Effects of Basal-Resource Augmentation on Intraguild Predation and Decomposition in a Soil Food Web

BY

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THESIS

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This thesis is dedicated to my husband, Lee T. Ayres, who provided me with the opportunity to pursue this research, and to all the women to whom similar opportunities were, and continue to be, out of reach.

PREFACE

One of the most widely investigated areas of research in community ecology is the study of the effects of the transfer of energy on taxonomic and trophic diversity and composition. Though generalizations have been made based on results from theoretical models and microcosm research with a limited number of taxa, the ability to link these theoretical models to real world, complex systems is challenged by the lack the understanding of these complex systems, and the level of feeding specialization of these taxa. Additionally, the most complex systems are also the most diverse, and comprise taxa that are minute, making temporally and physically large-scale research difficult, if not impossible.

As first an acarologist and entomologist by training, I have an inordinate fondness for mites, to play on the famous quote by Haldane. For this, I have David J. Horn, emeritus professor, and Hans Klompen, director of the Acarology Laboratory, both from The Ohio State University to thank. Their sharing of even parts of their vast knowledge with me encouraged in me the idea that the small animals, in a way, have preferences and motivations, too. I chose the microarthropod community of the soil food web for this research because it is trophically and taxonomically diverse, displays complex trophic interactions, and is a rich source of data as the density of microarthropods can be 500,000 individuals per m^2 (Coleman et al. 2004). I have been encouraged in my inclination toward the small soil fauna of the world, and know I am not alone in my propensity, as I continue to find new studies and experiments investigating the impact of these small animals on the activity of soil microbes and the processing and release of elemental nutrients through changes to decomposition. I hope this work contributes to this body of knowledge for those who come after me, as did the work of those who came before me.

The question a layperson would ask is, what application does the understanding of the dynamics of soil food webs have beyond general knowledge? This is an important question to answer because the question itself reveals the inadequate job researchers have done in the transmission and explanation of scientific results from ecological work to a general public, a population that is continually making personal and political decisions that affect the global environment and the existence of organisms within

it. Understanding the impacts of changes to resources and energy flux, especially changes due to anthropogenic causes, has the potential to inform conservation efforts and the effects of rapid change on ecosystem level processes, such as decomposition.

I have many people to thank for their encouragement, and their acceptance, of my choice to leave a career in art to go work with "bugs"; David J. Horn, Doug Huston (The School of the Art Institute of Chicago), Mary Russell (Robert Morris University), and Karen Savage-Martin (The School of the Art Institute of Chicago). I am grateful to the past and present members of my thesis committee – David H. Wise, Hormoz BassiriRad, Henry F. Howe, Emily Minor, Liam Heneghan, and David E. Walter – for their generous guidance and suggestions, which aided me in greatly improving this research and this writing. I would also like to acknowledge my labmates, Nolan Bielinski, Amanda Henderson, Brook Herman, J. Cristian Martinez, Robin Mores, and, especially, Basil V. Iannone III and Matthew A. McCary, for their candid feedback in the development and analysis of this research. I am grateful to the staff and researchers at The Morton Arboretum in Lisle, IL, especially Gary Watson, Kurt Dreisilker, and Peter Linsner for their help in providing me with a research location, delaying previously planned work in the area while I completed this experiment, and sharing local weather data for The Arboretum with me to use in this research. Without their help this experiment and, ultimately, this dissertation could not have been completed.

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LIST OF ABREVIATIONS

AIC	Akaike's Information Criterion
CFI	Comparative Fit Index
CSTL	Cotton-Strip Tensile Strength
GSM	Gravimetric Soil Moisture
IGP	Intraguild Predation
LD	Litter Depth
PCFI	Parsimony-adjusted Comparative Fit Index
PCO	Principle Coordinates Analysis
PERMANOVA	Permutational Multivariate Analysis of Variance
PERMDISP	Permutational Analysis of Multivariate Dispersions
RAD	Ranked Abundance Distribution
RIGP	Reciprocal Intraguild Predation
RMSEA	Root-Mean-Squared Error of Approximation
SE	Standard Error
SEM	Structural Equation Model
SOM	Soil Organic Material
X^2	Chi square

SUMMARY

Predation between generalist predators that consume shared prey on a lower trophic level is termed intraguild predation (IGP). If the shared prey is a limited resource, intraguild predators are also competitors. Thus, the interactions between IG-predators, and interactions with their prey, potentially consist of a combination of top-down and bottom-up control processes. IGP is a ubiquitous module in food webs, and it is hypothesized to affect community structure and ecosystem processes through bottom-up and top-down control processes that differ in relative strength in response to different rates of input of resources to the base of the food web. The impact of changes in basal resources on interactions within the IGP module, and indirect consequences of changes in IGP interactions on ecosystem processes, have not been adequately investigated in mature, highly complex food webs. Additionally, the phenomenon of life-history omnivory -- the feeding on different trophic levels by different life stages – is common among IG-predators and thus adds to the complexity of patterns involving the IGP module. It is has been suggested that trophic-level omnivory may increase the likelihood of predator coexistence, and the consequences of its inclusion in theoretical models suggests that trophic-level omnivory may affect the behavior of real food webs.

Predictions based on the dynamics of IGP and life-history omnivory have rarely been examined in fully realized, multi-taxa food webs. The microarthropod community of the soil food web is an ideal system for addressing these predictions because of its trophic diversity and the presence of IGP and life-history omnivory, especially among mites (order Acari). Changes in the density of fungivorous soil microarthropods are known to affect the activity of fungi, the microbial organisms primarily responsible for the decomposition of detritus (dead organic matter) on the forest floor. This dissertation addresses two basic questions about the microarthropod component of a forest soil food web: (1) How does enhancement of the detrital resource base of the food web affect the role of IGP as a structuring force in the soil microarthropod community? and (2) How do resource enhancement and subsequent changes to the microarthropod community affect decomposition rate?

To answer these questions, a two-year experiment was conducted in a temperate, mixed-mesic research forest at The Morton Arboretum in Lisle, IL. Basal resources were augmented by adding an artificial high-quality detrital resource (chopped potatoes and mushrooms and *Drosophila* medium) to increase the abundance of saprophytic fungi. Each of 150 fenced circular 1-m^2 plots was assigned to one of three levels of detrital enhancement --- High (4x enhancement; n=50), Low (1x enhancement; n=50), or None (No enhancement; n=50). Fifty unfenced plots that received no enhancement served as Reference plots to reveal whether fencing likely had a large impact on the system. Artificial detritus was added every two weeks from July-September 2014 and April-September 2015. Litter and soil microarthropod samples were collected in July 2014 (initial conditions, before detrital supplementation started), October 2014 (end of year 1), April 2015 (prior to beginning detrital supplementation in year 2), and October 2015 (end of year 2). Litter depth, litter weight, soil organic matter (%SOM), and gravimetric soil moisture (GSM) determinations were also made for every plot at every sampling period. Differences between treatments in the decomposition rate of a standardized cotton-strip substrate were used to measure treatment effects on decomposition (likely due to changes in the density and/or activity of saprophytic fungi). The cotton-strip assay was conducted three times in year 2.

