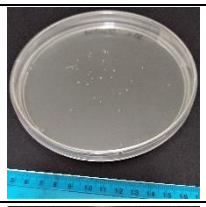
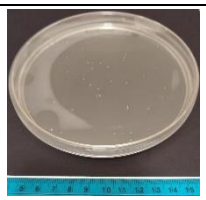
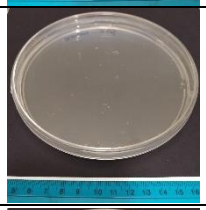
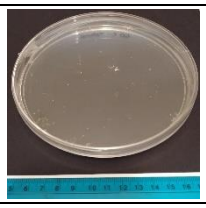
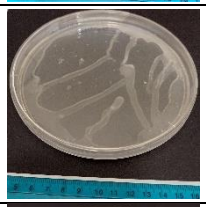
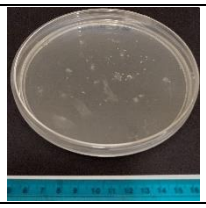
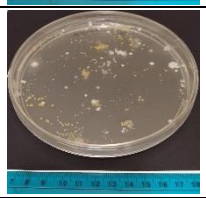
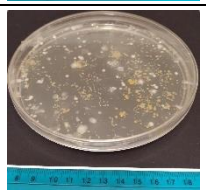
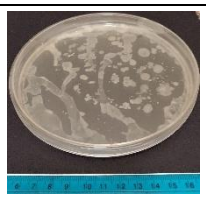
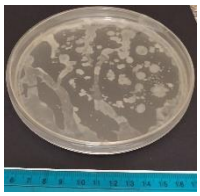
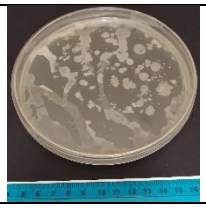
Collembola from the colonies are transferred to sterilized deli cups lined with sterile filter papers (11 μm pore size, Whatman #1 filter paper) that were moistened with sterilized DI water. After approximately 24 hours, the Collembola are moved to a new sterile lined deli cup. This process is repeated for 5 consecutive days (120 hours) prior to using the Collembola in experiments.

Prior to settling on this protocol, attempted sterilization techniques included diluted bleach, diluted ethanol, and sterile water baths in shakers and centrifuges. Due to the fragile nature of the collembolans, all other attempted protocols resulted in death. Sterilization by isolation over time, as described in this protocol, allows the collembolans to slough off any microbial fragments from their cuticle and pass any microbial fragments prior to using the collembolans in experiments. The only remaining contaminant is yeast, the food source given to the Collembola colonies in the lab. The yeast likely does not remove from the collembolans as well as the other microbes due to the yeast being unicellular.

In developing this protocol, it was determined that prolonging the sterilization procedure long enough to exclude all yeast led to significant Collembola mortality. Therefore, the protocol was optimized to maintain Collembola viability while removing the majority of microbial contaminants. This results of this developing this protocol suggests that experiments that are investigating Collembola-microbe interactions that are longer than 24 hours should follow a sterilization protocol to avoid interactions between the microbes of interest and the microbes brought into the experiment by the Collembola.

Sterilization Protocol Results

Table A.1.1. Images of petri dish arena (15 cm diameter) filled with potato dextrose agar over five days after adding collembolas.

Time Since Collembola Addition (hours)	**Unsterilized**		**Sterilized[1]**	
	30 Collembola	**60 Collembola**	**30 Collembola**	**60 Collembola**
0				
24				
48				
72				
96				
120				

[1]Collembola plated after undergoing the sterilization protocol still had yeast present. Water transfer from the deli cups was minimized, however whenever water droplets were carried over in the collembola plating more yeast growth occurs.

Appendix 2. Significance levels from the ANOVAs performed on species-level weed counts at each weekly check with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$). Interaction means not shown.

		Velvetleaf Count			Giant Foxtail Count			Yellow Foxtail Count			Lambsquarters Count			Pigweed Count			Waterhemp Count		
	soil treatment	(SS+NSS)	(SS)	(NSS)	(SS+NSS)	(SS)	(NSS)	(SS+NSS)	(SS)	(NSS)	(SS+NSS)	(SS)	(NSS)	(SS+NSS)	(SS)	(NSS)	(SS+NSS)	(SS)	(NSS)
Week 1	**P-Value**																		
	Soil*	**0.0047**			*At week 1 check we could not distinguish the foxtails - all foxtails are under yellow foxtail*			**5.21E-07**			**2.39E-05**			**4.74E-08**			**1.68E-07**		
	Seed Coat	**2.14E-10**	**2.01E-09**					**2.55E-14**	**2.33E-13**		**1.73E-12**	**1.32E-09**		**6.01E-12**	**4.42E-11**		**2.26E-07**	**1.55E-07**	
	Fauna	0.2511	0.7046	*0.0906*				**0.0046**	**0.0220**	0.2363	**0.0063**	**0.0464**	0.5111	0.2526	0.5197	0.2386	**1.46E-05**	**0.0008**	**0.0028**
	Fertilizer	0.5974	0.2376	0.1759				**0.63324**	0.8568	0.1994	**0.0042**	**0.0287**	**0.0067**	**0.0477**	0.1919	*0.0749*	0.8687	0.8456	0.6084
	Seed:Fauna	0.2009	*0.0757*	0.3333				0.2180	*0.0815*	0.2656	0.1659	0.3202	0.1508	0.3246	*0.0761*	0.6265	**0.0492**	**0.0249**	0.1182
	Seed:Fertilizer	0.3795	0.9694					0.1460	0.2692		0.4169	0.5356		0.8854	0.5167		0.5089	0.5088	
	Fauna:Fertilizer	0.5047	0.2829					0.5774	0.9383		0.4864	0.7413		0.2161	0.4769		0.3029	*0.0665*	
	Seed:Fauna:Fertilizer	0.2910	0.4302					0.8426	0.9196		0.3750	0.6514		*0.0618*	**0.0420**		0.2628	0.8901	
	Means																		
	Seed Coat																		
	MSC	6.0 B	4.8 B					18.2 B	18.2 B		10.8 B	8.1 B		19.6 B	13.5 B		19.0 B	13.6 B	
	SSC	12.4 A	11.1 A					41.0 A	41.0 A		21.2 A	18.5 A		36.0 A	29.9 A		29.6 A	24.2 A	
	Fauna																		
	NC	8.5	7.5	7.2				31.4 b	25.1 b	26.6	14.1 b	11.2 b	13.1	25.7	20.6	23.7	18.5 b	14.3 b	18.5 b
	LC	10.1	8.1	8.9				39.8 a	32.2 a	34.5	18.4 a	15.5 a	14.7	29.0	21.4	29.1	26.4 a	19.6 a	29.8 a
	HC	9.1	8.3	5.8				37.6 a	31.6 a	33.4	15.6 ab	13.2 ab	13.0	28.5	23.1	24.2	27.9 a	22.8 a	24.7 ab
	Fertilizer																		
	NF	9.4	8.5	6.5				36.8	29.8	34.1	17.6 A	14.8 A	15.6 A	29.5 A	22.9	28.3	24.4	19.1	24.9
	F	9.0	7.4	8.1				35.8	29.4	28.9	14.5 B	11.7 B	11.6 B	26.0 B	20.4	23.1	24.1	18.7	23.7
	Soil																		
	SS	7.9 b						29.6 b			13.3 b			21.7 b			18.9 b		
	NSS	10.5 a						42.9 a			18.8 a			33.9 a			29.6 a		
Week 2	**P-Value**																		
	Soil*	0.5118	NO SOIL EFFECTS		0.2547	NO SOIL EFFECTS		0.8555	NO SOIL EFFECTS		**4.75E-08**			**0.01189**			**0.00087**		
	Seed Coat	**6.44E-10**			**2.00E-16**			**2.00E-16**			**1.13E-13**	**5.90E-10**		**2.18E-05**	**0.00011**		**2.78E-06**	**1.80E-05**	
	Fauna	0.2774			0.5511			0.6206			*0.0668*	0.3147	0.2761	0.8165	0.8265	0.5005	**0.0132**	**0.0211**	0.5927

Fertilizer	0.8574		0.2951		0.9163		**5.80E-06**	**0.0027**	**2.49E-05**	0.1067	0.1713	0.4596	0.3897	0.1109	0.1512
Seed:Fauna	0.5503		0.2446		0.1702		0.2498	0.3559	0.6782	0.3947	0.4261	0.1946	0.2011	0.5783	0.7734
Seed:Fertilizer	0.7953		0.9760		0.6322		0.9377	0.6756		0.6550	0.7733		0.4132	0.8097	
Fauna:Fertilizer	0.8028		0.6926		0.1690		0.8433	0.6757		0.8486	0.5143		0.2081	0.5989	
Seed:Fauna:Fertilizer	0.4642		0.3970		0.1431		0.9996	0.8863		0.8453	0.7095		*0.0995*	*0.0972*	
Means															
Seed Coat															
MSC	9.3 B		11.0 B		21.1 B		45.3 B	36.3 B		10.3 B	9.0 B		9.5 B	7.9 B	
SSC	16.1 A		24.5 A		40.8 A		72.1 A	63.1 A		15.2 A	13.8 A		14.1 A	12.5 A	
Fauna															
NC	12.3		17.1		29.9		55.7	47.1	50.9	13.1	11.9	12.7	10.1 b	8.3 b	10.8
LC	13.6		17.5		31.5		62.8	53.3	56.6	12.8	11.2	11.6	12.5 a	10.8 ab	11.9
HC	12.1		18.6		31.4		57.6	48.8	55.2	12.4	11.1	10.9	12.8 a	11.6 a	10.5
Fertilizer															
NF	12.7		18.3		31.0		64.9 A	55.1 A	62.2 A	13.5	12.2	12.2	12.1	11.0	10.2
F	12.6		17.1		30.9		52.5 B	44.3 B	46.3 B	12.0	10.6	11.3	11.5	9.4	11.9
Soil															
SS	12.3		17.0		30.8		49.7 b			11.4 b			10.2 b		
NSS	13.0		18.5		31.1		67.7 a			14.2 a			13.4 a		
P-Value															
Soil*	0.4767	NO SOIL EFFECTS	0.6607	NO SOIL EFFECTS	*0.0888*	NO SOIL EFFECTS	**7.67E-07**			**0.0107**			0.1450	NO SOIL EFFECTS	
Seed Coat	**2.48E-11**		**5.48E-14**		**2.20E-16**		**7.34E-13**	**2.89E-10**		**0.0179**	**0.0238**		0.4524		
Fauna	**0.0186**		0.2092		**0.0009**		0.3049	0.4249	0.4301	0.5216	0.7257		0.2952		
Fertilizer	0.3665		0.3368		0.5054		**0.0002**	**0.0024**	*0.0999*	**0.0222**	*0.0779*		0.3741		
Seed:Fauna	**0.0395**		0.1688		0.1524		0.4374	0.6724	0.5676	0.8622	0.9638		0.5761		
Seed:Fertilizer	0.4115		**0.0345**		0.7573		0.1944	0.3247		0.891	0.7894		0.8791		
Fauna:Fertilizer	0.6373		0.6035		0.9454		0.2816	0.3784		0.2412	0.4453		0.1309		
Seed:Fauna:Fertilizer	0.1795		0.6911		0.4497		0.7936	0.9379		0.2689	0.2043		0.2435		
Means															
Seed Coat															
MSC	8.4 B		15.2 B		13.7 B		56.2 B	47.4 B		7.6 B	6.5 B		9.1		
SSC	15.8 A		25.8 A		26.8 A		84.4 A	75.6 A		9.7 A	8.6 A		9.7		
Fauna															

Week 3

	NC	11.5 ab		21.2			17.5 a			71.0	62.6	62.4	9.1	7.6	10.1	8.6			
	LC	13.7 a		21.1			21.1 b			72.5	63.6	68.6	8.8	8.0	8.4	9.7			
	HC	11.1 b		19.3			22.1 b			67.3	58.3	63.9	8.1	7.1	7.7	10.0			
Fertilizer																			
	NF	11.7		20.0			19.9			75.8 A	67.1 A	68.4	9.5 A	8.3	9.7	9.7			
	F	12.5		21.0			20.6			64.8 B	55.9 B	61.5	7.8 B	6.8	7.8	9.0			
Soil																			
	SS	11.8		20.3			19.2			61.5 b			7.6 b			8.7			
	NSS	12.4		20.8			21.2			79.1 a			9.8 a			10.0			
P-Value																			
	Soil*	0.7381	NO SOIL EFFECTS	0.6869			0.1504			**8.00E-04**			0.3498			**0.0414**			
	Seed Coat	**3.69E-09**		**2.54E-12**	**6.13E-09**		**2.00E-16**	**2.00E-16**		**4.82E-16**	**1.72E-11**		0.1465	0.1808		0.1390	0.1604		
	Fauna	**0.0406**		0.3460	0.5097	0.9857	0.7968	0.7289	0.4140	0.6839	0.9763	0.2729	**0.01524**	**0.0449**	0.2592	*0.0622*	0.2258	**0.0088**	
	Fertilizer	0.4997		0.1250	0.3847	0.1317	**0.0272**	0.1492	0.3000	**0.0099**	**0.0290**	0.2684	*0.0892*	*0.0829*	0.9406	0.1019	0.1297	0.4885	
	Seed:Fauna	0.2394		0.3597	0.5782		0.9269	0.9960		0.6989	0.6728		0.8759	0.9836		0.2089	0.4210		
	Seed:Fertilizer	0.6758		0.5835	0.5000		*0.0581*	0.1251		0.5486	0.8642		0.5272	0.9065		0.8606	0.9769		
	Fauna:Fertilizer	0.5082		0.2198	0.4319	0.7237	0.4411	0.7429	0.2999	0.3269	0.6769	0.4353	0.9499	0.9819	0.8123	0.9959	0.7488	0.1699	
	Seed:Fauna:Fertilizer	0.2072		0.2374	0.4669		0.3579	0.5234		0.7559	0.6900		0.4157	0.4281		0.2128	0.4231		
Week 4	**Means**																		
Seed Coat																			
	MSC	9.2 B		25.4 B	25.9 B		14.8 B	13.1 B		71.1 B	61.1 B		6.4	5.9		10.8	9.6		
	SSC	17.2 A		44.8 A	45.2 A		61.4 A	59.7 A		130.2 A	120.2 A		8.0	7.5		9.1	8.0		
Fauna																			
	NC	13.0 ab		33.7	33.9	25.2	37.2	35.1	16.5	102.2	91.1	81.8	8.4 a	7.9 a	8.3	11.5	10.2	15.1 a	
	LC	14.9 a		37.1	37.6	24.8	38.2	36.1	17.7	102.2	91.2	86.5	7.9 ab	7.6 ab	6.9	9.3	7.9	11.5 ab	
	HC	11.7 b		34.4	35.1	24.8	38.8	37.9	15.2	97.6	89.7	75.1	5.3 b	4.7 b	5.6	9.0	8.4	9.1 b	
Fertilizer																			
	NF	13.6		36.6	36.7	26.7	35.8 B	34.3	15.7	107.2 A	98.1 A	84.3	8.0	7.7	7.0	10.7	9.7	12.4	
	F	12.8		33.5	34.4	23.2	40.4 A	38.4	17.3	94.2 B	83.2 B	77.9	6.4	5.7	6.9	9.2	7.9	11.4	
Soil																			
	SS			35.5			36.4			90.7 b			6.7			8.8 b			
	NSS			34.6			39.8			110.7 a			7.7			11.1 a			