Detrital enhancement altered microarthropod community structure at the end of both years. Effects were pronounced for the community of common taxa but weak or absent for the community of less-common taxa. In the litter layer, community structure changed based on receiving any level enhancement, whereas, in the soil layer, the divergence in community structure was observed only in the High-level enhancement plots at the end of year 1. Divergence in the dispersion of communities in ordination space at the end of year 1 was observed only by High-level enhancement communities in soil with no difference in dispersion between treatments observed in the litter community. At the end of year 2, there was evidence of divergence in dispersion between all three treatments in the soil community with some evidence of difference in dispersion only between High-level and Low-level litter communities. There is no evidence that the changes observed in community structure over the course of this experiment were due to fencing.

In both litter and soil layers at the end of both years, the predatory mite family Parasitidae was 15x more abundant in High-level enhancement samples than the No enhancement control. Isotomidae, a fungivorous collembolan, was 7x more abundant in High-level versus No enhancement samples. Additionally, the minute fungivorous mite, Tarsonemidae (Prostigmata), increased in abundance due to enhancement in the litter layer only in both end-of-years. Tarsonemids were more abundant in High level plots than Low-level by 5x, and more abundant than No enhancement controls by 9x on average. Onychiuridae, also a fungivorous collembolan, was 2.5x more abundant in the soil layer in High-level versus No enhancement samples only at the end of year 2. In High-level enhancement litter samples, enhancement changed the dominant fungivorous taxon from family Tydeidae to Tarsonemidae, a mite family specializing on thin-walled fungal hyphae. This suggests a large abundance of fungal growth occurred in the High-level plots, specifically.

The IGP module consisted of two size classes of predaceous mites [IG-predators (larger taxa and age classes of generalist predators) and IG-prey (smaller taxa and age classes of generalist predators] and shared fungivorous prey (fungivorous mites and Collembola). Path analyses revealed a complex pattern of changes in the IGP module in response to detrital addition. One emergent pattern was the tendency for resource enhancement to increase the degree to which increases in abundance of smaller IG-prey positively affected densities of the larger IG-predators. The IGP interaction is the largest strength interaction in the Low-level enhancement group at the end of year 1. At the end of year 2, IGP was observed in all treatment groups, but the largest IGP interaction strength was found to occur in High-level samples. In Low-level enhancement plots, the IGP interaction was found to be the only existing interaction by SEM analysis. In year 2, a proxy for microbial activity (tensile strength loss of standardized cotton strips) was higher in High-level enhancement plots, followed by Low-level treatment plots. The most negative effect of fungivores on decomposition rate occurred in the Low-level enhancement plots. Since this is also the treatment where the only extant interaction is intraguild predation, this suggests the greater inhibition of microbial activity results from a combined effect of a moderate amount of microbial growth due to Low-level enhancement and intraguild predation, which produced a trophic cascade

positively affecting fungivores. IG-predators suppressed IG-prey, which led to increases in fungivores. Decomposition rate was highest in the High treatment, probably because saprophytic fungi were more abundant in those plots, and because fungivores had a negative impact on decomposition in the Low treatment.

I. INTRODUCTION

The importance of bottom-up and top-down control processes in food webs is a central theme in community ecology, and is central to our understanding of the effects of outside disturbances on a system. Intraguild predation (IGP), or the interaction between two generalist-predator groups that utilize the same limiting prey resources with the larger predator guild (the IG-predator) also consuming the lesser predator guild (the IG-prey) (Polis et al. 1989, Polis and Holt 1992), is a ubiquitous community module of omnivory that combines predation, competition, and theories of bottom-up and top-down control to make predictions regarding changes in community structure and coexistence. Added to this is the phenomenon of life history omnivory, or the scenario in which "different life history stages of a species fee(d) on a trophically different positions in a food web" occurs (Pimm and Rice 1987). This situation often includes larger adults consuming smaller juvenile predators of the same or different species in the absence, or reduced density of, preferred prey. Empirical ecological research has shown that both of these types of omnivory are common and capable of altering the composition of community structure. Life history omnivory occurs in microcosms with microarthropod predators and prey (Montserrat et al. 2012, Walzer and Schausberger 2013). Including IGP and life-history in theoretical studies reveals large impacts of these processes on food-web dynamics and stability (Polis et al. 1989, Holt and Polis 1997, Verdy and Amarasekare 2010, Wang and DeAngelis 2016). Nevertheless, predictions based on bottom-up and top-down control within the context of IGP and life history omnivory dynamics have rarely been empirically examined in complex, multi-taxa food webs, such as the microarthropod community of the detritus-based soil food web. This community is an ideal group for testing these predictions because of its trophic diversity and the presence of IGP and life history omnivory, especially among mites (order Acari).

The detritus-based soil-microarthropod food web (from now on "soil microarthropod food web") (Figure 1) is the focus of this study due to the large abundance of animals for evaluation, the ease with which they can be collected, and the known existence of IGP and life history omnivory within the web. Large predatory mites (IG-predator), smaller predatory mites (IG-prey), and fungivorous microarthropods

(suborder Oribatida, suborder Prostigmata, and order Collembola) constitute the majority of the IGP module of the microarthropod soil food web, and these are the taxa of focus in the following research. Though the term 'soil' varies in its usage, I define the detritus-based soil horizon (from now on "soil horizon") as including the layers of litter, humic soil, and mineral soil. Therefore, the soil microarthropod food web includes communities typical of each of these layers. Many soil microarthropods do differentiate by typical location in the soil horizon (Berg et al. 1998, Ponge 2000, Berg 2009) and utilization of resources typical of those layers (Ponge 2000, Potapov et al. 2016). It is reasonable, then, to predict that augmentation of resources may lead to differing effects, and different magnitudes of effect, on taxa typical of different layers, and this was incorporated into the sampling design of this experiment.

The structuring effects of IGP and life history omnivory are poorly understood in the soil food web because of the cryptic nature of the interactions, the difficulty of working with immature stages of microarthropods, and the fact that microarthropod taxa are extremely difficult to manipulate selectively outside of artificially constructed microcosms, as is typical of many perturbation experiments. However, it has proven feasible to manipulate the detrital resource base of this food web in nature (Chen and Wise, 1997, 1999, Scheu and Schaefer 1998, Maraun et al. 2001, Raub et al. 2014, Lawrence, submitted). By changing the quality and quantity of basal resources through artificial enhancement of detrital input (detritus defined as nonliving organic matter that came from living organisms), hypotheses based on IGP theory were tested in a soil food web with soil microarthropods (Acari and order Collembola) (Figure 1). Fungivorous microarthropods are known, in different resource-availability scenarios, to affect the growth and activity of saprophytic fungi in the soil food web positively (at low density) or negatively (at high density) through the consumption of hyphae. This can encourage or limit, respectively, the process of decomposition. And while an increase in fungal growth can increase the abundance of fungivores, top-down limitation by predators of fungivorous prey may affect the consumption of saprophytic fungi and decomposition. Therefore, fungivorous prey are an important resource to manipulate to investigate bottom-up and top-down control in the microarthropod-predator guild. The soil microarthropod community as a whole, then, plays a large role in regulation of ecosystem processes.