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CHAPTER 5

ORGANIC MATTER REDUCES THE EFFECTS OF *ISOTOMIELLA MINOR* ON *RHIZOCTONIA SOLANI* GROWTH IN A MINERAL SUBSTRATE

ABSTRACT

Microarthropod control of plant pathogens has not been established in field settings, however lab studies suggest that microarthropods could be an important control on pathogen growth. We conducted three complementary lab experiments to bridge this disparity in existing knowledge using *Rhizoctonia solani* and *Isotomiella minor.* The dominant mechanism in these interactions was investigated by allowing the pathogen-collembolan interactions to take place over 5 days in a controlled environment. The effects of the collembolans on the pathogen growth rate was determined using race tubes over a period of 14 days. The effects of the soil environment on these interactions was explored using soil material with no organic matter and soil material with high organic matter additions. The dominant mechanism in the *R. solani* and *I. minor* interactions was collembolan feeding on the pathogen, however there was potential for the collembolans to disperse the pathogen as there was viable pathogen structures on the cuticle and in the frass. Increasing Collembola abundances decreased the growth rate of *R. solani*. Collembola decreased the growth of *R. solani* in a soil material with no organic matter, however when organic matter was present this effect did not occur. Our findings suggest that it may be organic matter in soils that diminishes collembolan control of plant pathogens in field settings.

INTRODUCTION

Despite the known importance of soil processes in agricultural ecosystems (Crossley, Mueller and Perdue, 1992), the mechanistic and spatial dynamics of these processes remain poorly investigated. Soil microarthropods are known to mediate the microbial communities and the soil processes they drive (Soong et al., 2016). Managing soil biological processes is critical to improve crop production, especially in low-input sustainable cropping systems that aim to reduce external inputs. Plant pathogen control is of particular interest since this is an area where farmers often struggle to make agricultural systems more sustainable and less reliant on external chemicals inputs (Jerkins and Ory, 2016).

Microarthropods, especially Collembola, are fungal grazers that can potentially suppress microbial pathogens through grazing or transmit microbial pathogens by transporting spores on their cuticles or through their guts (Friberg, Lagerlöf and Rämert, 2005). There is considerably more evidence demonstrating the importance of microarthropod's consumption of pathogens compared to pathogen dispersal (Innocenti and Sabatini, 2018; Sabatini and Innocenti, 2001), though this may be due to the challenges associated with studying microarthropod dispersal of microbes. Despite the methodological challenges, there's evidence for both mechanisms occurring. The relative importance of these dueling mechanisms has yet to be compared, and the spatial dynamics of these interactions in soils remain a mystery.

Previous research investigating microarthropod-pathogen interactions has primarily been conducted in controlled lab experiments on agar media, with only a limited number of experiments investigating these interactions within a 3-dimensional physical environment (Innocenti and Sabatini, 2018). These lab studies reveal that Collembola consume pathogens and reduce their growth in small-scale petri-dish interactions (Sabatini and Innocenti, 2000a). Some

Collembola even preferentially feed on plant pathogenic fungi over other food sources (Sabatini and Innocenti, 2000b), however gut-content analyses indicate that collembolan diets are less restricted under field conditions than lab experiments would suggest (Tebbe, Czarnetzki and Thimm, 2006).

Field and greenhouse experiments do not consistently find that microarthropods interact with pathogens in a manner that results in pathogen control (Dromph and Borgen, 2001; Lartey, Curl and Peterson, 1994; Rickerl, Curl and Touchton, 1989). Microarthropods can move plant pathogens throughout the soil which can increase disease incidence; however, they can also reduce plant pathogen loads in soil by consuming the pathogens (Curl, Lartey and Peterson, 1988; Dromph, 2001). Field experiments often focus on plant health outcomes and do not explore the mechanisms driving these microarthropods-pathogen interactions (Lootsma and Scholte, 1997; Nakamura, Matsuzaki and Itakura, 1992; Sabatini and Innocenti, 2001).

The disparate findings from previous lab and field experiments indicate that the mechanisms driving interactions between microarthropods and pathogens, specifically consumption and dispersal, need further investigation to determine their relative importance in determining pathogen pressure in soils. There are also many environmental factors that would impact these mechanisms (Saitoh, Fujii and Takeda, 2014). Given the high spatial variability of both microarthropod and plant pathogen distribution in soils it is likely that the physical soil environment and the distribution of alternative food sources affects their interactions, however this remains a critical knowledge gap (Innocenti and Sabatini, 2018).

The Collembola species used in this series of experiments, *Isotomiella minor*, Schaffer 1896, commonly occur across a range of habitats including agricultural soils. Collembola can feed on microbes or decomposing organic matter in the soil (Lussenhop, 1992). These

experiments used the plant pathogen *Rhizoctonia solani,* which causes significant damage to many cereal, legume, tuberous, and other crops of economic importance across the world (Savary and Mew, 1996; Tredway and Burpee, 2001; Tsror, 2010). As a ubiquitous soilborne necrotroph, *R. solani* can survive by feeding as a plant pathogen or a saprotroph through the production of extracellular enzymes that break down cell walls and organic compounds (Ajayi-Oyetunde and Bradley, 2018). Additionally, the life cycle and reproductive structures of *R. solani* make this an ideal study organism to explore microarthropod-pathogen interactions.

The goal of this research was to enhance our foundational knowledge of the mechanistic and spatial nature of microarthropod-pathogen interactions in soil environments to bridge the disconnect between previous lab and field studies. To this end, we conducted three complementary lab experiments to investigate (1) the dominant mechanism in these interactions, (2) how collembolans effect the growth rates of pathogens, and (3) how the physical soil environment and the presence of organic matter impacts these interactions. We hypothesized that (1) the consumption would have a greater effect on pathogen growth outcomes than dispersal (2) Collembola would decrease pathogen growth rate and (3) the addition of organic matter in a physical soil matrix would reduce the effect of the Collembola on pathogen growth.

METHODS

This series of experiments used a common fungal plant pathogen, Rhizoctonia solani, and the collembolan species *Isotomiella minor*, Schaffer 1896, which commonly occur across a range of habitats including agricultural soils. Each of the experiments included 20 replicates of each Collembola treatment (no Collembola (control), 30 Collembola, 60 Collembola).

To isolate the Collembola interactions with *R. solani*, a Collembola sterilization protocol was developed to remove other microbes. Colonies of *I. minor* are maintained in the lab. In a

sterile hood, Collembola from the colonies were transferred to sterilized deli cups lined with sterile filter papers that were moistened with sterile water. After approximately 24 hours, the Collembola were moved to a new sterile lined deli cup. This process was repeated for 5 consecutive days to minimize viable microbes prior to using the Collembola in the experiments (Appendix 1).

Experiment 1

The first experiment investigated how the interactions between the Collembola treatments and *R. solani* impact the dominance of the dueling mechanisms, Collembola consumption vs. dispersal of pathogens (via cuticle or gut). Interaction arenas were created by filling sterile 150 mm petri dishes halfway with potato dextrose agar (PDA). A *R. solani* isolate (5mm diameter), composed of dense hyphae, was placed in the center of the arena and allowed to grow to a diameter of 2 cm. The Collembola treatments were then added to each arena and allowed to interact with the pathogen for five days.

After the 5-day interaction period ended, colony diameter was measured at three locations and any fragmentation was recorded. Images were taken of each arena to later analyze for pathogen growth and dispersal using ImageJ (Rasband, 2018; Schneider, Rasband and Eliceiri, 2012). The collembolans were removed from the arena and split into two equal groups. Half of the collembolans were rinsed to remove pathogen fragments from the cuticle, then the rinse solution was plated onto PDA plates to determine if viable pathogen structures were present on the cuticle. The remaining collembolans were kept alive in a sterile petri dish (5 cm diameter) with a moistened sterile filter paper for three days. The filter paper was then scraped for frass, and four frass pellets were selected at random from the accumulated material and plated onto PDA plates to determine if viable pathogen structures passed through the collembolan gut.

Finally, the PDA in the interaction arena was spatially sectioned to verify the sections of the arena with *R. solani* present. Spatial sectioning was done using a custom 3D printed petri dish area divider (Appendix 2). The divider spatially divides the petri dish areas into 30 sections of approximate equal areas (average area = 460 mm^2), excluding the middle circle of initial pathogen growth (2cm diameter; 290 mm^2 area).

Experiment 2

The second experiment explored how Collembola effect pathogen growth rates. Glass race tubes (16mm diameter x 16.5" overall length, both ends bent 45°) were prepared by filling the bottom half of the tube with PDA when placed horizontally and marking the tube with distance measurements at each centimeter interval. An *R. solani* isolate (5mm diameter) was placed at the starting end of the tube (0 cm) and allowed to grow until it reached the 4 cm mark on the tube. The Collembola treatments were added to the opposite end of the tube to where the pathogen was placed. The race tube was then inverted and tapped gently to randomly distribute the Collembola throughout the race tube. After 5, 7, and 14 days the growth of *R. solani* was measured. Growth rate was calculated as the distance of R. solani growth (cm) divided by the number of days the interaction had occurred.

Experiment 3

The third experiment investigated how the Collembola-pathogen interactions were affected by organic matter (OM) presence in a soil environment. Calcined, non-swelling illite clay granules, sieved to include only particles with diameters between 1mm and 4mm, were used as an absorbent mineral substrate that mimics the physical and spatial 3-d properties of a coarse soil (Turface MVP, Profile Products, Buffalo Grove, IL). The clay granules also lack organic matter. For the OM present soil treatment, fresh alfalfa aboveground plant tissue was dried and

ground to 2 mm using a Wiley mill (Thomas Wiley Mills, Thomas Scientific, Swedesboro, NJ). The alfalfa was then mixed with the Turface to create arenas with 2.25% organic matter; 1.63 g of alfalfa was added per arena (72.5 g Turface - average per arena). The alfalfa green manure was 6.15% nitrogen (C:N ratio = 7:1).

Using the same sterile 150 mm petri dishes from Experiment 1, an *R. solani* isolate (5mm diameter) was placed in the center of the arena and allowed to grow directly on the sterile petri dish for 1 day to stabilize the pathogen in the center of the arena. The areas were then filled halfway with the sterilized clay granule treatments. After approximately 2 days, once *R. solani* reached a diameter of 2 cm within the arenas, the Collembola treatments were added. Sterilized collembolans were counted for each arena under a microscope into sterile specimen cups, and were then transferred using gentle tapping to ensure random distribution throughout the arena.

After 5 days the interaction arenas were spatially sectioned using the arena divider to determine which rings (1 cm width) of the arena had *R. solani* present. The clay granules in each 1 cm arena section were gently mixed, then subsampled and plated on PDA. After 7 days the plates were checked for *R. solani* presence.

Statistical Analysis

All data analyses were performed in R version 3.4.2 (R core team, 2017). We used analysis of variance (ANOVA) to test for differences in each continuous response variable using the *lmer* function in the 'lme4' package. The Collembola treatment, was included as a fixed effect, and a random replicate effect was included to account for potential variability due to the day the replicate was started. The data met the assumptions of normality and homoscedasticity for the ANOVAs. Pairwise mean comparisons were made by using Fisher's LSD method, with Tukey adjustment and significance was declared for $P \leq 0.05$.

The model for the area of *R. solani*, as determined by ImageJ, also included the area of yeast as a fixed variable to determine if the yeast affected the growth of *R. solani*.

Each presence/absence response variable was analyzed using a Chi-square test on a generalized linear model using the *glm* function with a binomial distribution. The Collembola treatment was the fixed effect in this model. The cuticle viability response variable also included the number of Collembola in the cuticle wash as a fixed variable to account for difference in the number of collembolans used in the cuticle wash process for each replicate.

A linear model was used to determine the relationship between the manual measurements of the area *R. solani* and the ImageJ analysis of the area of *R. solani* using the *lm* function.

RESULTS

Experiment 1

The presence of Collembola reduced the growth of *R. solani*, as manually measured by diameter and the number of divider sections where the pathogen was present and well as determined by image analysis using ImageJ (Table 1). The manual measurements and ImageJ measurements of the area of *R. solani* were highly correlated ($R^2 = 0.988$, $p = <2.2E\text{-}16$). The growth of yeast in the arenas was not affected by the Collembola density (Table 1), and the yeast did not affect the area of *R. solani* growth.

Pathogen dispersal by the Collembola, as determined by new *R. solani* growth apart from the original colony, was not affected by the Collembola treatment (Table 1). There were viable pathogen structures found on the cuticle and in the frass of the Collembola (Table 1; Figure 1).