I predicted that the responses of densities of fungivorous microarthropods to detrital enhancement would differ depending on differences in size, life history stage, and location in the soil horizon. Oribatid mites (Oribatida) are major fungivores in the soil food web. They are mostly parthenogenic group, and there is evidence that females of many oribatid species always contain eggs and are constantly ovipositing, primarily in highly fragmented litter and the adjacent lower humus layer (Smrz 1989). Consequently, most oribatid individuals found in lower humus and highly fragmented litter layers are juveniles (Mitchell 1978). In the upper portion of the litter layer, oviposition is often arrested and juvenile oribatids are much less abundant. The other abundant group of fungivores, the Collembola, also includes taxa with characteristic locations within the soil horizon, exhibiting oviposition patterns similar to Oribatida (Hopkin 1997). I predicted that adding detritus would promote the growth of saprophytic fungi, leading to increased reproduction and higher densities of oribatids and Collembola. I expected the mite predators living in highly fragmented litter and humic soil layers to be the first predators to benefit because they are in closest proximity to newly emerging prey. These predators, referred to as "IG-prey" in the following sections, are the smaller species of mite predators and juveniles of the larger mite predators. Larger predators will be referred to as "IG-predators" (explained later). I expected IG-prey to initially reduce recruitment of fungivorous mites and Collembola because they are primarily consuming eggs, larvae, and early-stage juveniles of these taxa, which are deeper in the soil (Schneider and Maraun 2009). I expected this increased feeding on fungivorous prey to contribute to increased biomass in higher trophic levels (i.e. the IG-predators), as conceptualized by Hairston et al. (1960) and many others.

It is my hope that this research will further characterize the strength of bottom-up and top-down limitation on the detritus-based soil food web in the context of IGP by analyzing "snapshots" of resultant structural changes in response to increased input of basal resources to the food web. This research also aims to help bridge patterns in community and ecosystem ecology by comparing changes in the structure of the soil microarthropod community with patterns in decomposition. With these goals in mind, I sought to answer, *how does manipulation of energy and nutrients in the form of basal-resource enhancement*

affect the trophic and taxonomic structure of the soil microarthropod community, given the existence of IGP and life history omnivory at higher trophic levels? In particular:

- How do short- and intermediate-term inputs of detrital enhancement affect the abundance and age-structure of communities of predators and their prey?
- How does sustaining an enhanced input of detritus over the long-term change trophic and taxonomic structure of the soil microarthropod community?
- How do changes in abundance and composition of microarthropod fungivores affect decomposition?

Knowledge of the biology of soil microarthropods leads to several hypotheses (Figure 2):

1. Change in patterns of community structure of soil microarthropods will be driven by an increase in the abundance in quickly reproducing fungivores in the humic layer caused by increased detritus over the **short term**. These particular microarthropods are parthenogenic and reproduce quickly in this part of the soil horizon, such as many Collembola (Hopkin 1997).
2. Increasing enhancement over the **intermediate-term** will result in an increase in both litter and humic layer fungivores. Abundance of IG-prey will continue to increase in abundance due to the increase in fungivore immature stages.
3. IG-predators, which are relatively large and mobile, will increase in abundance **within 6 months** due to the increased abundance of all fungivores. The increase in IG-predators will result in a reduced abundance of IG-prey (Holt and Polis 1997, Mylius et al. 2001)
4. Since high rates of consumption of fungal hyphae by fungivores can affect fungal growth rates, decomposition rate will lower in plots with higher densities of fungivores, and will be elevated in plots with lower densities of fungivores.

In the following sections I will summarize the theories defining intraguild predation, current knowledge of the roles of bottom-up and top-down control processes in structuring the soil food web, the history of resource perturbation experimentation in soil food webs, and the influence of changes to the microarthropod community on fungal activity and decomposition. This framework will provide appropriate background support for results and conclusions of this research.

A. Background

1. Intraguild Predation and Life History Omnivory

The IGP (IGP is defined as two generalist-predator groups that utilize the same limiting prey resources with the larger predator guild (the IG-predator) also consuming the lesser predator guild (IG-prey)) community module that includes life history omnivory comprises a set of interactions that make it exceptionally suited for the investigation of the strength of bottom-up and top-down control in the detritus-based soil food web. Though IGP and life history omnivory are now known to be common, how they affect the structure of communities is poorly understood in natural, complex food webs such as occur in soil, although theoretical models and microcosm studies provide some basis for predictions. IGP (Figure 3) was modeled and characterized most notably by Holt and Polis (Polis et al. 1989, Polis and Holt 1992, Holt and Polis 1997) and was thoroughly documented in an empirical example by Polis (1991). IGP in food webs can lead to system instability (Holt and Polis 1997, Amarasekare 2008, Wang and DeAngelis 2016), yet IGP is widespread. In a recent meta-analysis of 113 food webs, Arim and Marquet (2004) concluded that IGP is widespread among taxa in many different ecosystems, is based on clearly-defined biological or behavioral characteristics of the trophic species (as also suggested by Oelbermann and Scheu (2010)), and has the ability to affect the abundances and distribution of the species involved, as suggested by Polis et al. (1989). Therefore, understanding aspects of life history, feeding behaviors, and other trophic characteristics is critical to formation of predictions and result interpretation.

Theories on IGP interactions predict that this type of trophic-level omnivory can organize community structure in a number of ways depending on the strengths of bottom-up and top-down

limitation in the system being perturbed. These theories can be roughly categorized by the parameter or process that they are emphasizing: diversity (or dominance) within the food web, coexistence of the IG-prey and IG-predator, and the effect of productivity on trophic interactions. It is this last variable that was manipulated in this research. Figure 4 diagrams the predicted dynamics of a system subject to more bottom-up versus top-down control and the same system under more top-down versus bottom-up control. Figure 5 maps the predicted relative change in standing crops of the IG-predator, IG-prey, and fungivore guilds in a system subject to more bottom-up control (Figure 5A) and more top-down control (Figure 5B) over the course of a basal-resource enhancement experiment.

With increasing resource productivity, the abundance of the IG-predator will increase and IG-prey will decrease. Due to the increase in abundance of the shared resource, the IG-prey becomes a larger proportion of the potential prey for the IG-predator. The IG-predator, because it is less efficient (reduce prey to low densities and subsist on these low levels of prey) than the IG-prey in utilizing the shared resource, feeds more heavily on the IG-prey when IG-predator productivity increases, thereby, creating opportunity for increased survival of the shared resource. Thus, increased input of the basal resource leads to increased productivity of the shared resource, which leads to increased productivity of the IG-prey, leading to higher densities of IG-predator, a result predicted in a system subject to strong bottom-up control (Figures 4 and 5A). The increase in IG-predator abundance **eventually** lowers densities of IG-prey, which causes densities of the shared resource to increase, a phenomenon typical of a system subject to top-down control (Figures 4 and 5B). Thus, increasing the resource base of the food web is predicted to produce a "delayed" trophic cascade (Paine 1980) within the IGP module that leads to further increases in densities of the shared prey (Figure 5B). This is reflective of the model of Fretwell and Barach (1977) and Oksanen et al. (1981) in which top-predators are bottom-up limited, the adjacent trophic-level (IG-prey) is limited by top-down control, and the next level down (the common resource) is bottom-up limited, for large and small length food chains. Previous findings from simple microcosms involving protists (Morin 1999) and parasitoids (Borer et al. 2003) support these predictions, as do some studies on predatory mites (Pugh and King 1985, Lister et al. 1987).