Table 1. Significance levels from the ANOVAs performed on the metrics from experiment 1 with means ($P < 0.05$, bolded). Means with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

	Manual Measurements							**ImageJ Measurements**	
	Average Diameter of *R. solani*	**Area of *R. solani***	**Sections with *R. solani***	**Connectivity**		**Cuticle Viability**	**Frass Viability**	**Area of *R. solani***	**Area of Yeast**
	cm	cm^2	count	binomial		binomial	binomial	cm^2	cm^2
P-Values									
Collembola Treatment	**2.20E-16**	**2.20E-16**	**3.39E-16**	0.2146		**6.28E-10**	**0.0067**	**1.75E-07**	**1.63E-14**
					# Collembola in cuticle wash	0.2303		Area of yeast 0.07851	
Means									
Collembola									
None	10.53 a	87.9 a	20.63 a	1.00		0.00 b	0.00 b	73.3 a	0.00 b
Low	5.91 b	29.4 b	9.10 b	0.90		0.84 a	0.20 a	31.4 b	42.67 a
High	5.57 b	27.5 b	8.33 b	0.95		0.43 a	0.29 a	30.5 b	43.03 a

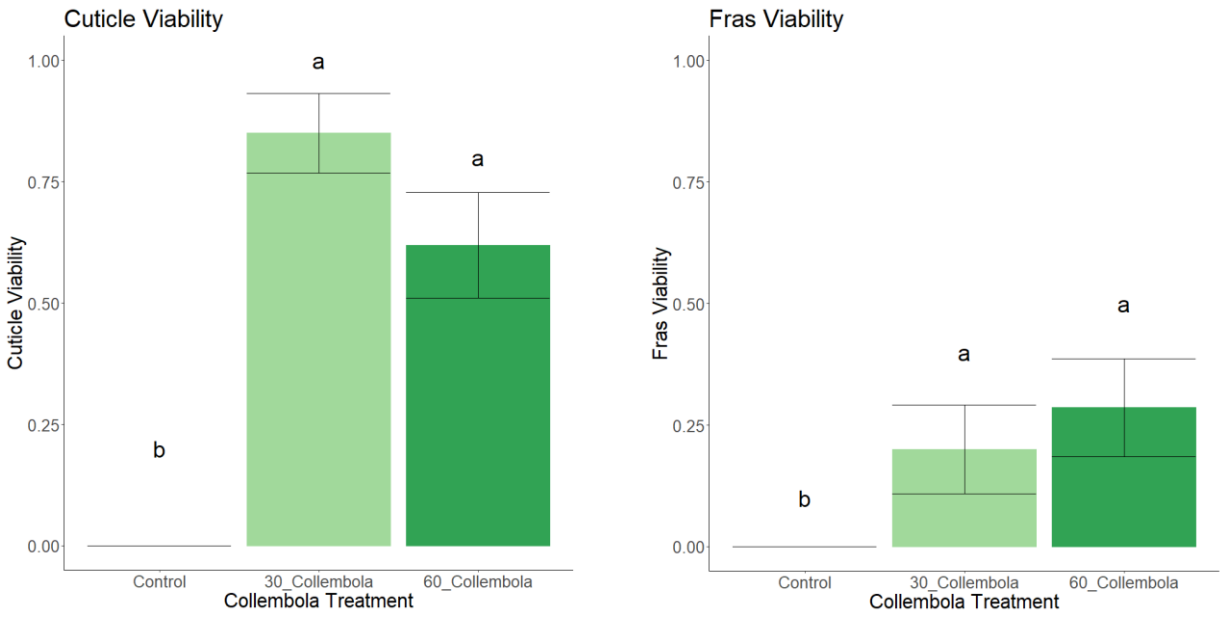

Figure 1. Cuticle viability (A) and frass viability (B) of pathogen. Bars with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

Experiment 2

The daily growth rate of *R. solani* was affected by the Collembola treatments and time (Figure 2). The high Collembola abundances reduced the growth rate compared to low abundances and the absence of Collembola. The growth rate of *R. solani* 5 and 7 days after experiment initiation did not differ, however the growth rate differed on the 14th day compared to earlier measurements.

The growth of *R. solani* was not affected by the Collembola treatments after 5 days. After both 7 and 14 days the race tubes with high Collembola abundances decreased the total amount of pathogen growth compared to those with no Collembola present (Figure 3).

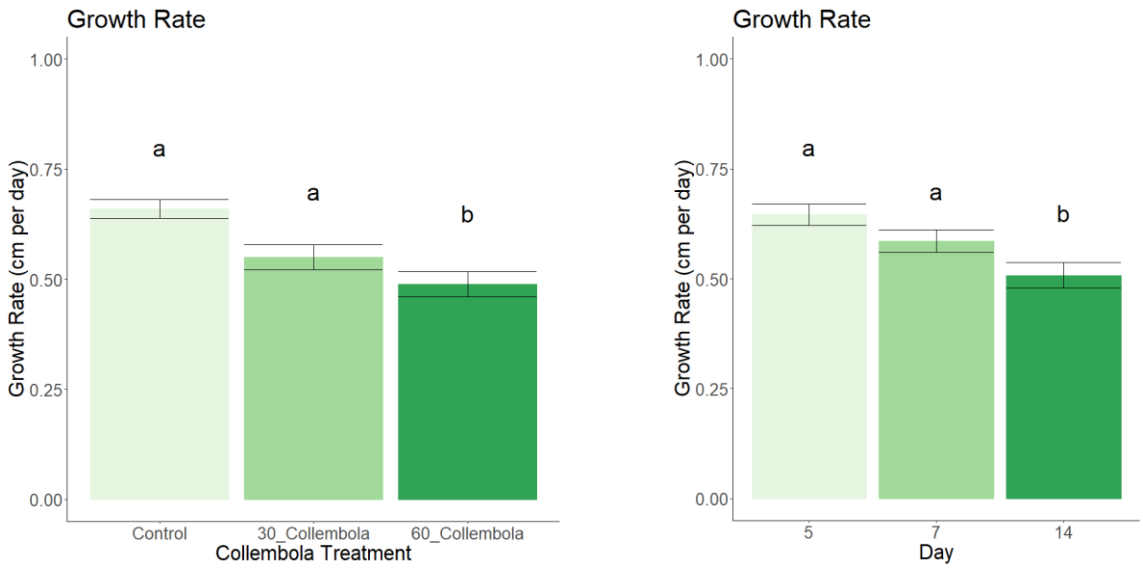

Figure 2. Growth rate of *R. solani* by Collembola treatments and time. Bars with the same letters are not significantly different (Fisher's LSD, P > 0.05).