As implied by the above reasoning, coexistence of the three trophic groups involved in IGP (IG-predator, IG-prey, and the common resource) has been theorized to occur if the IG-prey is better at exploitative competition for the shared resource than the IG-predator (Polis and Holt 1992, Holt and Polis 1997, Mylius et al. 2001). The IG-predator should, theoretically, gain significantly from consumption of IG-prey (Holt and Polis 1997) and because of this the IG-prey could go extinct and the common resource increase in abundance. But the IGP interaction may continue to exist if competition between the IG-predator and IG-prey is particularly weak (Mylius et al. 2001) and/or these trophic groups are comprised of multiple species. Coexistence can also occur, even with exploitative competition, if there is some level of resource partitioning. Holt and Polis (1997) point out that there is an obvious niche difference between IG-prey and IG-predator, namely that the IG-predator has the advantage of being able to consume the IG-prey for great gain. This does not mean, however, that predation between IG-predator and IG-prey is unidirectional. Life history omnivory and reciprocal intraguild predation can vary the direction of predation between the IG-prey and the IG-predator.

Life history omnivory (Pimm and Rice 1987) occurs in a predatory guild when the guild is trophically structured by developmental stage, leading to reciprocal intraguild predation, or RIGP. In other words, juvenile IG-predators will, in some cases, become prey for larger, more mature stages of IG-prey. ***This pattern is extremely common across food webs*.** There are many co-varying aspects which change for individuals as development progresses and these probably all contribute to life history omnivory. Size is widely known as an important structuring factor (Yodzis and Innes 1992, Jonsson and Ebenman 1998, Woodward and Hildrew 2002, Cohen et al. 2003, Emmerson and Raffaelli 2004, Woodward et al. 2005, Brose et al. 2006a, Brose et al. 2006b, Brose 2010, Arim et al. 2010) due to the difference in predation risk for a small versus large animals, the increase in susceptibility to environmental factors for a small versus large animals, and, for small generalist predators, limitation in the spectrum of resources available for consumption. Additionally, body size can be a factor in resource differentiation in physically complex environments. Janssen et al. (2007) found in a meta-analysis of studies on IGP interactions that IG-prey abundance was reduced more often in physically unstructured

habitats than structured ones, suggesting that physical structure weakens the IGP interaction (Janssen et al. 2007) and increases the likelihood of coexistence. While the likelihood of coexistence has recently been disputed (Reichstein et al. 2013), there is common agreement that the IGP interaction does weaken with complexity of habitat structure.

For juvenile IG-predators, having to compete for resources with the more efficient adult IG-prey can have the effect of reducing recruitment of IG-predators to more mature life-stages. This prediction is supported by some empirical work on food webs (Montserrat et al. 2012), and models that suggest the likely existence of moderate to high levels of life history omnivory. Pimm and Rice (1987) found that without life history omnivory added to models, the communities with more than two trophic-level omnivores were rarely stable (all species and cycles exist at the end of the model run). When added, the number of model communities still in existence after the model run increased by 22%. Hin et al. (2011) addresses the case of life history omnivory and IGP in a stage-structured theoretical model by examining the effects of resource specificity by developmental stage. Their conclusion points to coexistence between the IG-predator and the IG-prey being increasingly likely as resource specificity increases and, therefore, competition (top-down control) is reduced.

Age-restriction in predation, by any process, has been theorized to provide a partial escape from predation for IG-prey leading to coexistence of IG-predator and IG-prey (Holt and Polis 1997). However, it is common for interactions involving age structure to be ignored in empirical studies of soil microarthropods by either lumping juveniles with adults, or not taking juveniles into account at all (Polis 1991). Though modeling and simple microcosm work have been pursued to evaluate different scenarios in communities that may be bottom-up or top-down limited, contradictions to theory exist, resulting in further questions. Alternative stable states involving IGP interactions may exist, but many of the models on which predictions are based are calibrated with data from microcosm and parasitoid studies, both very different, limited-interaction scenarios than are seen in mature communities. Perturbation experiments under field conditions continue, then, to be a necessary experimental technique for understanding how

bottom-up and top-down limitation affect community structure and dynamics when communities are disturbed.

2. Bottom-Up and Top-Down Limitation in the Detritus-Based Soil Food Web

In the soil microarthropod community, both IGP and life history omnivory are present in the predatory mite trophic level and, therefore, this community is a good model for evaluating the relative strengths of bottom-up and top-down control. As mentioned previously, large predatory mites (IG-predators), smaller predatory mites (IG-prey), and fungivorous microarthropods (Oribatida, Prostigmata, and Collembola) constitute the majority of the IGP module of the soil microarthropod food web.

Past investigations of top-down and bottom-up control processes suggest that both forces affect the structure and dynamics of soil food webs. Furthermore, both types of population limitation are components of the IGP module in food webs (Figure 4). Hairston et al. (1960) made the case that decomposers, producers, and predators are food-resource limited, and this affects diversity and trophic structure of the food web (bottom-up control). With an increase in available basal resources, biomass accumulates in successive trophic levels, consequently diversifying prey and increasing biomass in the predatory trophic level, which leads to top-down control of prey (Hairston et al. 1960, Oksanen et al. 1981). There is a difficulty in this conceptualization of control within the soil food web, however, because there is a great deal of feeding redundancy due to both classical omnivory and trophic-level omnivory (i.e. feeding on two or more trophic levels) (Walter 1987) and resource switching (Levin et al. 2001, Siepel 1994).

In microcosm experiments examining top-down and bottom-up control within the soil microarthropod community, support for both types of control have been observed, as suggested should be the case in the work of Bardgett and Wardle (2010), Rooney et al.(2006, 2008), Moore and de Ruiter (2012), and de Ruiter et al.(1995). Top-down control was observed to occur in microcosms by Schneider and Maraun (2009), who found predatory mites will feed on and reduce populations of Collembola, Protura, less-sclerotized mites, and mites of medium size (200-300 μm). This occurred because the diets of larger predatory mites exclude highly sclerotized adults that are more difficult to utilize as prey (Atlas

and Palen 2014). Very small mites tend to be less-sclerotized juveniles (though not exclusively) that inhabit deep soil pores, which large predators cannot access (Schneider and Maraun 2009, Walter et al. 1988); thus, the larger predators have less of an impact on populations of smaller species and smaller juvenile stages of large species.

In communities with a number of generalist-predator species, age structure can determine the direction of limitation within a community. In a food-chain microcosm study using two species of mites in the family Phytoseiidae (order Mesostigmata), when the shared pollen resource is at high levels, only IG-predator larvae (a non-feeding, non-motile stage) and eggs were affected by adult IG-prey. IG-prey reproduction was highest when provided only the shared resource and IG-predator larvae. This leaves open the possibility that fully-realized populations of IG-prey or IG-predators will consume juveniles of the other group, preventing an immigrating population from establishing (Montserrat et al. 2012), and create a new trophic-group dominance. In this case, "top-down" and "bottom-up" controls are relative, which is an important aspect in predicting the effects of IGP on a community experiencing a change in the rate of energy flow.