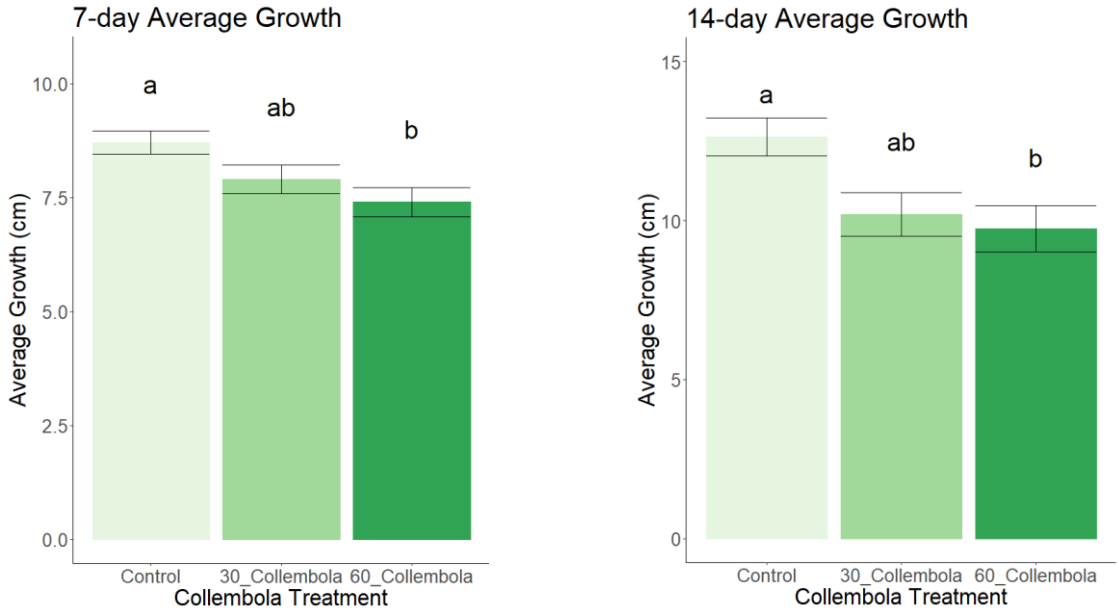

Figure 3. Growth of *R. solani* after 7 (A) and 14 (B) days. Bars with the same letters are not significantly different (Fisher's LSD, P > 0.05).

Experiment 3

The growth of *R. solani* was affected by the interaction of the Collembola and soil treatments (Figure 4). In the no OM soil, the high Collembola abundances decreased the pathogen growth compared to the low and no Collembola abundances. In the soil with OM the Collembola did not affect the pathogen growth.

The connectivity of the pathogen growth was not affected by the Collembola or soil treatments ($p = 0.4537$ and $p = 0.1717$, respectively). There was connectivity of pathogen growth in 96% of the arenas.

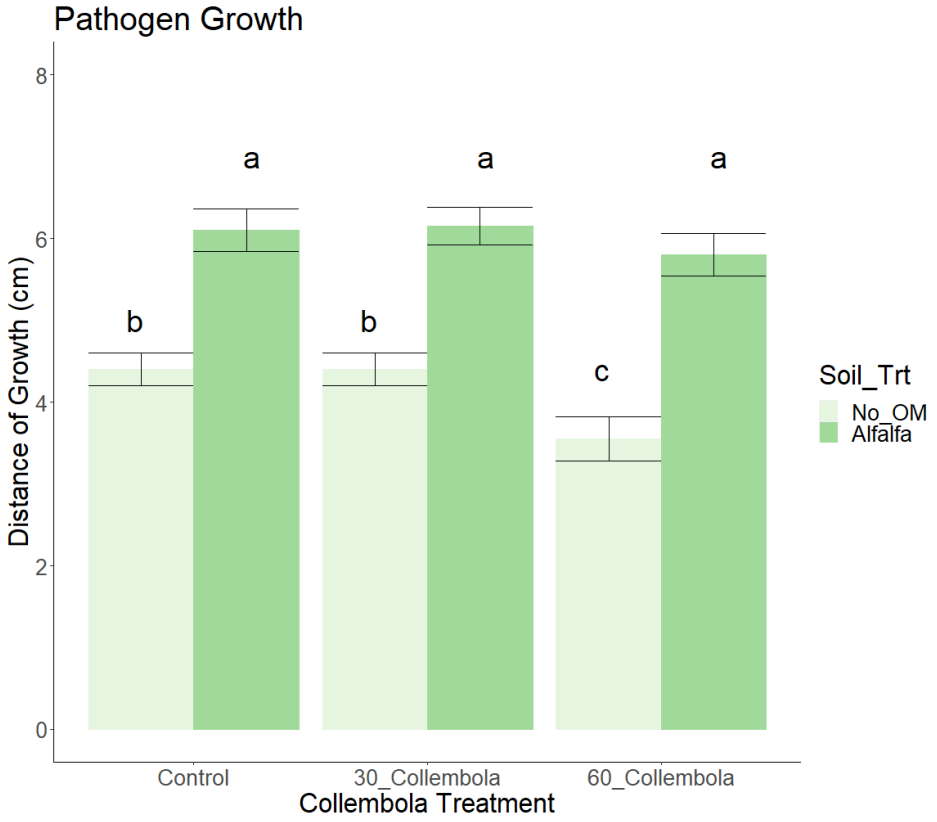

Figure 4. Distance of growth of *R. solani* within soil and Collembola treatment interactions. Bars with the same letters are not significantly different (Fisher's LSD, $P > 0.05$).

DISCUSSION

We observed that in favorable conditions the dominant mechanism of the *I. minor* and *R. solani* interactions was consumption, as there were no signs of pathogen dispersal by the collembolans. Previous work investigating the dispersal of pathogens by collembolans has found mixed evidence of the spread of fungal pathogens by the fauna (Nakamura, Matsuzaki and Itakura, 1992; Sabatini and Innocenti, 2001; Wiggins and Curl, 1979). However, in this experiment there was the potential for the Collembola to move *R. solani* as viable pathogen structures were recovered from both the cuticle and frass of *I. minor*. The cuticle wash had greater pathogen structure viability compared to the frass that was plated, though this could be the result of the different starting pools of fungal structures obtained from the differing sampling protocols.

The passage of the pathogen structures through the gut may have directly reduced their viability, or what happened to the frass pellet after defecation could have indirectly reduced pathogen viability. Similarly, in a study using field collected collembolans (*Entomobrya nivalis* Linnaeus 1758, *Orchesella flavescens* Bourlet 1839 and *Pogonognathellus longicornis* Tullberg 1871) plated collembolan appendages and gut samples resulted in fungal propagule germination 32% and 22.6% of the time, respectively (Anslan, Bahram and Tedersoo, 2016). Studies have confirmed that the passage through collembolan guts can damage fungal spore germination rates, in some cases by up to as much as 73.5% (Dromph and Borgen, 2001; Lussenhop, 1992; Nakamori and Suzuki, 2010; Sabatini, Ventura and Innocenti, 2004).

In each of these experiments the growth of *R. solani* was connected, with no signs of dispersal by *I. minor* as determined by the presence of disconnected pathogen growth. This would suggest that there was little dispersal of pathogens by collembolans under the conditions

used for this experiment. However, the dominant mechanism of these interactions may be affected by the length of time of the interaction or the favorability of the environmental conditions for the collembolans. Unfavorable conditions, such as the presence of predators, high moisture, or soil compaction, likely would affect pathogen-microarthropod interactions. Research on other epigeic fauna has found that the fear of predation affects prey in a manner that alters their movement (Ninkovic *et al.*, 2013) and decreases prey feeding behaviors (Hermann and Thaler, 2014; Williams and Wise, 2003), however little research has explored these effects in soil microarthropod communities.