An aspect key to the concepts of coexistence and dominance within the IGP topology is that competition, a type of top-down control, is a strong community-structuring force affecting access to resources. Though there is empirical evidence of competition between fungal taxa (Wardle 2006), within the fungivorous Collembolan and soil mite communities there is little evidence of competition, nor is there evidence of trophic (Schneider and Maraun 2005, Schneider et al. 2005) or temporal (Norton and Behan-Pelletier 2009) niche partitioning in fungivorous mites, such as the oribatids. Adult predatory mite populations are comprised of generalists who utilize many similar prey items (Walter and Proctor 2013), so their diets tend to be relatively stable in diversity if not taxonomic composition. Herein lies a discrepancy in utilizing predictions of IGP interactions regarding these communities; omnivory and resource switching weaken interactions thereby reducing competition. This may result in weaker observed interaction strengths than may be observed in a microcosm or simple three-species system. Other fauna, such as nematodes, are important components of the entire soil food web, but they are not included, as

their addition would change the size and trophic scales of the research to a level of complexity where resultant ecological patterns are likely to be elusive. Additionally, caution must be used in categorizing guild or trophic groups at a scale this broad (Schmitz and Suttle 2001, Attayde and Hansson 2001, Oelbermann and Scheu 2010). However, by dividing groups by size/developmental stage, known resource consumption from the literature, and typical location in the soil horizon, as is being proposed here, major behavioral and dietary restrictions are being included by proxy.

3. Energy/Nutrient Manipulation Experiments

Bottom-up effects on primary and secondary consumers in soil food webs due to augmentation in basal resources have been investigated in a few microcosm studies (Schneider and Maraun 2009, Montserrat et al. 2012), and in field experiments (Chen and Wise, 1997, 1999, Raub et al. 2014, Lawrence and Wise, submitted), with mixed conclusions. In a "press" perturbation (Bender et al. 1984) experiment similar to the one being proposed, Chen and Wise (1999) utilized a food enhancement of mushrooms, potatoes, and *Drosophila* media to elevate abundance of fungivores in order to uncover the strength of bottom-up control processes affecting the community of arthropod predators in the litter layer. In replicated treatment and control plots, positive responses in productivity were observed throughout all trophic levels; they were especially strong among microarthropod fungivores. Mites comprised 58% of total arthropods extracted from litter, and they doubled in density in plots receiving the food treatment. However, mites were not determined to higher taxonomic or trophic resolution, nor were they separated according to age structure. Collembolan families (excluding Neelidae, which are found predominately in soil horizons below the litter layer) increased in all food enhancement plots to three times that of control plots after 15 weeks. This work demonstrated a strong capability of increasing the abundance of individuals in the fungivore community, and the capability of increasing the abundance of individuals within, at least some portion of, the soil mite community. Given the lack of knowledge of species composition at the end of the experiment, one can reasonably make the assumption that this increase occurred within taxa capable of reproducing quickly and such as some Mesostigmata and Prostigmata.

The long-term field experiment of Lawrence and Wise (submitted), which examined effects of detrital enhancement on primary and secondary consumers in the litter layer, was similar in approach to the research in this dissertation. The community chosen included both macro- and microarthropods and the analysis was not intended to evaluate IGP interactions directly. Their press perturbation experiment over 3 years utilized the same detrital enhancement combination as Chen and Wise (1997, 1999). Though the results are complex, increased densities of six collembolan families were observed in plots receiving enhancement in at least one of the three years. Some collembolan families responded positively to enhancement in the first year, but had a declining response over time, as with Tomoceridae and Onychiuridae. Cursorial spiders increased in density over two seasons due to higher survivorship in the Spring caused by increased numbers of active Collembola. The importance of performing press perturbations over the long-term is exemplified here as some groups, such as pseudoscorpions, were negatively affected by the enhancement only over the long-term. Lawrence and Wise (submitted) concluded there was support for some top-down and bottom-up control as some taxa were heavily preyed upon due to the increase in some predators and other taxa were advantaged by the increase in prey. Overall, there was not an overwhelming response leading to a conclusion of strong bottom-up limitation in soil food webs. Lawrence and Wise suggested the use of structural equation modeling (SEM) to analyze the strength of direct versus indirect effects would assist in understanding when low or no responses by fungivores indicated the absence of food limitation (bottom-up control) or reflected increased mortality from predators whose densities responded to increases in other prey taxa. However, many more replicates than utilized by Lawrence and Wise (submitted) are required for SEM (Grace 2006, Byrne 2016). Raub et al. (2014) did not find pervasive evidence that there is bottom-up limitation; however, Raub et al. evaluated a tropical system, which may not be comparable to the temperate locations used by both Chen and Wise (1999) and Lawrence and Wise (submitted).

Other detrital resources have been used which relate more to use as fertilizer in organic farms. In a long-term experiment comparing treatments of organic fertilizer (straw, bran, chicken dung, and pressed cottonseed waste) and artificial chemical fertilizer (ammonium bicarbonate, urea, and calcium super

phosphate), Cao et al.(2011) found soil organic content, K (potassium), total N (nitrogen), and available N increased in the organic treatment, but due to increased P (phosphorus), fungi were suppressed and reduced abundances for mite fungivores. However, the organic treatment in this experiment, represents a detrital enhancement treatment, which Cao et al. (2011) concluded increased abundances of predatory Mesostigmata because the treatment created heterogeneous spatial habitat and food resources and for a larger diversity of prey types (Cao et al. 2011). The enhancement I utilized was not intended as a fertilizer and did not cause the issues Cao et al. (2011) experienced, as the enhancement has been shown to increase fungal growth (Lawrence and Wise, submitted). However, it is possible that some differences in spatial heterogeneity of detritus may occur which may benefit predators.

4. Soil Microarthropod Life-History Characteristics

For this research, predictions for the responses of members of the soil microarthropod community to enhancement were developed from multiple life history and community sources. It is well known that different soil microarthropod taxa inhabit different layers of the soil horizon (Berg et al. 1998, Coleman et al. 2004, Berg 2009, Potapov et al. 2016) and have evolved morphological and behavioral characteristics (or, in some cases, lost them) in adaptation to their typical environment. For Collembola, there are clearly typical locations for some families in a particular soil horizon (Ponge 2000) and their diets have been found (through physical gut-content analysis (Ponge 2000) and isotopic work (Potapov et al. 2016)) to be distinctive based on their typical location. Additionally, Collembola have been found to form intense aggregations within one layer based on the presence of ephemeral food resources (Verhoef and Nagelkerke 1977), which leads to increased heterogeneity of distribution on the forest floor especially in litter (Berg 2009).

It is also important to note here that there are many soil parameters that have been shown to affect the soil microarthropod community and could have been altered by adding high-quality detritus to the system. Two most likely parameters are litter depth (or litter duff) and soil moisture. Litter depth (Nielsen et al. 2010, Steffen et al. 2012), and complexity (Hansen and Coleman 1998, Hansen 2000, Ilieva-Makulec et al. 2006, Sulkava and Huhta 1998, Usher and Parr 1977) tend to be important because

they both provide spatial and food-resource heterogeneity that might sustain a higher diversity of microarthropods. Soil moisture is often an important variable for soil microarthropods (Verhoef and van Selm 1983, Choi and Ryoo 2003, Xu et al. 2012), with higher densities usually observed in more moist soils (Hutson and Veitch 1987). Higher temperature reduces collembolan reproduction when water is already in short supply (Xu et al. 2012). Soil mites and Collembola show greatest densities at temperatures typical of their location of collection, with temperate deciduous forests having highest densities around 10 °C (Petersen and Luxton 1982). In general, litter performs a buffer-like function, preventing the humic and mineral soil layers from undergoing extreme environmental changes (van Straalen 1985, Sayer 2005), so typical seasonal temperature fluctuations with no associated drought were not expected to negatively impact soil microarthropods.

Since oribatid mites are slower to mature (Norton 1990, Siepel 1994) than Collembola, I expected to observe overlapping developmental stages of Collembola before oribatid mites could respond reproductively. When resources increase for Oribatida and especially Collembola, the IG-prey should be the first beneficiaries because eggs and early stage juvenile microarthropods constitute a large part of their diet (Lindquist et al. 2009, Montserrat et al. 2012). IG-prey are more likely to be in close proximity to eggs and larvae due to their typical position in deeper soil layers. An increase in abundances of the mature stages of Collembola will benefit the IG-predator (König et al. 2011, Chauvat and Wolters 2014) and epigeic Collembola will be severely reduced by predation (Ernsting and Joosse 1974, Ernsting 1977). By first increasing the density of eggs and juvenile stages of a shared prey resource, it is more difficult for the IG-predator to exclude the IG-prey in the system and, therefore, make coexistence more likely, as suggested in theoretical work by Holt and Polis (1997).

5. Influence of the Microarthropod Community on Ecosystem Processes

The above sections detailed theories about food-web and community dynamics as rationale for this research, and explained why the community of soil microarthropods is an excellent candidate for testing theories on the dynamics of the postulated IGP food-web module. This community

also serves as a model for investigating indirect effects of community-level change on ecosystem-level processes, as microarthropods are known to directly and indirectly affect rates of decomposition and nutrient cycling (Moore et al. 1988). For example, the presence of *Scheloribates moestus* Banks (suborder Oribatida) increased microbial respiration rates in oak and corn litter by 19% and 17%, respectively (Wickings and Grandy 2011). Additionally, Wickings and Grandy (2011) observed a nitrate concentration over 35 times greater in decomposing corn litter with mites present, as well as a 4-fold increase in dissolvable organic nitrogen. The reason for this is the propensity for soil microarthropods to assist in the propagation of microbes.

Soil mites can affect the dispersal and growth of decomposer microbes (specifically fungi) by increasing dispersal and comminuting detritus. Predatory mites can alter decomposition rates indirectly by reducing densities of fungivorous microarthropods. Mites can carry viable fungal spores and other propagules in crevices in the exoskeleton and internally in the digestive tract (Lussenhop 1992, Walter and Proctor 2013). Renker et al. (2005) examined LSU and ITS DNA of fungal origin from 4 species of oribatids and found 31 fungal taxa; 16 from the body surface and 15 (some the same) from the digestive tract. In another study, Pherson and Beattie (1979) found 7 fungal genera on soil mites and 6 on Collembola through plate culturing. This capacity to carry and disperse fungal spores benefits fungal communities. Visser et al.(1981) observed in a microcosm experiment that respiration (measured by O_2 uptake) within litter increased significantly due to deposition of fungal spores by Collembola, and not by Collembola grazing on fungal hyphae.

Oribatids and Collembola can also affect fungal growth by comminuting litter and by promoting or retarding fungal activity depending on the density of fungivorous arthropods in the system. Low-level grazing can increase growth (Visser 1985, Moore et al. 1988) while no grazing and heavy grazing retard fungal growth (Parkinson et al. 1979, Hedlund and Sjögren Öhrn 2000). High densities of fungivorous mites could inhibit certain fungi (Edwards and Stinner 1988, Klironomos and Kendrick 1995, Chauvat and Wolters 2014) enough to affect the growth of plants (Edwards and Stinner 1988, Klironomos and Kendrick 1995). Bengtsson and Rundgren (1983) observed collembolan grazing of fungi increased fungal

respiration when the Collembola were periodically removed and the mycelia had a brief recovery period (five days). Feeding type may also play a role in the effect fungivore consumers have on fungi. Based on an experiment using an assemblage of five oribatid species, Siepel and Maaskamp (1994) suggest that the rate of compensatory growth (compensatory growth is defined by Lussenhop (1992) as "increased productivity or mass relative to a control due to grazing") of the fungi is related to the whether the fungivore is a piercing-sucking browser that consumes cell contents with little damage to cell walls, or is a grazer that must chew through or engulf cell walls. Additionally, they suggest that the consequences for fungi also depend on the rate of assimilation of nitrogen from chitin by the assemblage of mites, with mites assimilating more nitrogen being those that damage and ingest hyphal cell walls. They suggest this aspect is more important to overall effect than simply fungivore density.

Finally, predaceous mites can indirectly affect fungal growth and the decomposition of litter through predation on fungivores, though evidence of the direction of the effect is contradictory. In a microcosm experiment using wheat litter and a mixture of fungivores, microcosms with a mesostigmatid predator, *Hypoaspis aculeifer* (G. Canestrini) had more fungal biomass (as measured by quantity of ergosterol) and higher rates of nitrogen mineralization than microcosms with fungivores and no predator (Cortet et al. 2003). This result was contradicted by Cole (2004) who observed nitrate and total available nitrogen were reduced in the presence of predatory mites. The difference in these experiments is the presence of one species (Cortet et al. 2003) versus many species of predatory mites (Cole et al. 2004). Hedlund and Sjögren Öhrn (2000) also observed an increase in fungal biomass and respiration of fungi in the presence of predators in a microcosm study with *Folsomia fimetaria* (Collembola) and *H. aculeifer*. In a desert system where prostigmatid mites are the keystone predators, Santos et al. (1981) observed that prostigmatid predation (specifically by the family Tydeidae) on microbivore nematodes resulted in increased decomposition of buried litter. The interactions between microarthropods and fungi in real communities (i.e. not microcosms, but in nature) occur in a complex environment. Alteration in rates of fungal growth and decomposition can occur, but the magnitude and direction of the effects are highly dependent on the mite taxa present, their abundance, and feeding ecology.

B. Methods

Resource perturbation press experiments were initiated in July 2014 and conducted within years 1 (2014) and 2 (2015) at The Morton Arboretum in Lisle, Illinois, USA. The site of the experiment is a mixed mesic temperate forest bordering the remains of a pin oak (*Quercus palustris*) plantation. Previous management practices included prescribed burning and European buckthorn (*Rhamnus cathartica*) removal, though many exotic invasive herbaceous plants, such as garlic mustard (*Alliaria petiolata*), existed at the site.

In June 2014, 200 circular 1-m^2 plots were established over a 21-day period within an approximate 1-ha area of forest. Plots were divided evenly into five rectangular blocks, each 12.2 m x 15.2 m (40 ft x 50 ft.). Plots were installed in a stratified design with daily installations spread across blocks and the four treatment types (see below). Approximately 10 plots were installed per day. One hundred and fifty of the 200 plots were fenced with aluminum flashing 25.4 cm (10 inches) wide (Midland Hardware, location), which was painted brown on one side and white on the other. Fencing was installed to limit immigration and emigration of soil microarthropods, and to contain the detrital enhancement within the plot, as wind, heavy rain or animals might have dispersed some of it otherwise. Fencing was buried approximately 7.6 cm (3 inches) into the ground surrounding the plot, while leaving the inside of the circular plot itself undisturbed. Another 50 plots were marked on the perimeter with Presco^{TM} steel wire stake flags (Forestry Suppliers, Inc., Jackson, Mississippi) but left unfenced as an untreated control (from now on referred to as Reference plots). The intent of the Reference plots was to assess whether fencing alone could influence the soil microarthropod community.