This research confirmed that *I. minor* does indeed reduce the growth of *R. solani*. Interestingly, *I. minor* not only reduced the overall growth of *R. solani*, but also its growth rate. *R. solani* has been reported to grow at rates up to 0.15 - 1 mm per hour (3.75 - 24 mm per day) under lab conditions, though the rates vary based on environmental conditions such as moisture and temperature (American Phytopathological Society, 1970). The high Collembola abundance treatment reduced the *R. solani* growth rate by 30%, from 6.57 mm per day (control) to 4.62 mm per day. Reducing pathogen growth rates by this amount has the potential to reduce disease spread between plants in agricultural fields with typical row spacings of around 76 cm. To our knowledge this is the first study to investigate these interactions over time, allowing for the determination of how collembolans affect pathogen growth rates and further extrapolation on the broader impacts of collembolan feeding on the movement of pathogens.

The presence of organic matter reduced the effects of *I. minor* on *R. solani* growth in a mineral matrix, however the physical structure of the mineral matrix itself did not appear to impede *I. minor* feeding on *R. solani*. Prior research has found that physical environments with high porosities, such as the mineral substrate used in this experiment, are less likely to affect

microarthropod communities (Saitoh, Fujii and Takeda, 2014). A soil environment with lower porosity may affect the interactions between microarthropods and plant pathogens.

These findings suggests that soil organic matter composition may explain some of the variability observed in field experiments testing the role of soil invertebrates on plant pathogens. Soil organic matter is known to alter many aspects of soil biological activity and function. Organic matter serves as a food resource for both soil microbes and invertebrates, while also changing soil abiotic conditions like water holding capacity and porosity (Kampichler and Bruckner, 2009; Lal, 2020; Minasny and McBratney, 2018; Onemli, 2004; Seastedt, 1984).

In this study, the additional organic matter may have served as a food source for *I. minor*, thus reducing feeding pressure on *R. solani*. Additionally, the uniform accessibility of the added organic matter may have reduced the need for *I. minor* to explore the mineral matrix as extensively as in its absence. Alternatively, *R. solani* growth may have been enhanced by OM additions as these fungi are well known for their ability to survive saprophytically on detritus (Bailey, Otten and Gilligan, 2000).

The findings from this experiment help explain why we do not observe pathogen control by microarthropods in field and greenhouse studies as we would have expected to, based on previous lab studies highlighting their preferences for feeding on pathogenic fungi (Innocenti and Sabatini, 2018). However, the interactions between microarthropods and plant pathogens occur within the context of many other environmental variables in addition to the physical soil environment and organic matter resources for the organisms that affect these dynamics. Future research should investigate how community interactions effect the role of soil microarthropods in plant pathogen management.

Acknowledgements

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Appendix 1 - Collembola Sterilization Protocol

All steps for the Collembola sterilization protocol are completed in a sterile hood. All materials are sterilized using an autoclave for 20 minutes.

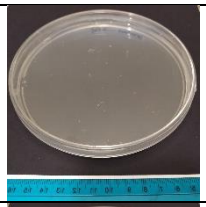
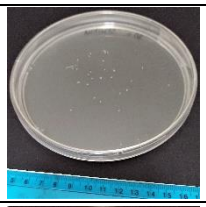
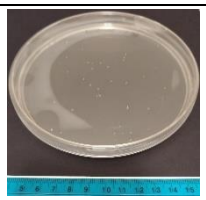
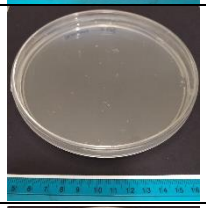
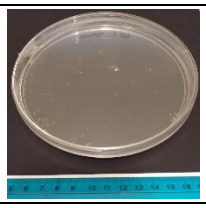
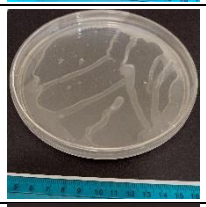
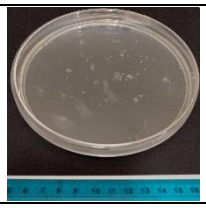
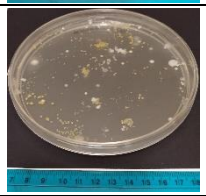
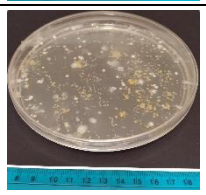
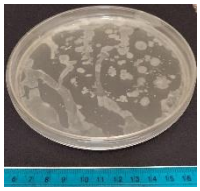
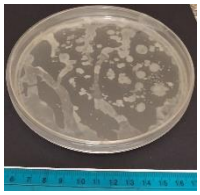
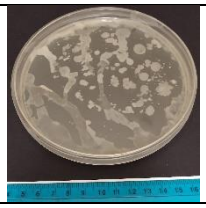
Collembola from the colonies are transferred to sterilized deli cups lined with sterile filter papers (11 μm pore size, Whatman #1 filter paper) that were moistened with sterilized DI water. After approximately 24 hours, the Collembola are moved to a new sterile lined deli cup. This process is repeated for 5 consecutive days (120 hours) prior to using the Collembola in experiments.

Prior to settling on this protocol, attempted sterilization techniques included diluted bleach, diluted ethanol, and sterile water baths in shakers and centrifuges. Due to the fragile nature of the collembolans, all other attempted protocols resulted in death. Sterilization by isolation over time, as described in this protocol, allows the collembolans to slough off any microbial fragments from their cuticle and pass any microbial fragments prior to using the collembolans in experiments. The only remaining contaminant is yeast, the food source given to the Collembola colonies in the lab. The yeast likely does not remove from the collembolans as well as the other microbes due to the yeast being unicellular.

In developing this protocol, it was determined that prolonging the sterilization procedure long enough to exclude all yeast led to significant Collembola mortality. Therefore, the protocol was optimized to maintain Collembola viability while removing the majority of microbial contaminants. This results of this developing this protocol suggests that experiments that are investigating Collembola-microbe interactions that are longer than 24 hours should follow a sterilization protocol to avoid interactions between the microbes of interest and the microbes brought into the experiment by the Collembola.

Sterilization Protocol Results

Table A.1.1. Images of petri dish arena (15 cm diameter) filled with potato dextrose agar over five days after adding collembolas.

Time Since Collembola Addition (hours)	**Unsterilized**		**Sterilized[1]**	
	30 Collembola	**60 Collembola**	**30 Collembola**	**60 Collembola**
0				
24				
48				
72				
96				
120				

[1]Collembola plated after undergoing the sterilization protocol still had yeast present. Water transfer from the deli cups was minimized, however whenever water droplets were carried over in the collembola plating more yeast growth occurs.