1. Detrital Enhancement Treatment

The treatment was a detrital enhancement intended to 1) bolster the abundance of saprophytic fungi for consumption by fungivore prey in the detrital system and 2) supplement the fungal community by direct application of fungi to ambient detritus already in plots. Fungi are known to respond productively to multiple resources, including starch substrates and other fungi. A portion of the detrital enhancement treatment was a mixture of white potatoes that were peeled and chopped using a manual

culinary chopper, and white button mushrooms sliced and then coarsely chopped using an Ulu knife. Mushrooms and potatoes used in the dispersed treatment were prepared several days ahead of dispersal and frozen. The amount of potato and mushroom for one plot was measured using a standard laboratory balance and then bagged in a quart Ziploc™ freezer bag and kept at -4°C until the morning that treatments were to be dispersed in the field. To encourage the growth of microbes on the forest floor, standard dry *Drosophila* medium flake (Carolina Biological Supply, Inc.) was also a component of the treatment. The amount of medium to be added to a single plot was bagged separately from the rest of the treatment for that plot. *Drosophila* medium was dispersed in a plot immediately before the chopped mushroom and potato were dispersed. Three levels of treatment were assigned to the plots fenced with Aluminum flashing to gauge whether a threshold exists for the responses measured:

- HIGH treatment (x4) – 400 g chopped mushroom (wet weight), 400 g chopped potato (wet weight), 40 g Drosophila medium (dry weight)
- LOW treatment (x1)– 100 g chopped mushroom (wet weight), 100 g chopped potato (wet weight), 10 g Drosophila medium (dry weight)
- NO treatment – no treatment dispersal.

The dried mass of potato and mushroom has been determined to be one-tenth the mass of the non-dried product in previous research. The masses of the *Drosophila* medium were chosen to equal the dried masses of the potato and mushroom. This enhancement combination is known from previous work to increase overall abundance of soil mites and Collembola (Chen and Wise 1997, Chen and Wise 1999) Similar rates of addition of this amount of artificial detritus increased fungal densities as measured by ergosterol content (Lawrence and Wise, submitted). The detrital enhancement treatment was applied every two weeks from mid-July through late September in 2014 (6 times) and from mid-April through late September in 2015 (11 times).

2. Microarthropod Sampling

Soil microarthropods were sampled, and environmental parameters were measured, at four times periods: July 2014 (initial conditions prior to first enhancement dispersal, 10-18 July), October 2014 (end of year 1, 27 September - 25 October), April 2015 (year 1 conditions prior to first enhancement dispersal of year 2, 11-18 April), and August 2015 (end of year 2, 8-15 August). The hypotheses I investigated are based on knowledge from previously published regarding the typical location in the soil horizon that certain taxonomic groups, specifically soil mites and Collembola, are known to inhabit. Therefore, separate humic soil and litter communities of microarthropods were sampled separately at every sampling event. Litter samples were taken for each plot using a "grab" technique, in which a sample the diameter of the collector's hand was extended fully and all litter within that area "grabbed" with one hand and bagged immediately in a Ziploc^{TM} bag. Soil samples were collected from the center of the area where litter was just collected using a standard bulb planter (Home Depot) ~6 cm in diameter and ~7 cm long, which was inserted into the ground using a twisting motion and lifted out with the soil sample inside. Soil samples were immediately bagged in Ziploc^{TM} bags for transport back to the lab. Soil and litter samples were kept in coolers for transport to the laboratory and stored at 11°C until they could be extracted. Arthropods from litter and soil samples were extracted separately one to three days after collection in a modified Berlese / Tullgren funnel (Southwood 1978) into 70% ethanol. Mites and Collembola were identified to family. Other microarthropods that were not part of the originally designated food web taxa were identified to either the family or order level, depending on ease of identification, as they were not going to be included in the final analysis. Most microarthropods were stored in 70% ethanol after sorting and identification. Most sorting was done under a high-resolution dissecting microscope, but approximately 200 specimens of mites and Collembola were chosen for mounting onto glass slides for further taxonomic identification. Both mites and Collembola specimens were cleared of internal tissue using lactophenol or laboratory-grade specimen clearing fluid (BioQuip Products, Inc.) for 1 to 7 days depending on the level of sclerotization of the specimen. Specimens were

then mounted into slides using PVA mounting medium (BioQuip Products, Inc.) and placed in an oven at 50°C for approximately one week.

3. Litter Parameters

Concurrently with collecting samples for microarthropod extraction, litter depth in each plot was estimated to the closest 0.64 cm (~0.25 inch) using a metal tape measure. Additionally, after microarthropods had been extracted from litter samples, the litter was re-bagged and weighed later using a standard laboratory balance. Litter weight was determined for plots in the final three sampling events, but not for the initial conditions in July 2014.

4. Soil Parameters

Concurrently with the collection of soil samples for microarthropod extraction, a small quantity of soil (50-100 g) was collected from the remaining hole for determination of percentage organic content of the soil (%SOM) and gravimetric soil moisture (GSM). Data was collected on these parameters to be used as covariates because soil fauna are known to be desiccation sensitive (Petersen and Luxton 1982, Lindberg and Bengtsson 2005) and thus differences in soil moisture between plots could affect the microarthropod community independently of the detrital treatment. Soil organic material is a factor in the amount of moisture soil can contain. Additionally, these two parameters can directly affect fungal growth (Brockett et al. 2012) and therefore, decomposition (see next section). To determine GSM, fresh soil samples were gently packed in pre-weighed aluminum weighing tins, weighed using a standard laboratory balance, and placed in a drying oven at 50°C for 24 hours. Samples were immediately weighed again after drying and this weight was recorded. Gravimetric soil moisture was calculated to be:

$$\text{(Wet weight of soil - Dry weight of soil)/(Dry weight of soil)}$$

SOM was determined by the loss-on-ignition method (Ball 1964). After GSM was determined, the same soil sample was combusted in its tin in a Muffle furnace at 500°C for 8 hours. The remaining mineral

content was allowed to cool overnight and weighed using a standard laboratory balance. Soil organic material proportion was calculated to be:

(Soil weight before combustion – Soil weight after combustion)/(Soil weight before combustion)

5. Decomposition rate / Microbial Activity Measured by Cotton Strip Assay

The determination of treatment effects on the activity of microbes that decompose cellulose was accomplished using the "cotton strip assay" to measure changes in a standardized cellulose substrate (Latter and Howson 1977, Howard 1988) three times in year 2 (July 2015, August 2015, and September 2015). Decomposition rate estimated this way gives an estimate of the rate of carbon mineralization from cellulose, which is primarily a function of fungi in temperate forest systems (Coleman et al. 2004). Decomposition rate can be used to evaluate patterns across detrital treatments that might relate to SOM content, GSM, and effects of community structure and abundances of taxa on soil processes. Forty plots were randomly chosen to be in the assay at each of the three sampling periods in 2015. The remaining 160 plots were randomly assigned to be assayed at only one of the three sampling periods. Eighty-nine cotton strips were buried in July, 97 strips in August, and 94 strips in September/October (one strip disappeared during burial).