Appendix 2 - Petri Dish Divider

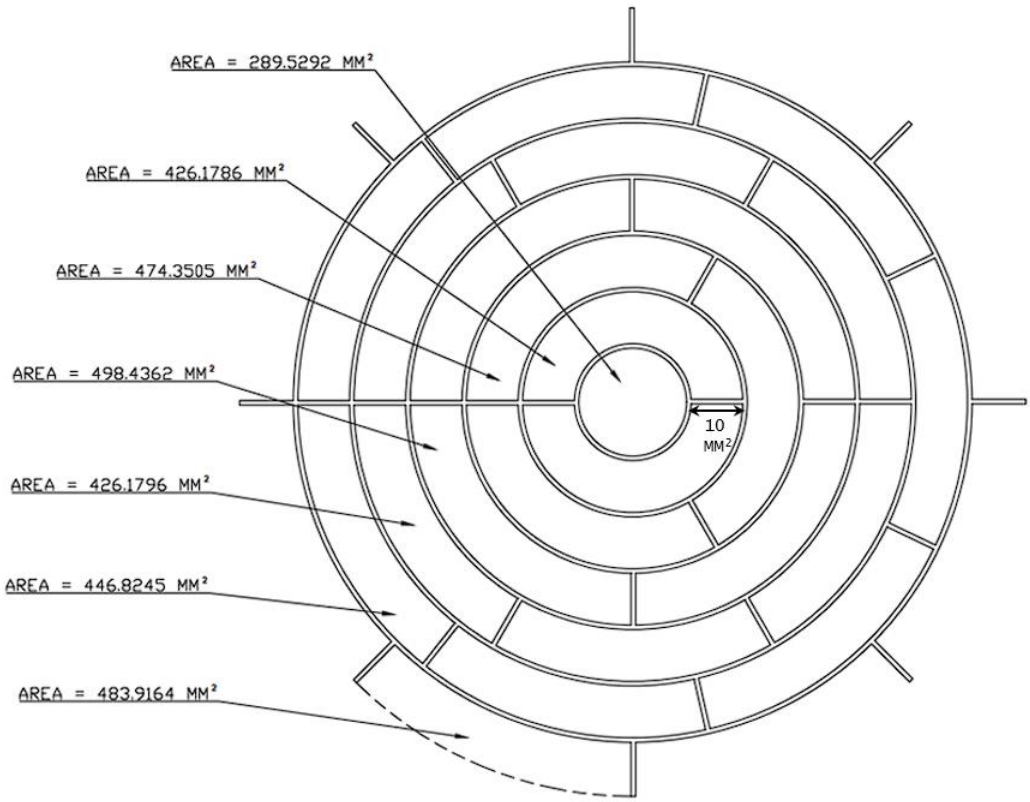


Figure A.2.1. Image of the petri dish divider tool created in AutoCAD software. The divider spatially divides a 15 cm diameter petri dish into 30 sections of approximate equal areas (average area = 460 mm^2), excluding the middle circle of initial pathogen growth (2cm diameter; 290 mm^2 area). The divider tool was 3-d printed with 0.8 mm wall thickness.

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CONCLUSIONS

Soil microarthropods play an important role in many soil biological processes that are central to crop production. Through this work I have synthesized our current understanding of soil microarthropods on crop production and have attempted to highlight their multi-faceted role in cropping system management. I endeavored to understand how soil microarthropods may influence soil fertility, weed, and pathogen management.

The literature indicates that the overall effects of microarthropods on plants is positive. This research supports that conclusion that microarthropods generally have positive effects on crop production. Within a systems-level field experiment we found that microarthropods are a central determinant of crop productivity. The microarthropods had more positive effects on bean production when there are more food resources available, highlighting the importance of feeding a soil food web to feed a crop.

I then investigated the role of microarthropods in nitrogen cycling. In the greenhouse we found that microarthropods, both single species and diverse communities, stimulate nitrogen cycling and enhance crop nutrient status. As microarthropod abundance and diversity increased, microarthropods exerted a greater number of effects on soil microbial activity. These effects enhanced 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 outcomes primarily through their effects on soil biological processes.

In another set of experiments, I examined how microarthropods could potentially affect weed communities. Promisingly, the Collembola had decreased total weed biomass production by up to 23%. The Collembola decreased broadleaf weed biomass (up to 45% reduction for certain species) more than the grass weed biomass. Our findings indicate that Collembola, and

microarthropods in general, likely have the potential to play a role in weed management decisions in agricultural systems.

Lastly, I delved into the mechanisms and spatio-temporal dynamics of microarthropod-plant pathogen interactions. This work helped bridge the disparities in findings from previous lab and field studies. Our findings suggest that the organic matter in soils may be the reason that we do not observe microarthropod effects on pathogens in field studies.

From this work it is evident that soil microarthropods play a role in all aspects of crop management. The studies span applied and mechanistic research to begin creating a foundation for utilizing soil microarthropods in crop management.

APPENDIX I

COMMENTARY ON MICROATHROPOD HANDLING FOR EXPERIMENTAL USES

Manipulating microarthropod treatments in controlled greenhouse and lab experiments is a common practice. Published peer-reviewed journals leave little room for commentary on best practices for microarthropod handling, therefore this commentary may serve to fill this technical gap and aid new researchers in carrying out their experiments.

Techniques for counting and moving living microarthropods are rarely spelled out in experimental methods, though water floatation has been mentioned previously for moving collembolans (Wiggins & Curl, 1979). The use of water to handle collembolans has proven to be very helpful. This water transfer method can also be carried out in a sterile hood with sterilized equipment and water for experiments where contamination is a concern.

When placed in a container with water the collembolans will float and create a raft since they are hydrophobic (Gundersen et al., 2014). A plastic pipette can then be used to suck up dozens of collembolans at a time. If collembolans are placed in a container with a small amount of water, so that the water does not completely cover the bottom of the container, the collembolans will gather on the dry area of the container. The container can then be tilted to move the water over the collembolans. This will trap the collembolans in air bubbles under the water, which makes it easier to suck up many collembolans at once. Alternatively, the pipette can be place under the water surface, then gently raised up underneath a group of collembolans which will climb onto the pipette. This second technique is better for moving smaller quantities of collembolas.

Mites prove to be much more difficult to handle in comparison to collembolans, though

other studies have manipulated mite abundances in controlled experiments (Acharya et al., 2019; Thakur et al., 2015; Thakur & Eisenhauer, 2015). It is possible to move individual mites using paint brushes, though this is much slower compared to moving dozens of collembolans at a time. Unfortunately, in experiments where sterility is a concern, as to not contaminate the experiment with additional microbes, paint brushes do not work since they cannot be sterilized efficiently. In an attempt to manipulate predatory mite abundances in a sterile experiment, I found the best way to move live mites individually was via a sterilized scalpel. The mites appear to be attracted to the blade when pressed against the bottom of their container at a 45° angle. The mites will run onto the blade surface. This behavior may be due to the light reflectance of the blade or the conception of shelter to the mites. The mites then can be gently tapped off the blade to move them, though they do not jump as the collembolans do, so it is much more difficult to get them to move off the scalpel. This is still a much slower process than moving collembolans via water, which can also be done in a sterile manner.

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