The cotton strip assay utilizes a standardized cotton fabric as a medium for microbial growth. For this assay, 100% cotton utility fabric (JoAnn Fabrics) was cut along warp threads into 10.2 x 25.4 cm (4 x 10 inch) strips. Strips were packaged into five-strip groups and wrapped in heavy-duty aluminum foil (Jewel). Aluminum packages were autoclaved for 40 minutes to remove any microbes that might have been present before the beginning of the assay. Cotton strips were stored in the aluminum packages until being transported to the field. A flat garden spade was used to make a vertical slit in the ground, the spade was removed, and a cotton strip was wrapped over the bottom end of the spade, which was then inserted into the vertical slit at least 15.2 cm (6 inches). The spade was then removed, leaving the strip in place, and soil was pushed back to make contact with the length of the strip. Strips were left buried from 8-12

days and then retrieved. Strips were placed back into their original aluminum packages with Whatman™ filter paper placed in between strips. These were then transported to the lab and placed in a -4°C freezer until they could be cleaned and prepared to be torn. Strips were removed from the freezer and cleaned in groups of five strips. The five strips were placed into a bath of 3 L of deionized water and gently removed of cemented soil for 15 minutes. Strips were removed from the water and excess water was allowed to drip off of the strips for 15 seconds. Strips were then placed in a bath of 3 L of 70% ethanol for 45 minutes to eliminate the chance of continued microbial growth on strips colonized by fungal hyphae. Strips were then placed on absorbent Labmat™ bench liners and allowed to dry under rapid air movement at ambient room temperature. Cleaned strips were torn using a tensometer (TestResources, Model 100P225-6, Shakopee, MN) and the max load, % at elongation, and load at break were recorded.

Cotton strip tensile strength loss (CSTL) is calculated as the difference between the average of "control" strips, which were not buried, and the force (N) required to tear the strip that was buried. The maximum load on a strip before tearing can also be utilized to calculate a rate of decomposition, or "rotting rate" (*R*), with the equation (Correll et al. 1997):

$$R = \left(\frac{1}{t}\right)\left[\left(\frac{y_o}{y}\right) - 1\right]^{\frac{1}{3}}$$

where y = tensile strength (N); y_0 is the initial tensile strength (N, as measured from cotton strips used as treatment controls), and t is the time the cotton strip was buried (usually in the unit *days*).

6. Data Analysis

More soil and litter samples were collected over the two years than could be sorted and identified because of the time required to process so many samples (2x200 = 400 per date). All 2014 samples were analyzed: initial conditions for the entire experiment year (July 2014 (year 1); soil, n = 200; litter, n = 200) and a fall sample (October 2014 (year 2); soil, n = 200; litter, n = 200). Four sets of samples were taken in 2015 (April, July, August and October), but samples from July and October were not sorted and identified. Furthermore, a randomly selected subset of the 400 April 2015 samples (initial

conditions for year 2) was analyzed (soil, n = 90; litter, n = 90; no Reference plots). The final samples analyzed came from the second-to-last sampling event in year 2 [August 2015; soil, n = 199; litter, n = 199 (one sample was lost)]. Samples were collected in October the first year to allow communities the maximum time under enhancement conditions before cool fall weather arrived. Although samples were also collected in October 2015, the August 2015 data was chosen as the endpoint for year 2 because of the relatively few number of individuals in the samples from October 2014. It was felt that in August the temperature and moisture conditions would have been more favorable for fungal growth and for mite and Collembola activity and reproduction. The April 2015 samples were selected for analysis because they would reveal any residual effects of detrital addition from year 1 as well as reveal initial conditions for year 2, before the addition of detritus started.

For the first part of this analysis, I investigated structural changes to the communities of "common" and "uncommon" taxa due to enhancement. I defined taxa that were collected with a frequency, on average, of at least one individual every time I sampled a plot (soil and litter samples combined) as "common". The other taxa I considered "uncommon". In other words, "common" taxa are those collected in an abundance greater than 690 over the entire course of the experiment. This successfully separated the taxa that responded to enhancement the most from those that did not. For each of the two community types, multivariate analyses were done with litter and soil samples analyzed separately, and also pooled.

Patterns of abundance were first visualized using a ranked abundance distribution (RAD) based on total taxonomic abundances during the two-year experiment. RADs were calculated for the litter and soil communities separately and are presented in Appendix A.

Overall patterns of variation in response to the detrital enhancement were visualized using a Principle Coordinates Analysis (PCO) using the Bray-Curtis index of dissimilarity. Pearson correlations between the taxa and PCO axes were also plotted to visualize which taxa were most likely influencing the distribution of communities in ordination space. Pearson was chosen for this because this is most appropriate for data sets of true values as opposed to ones based upon ranks (i.e. NMDS – Nonmetric

Multi-Dimensional Scaling). The PCO was calculated for each set of community samples per sampling date with litter and soil communities combined and separately.

I performed a permutational multivariate analysis of variance (PERMANOVA, 9999 permutations of each community data set, Type III S, Anderson 2006). To do this, I transformed abundance data by adding 0.1 to all abundances and then took the fourth-root. Because this data set contained multiple samples with zero individuals collected, or "double zeros", adding 0.1 allowed PRIMER-E, which I used for the majority of my multivariate analyses, to create a dissimilarity matrix from my data. To test how different within-community dispersions may be across communities, I performed a permutational distance-based test for homogeneity of multivariate dispersions (PERMDISP) (Anderson 2006). This test reveals whether some community treatment groups cluster in ordination space more tightly than others or, in other words, are more alike than other treatment groups. This was done as a pairwise comparison between the three treatment groups.

Structural equation models (SEM), in the form of modern path analyses, were used to evaluate direct and indirect effects of IGP trophic groups and soil variables for July 2014, October 2014, April 2015, and August 2015. In path analyses all variables are observed as opposed to some being latent. Latent variables were not included in order to reduce the number of variables for better model fit; also, the system of potential interactions could be defined clearly without using latent variables. For the SEM analyses taxa were combined into larger trophic categories. The taxa included in these trophic groups can be seen in Table XXV, Appendix C. The community data were fourth-root transformed prior to model implementation in order to improve normality of the data. The condition (necessary for SEM) of multivariate normality is met if each variable has a kurtosis of 7 or less, and the overall multivariate critical ratio of 5 or less (Byrne 2016). The fourth-root transformation was sufficient to satisfy these conditions for October 2014, April 2015, and August 2015 analyses. The analysis for July 2014 (initial conditions) required removal of four statistical outliers to make the data multivariate normal.

Reference and No-Treatment data were combined and included together to comprise the No-Treatment category for both October 2014 and August 2015 data sets. This decision was made based on

the PERMANOVA performed on data presented in Chapter 2 (Table I and Table IX), which revealed that Reference and No-Treatment communities did not differ in overall structure. I assessed the fit of the model using three recommended statistics (Grace and Bollen 2005, Grace 2006, Byrne 2016); χ^2 Goodness-of-fit, the Root-Mean-Squared-Error of Approximation (RMSEA), and the Comparative Fit Index (CFI). Tests for multi-group invariance were performed to assess the statistical significance of differences in path estimates between the three treatment groups.

Differences in χ^2 values from Unconstrained and Constrained structural equation models were compared to evaluate the existence of interaction-pathway invariance between treatment groups. Both Unconstrained coefficients were calculated and are presented in path diagrams. Though standardized estimates are common in the literature, unstandardized coefficients are used when comparing interaction strengths between models or between treatment groups, as I am doing. Standardized estimates, which are unstandardized coefficient estimates standardized by variable standard deviations, are not as appropriate for this purpose (Byrne 2016, Grace 2006).

PCO, PERMANOVA, and PERMDISP analyses were performed using PRIMER-E/PERMANOVA (Anderson et al. 2008). RADs were calculated and plotted using R statistical computing language (R Development Core Team 2013). SEM analyses were performed using SPSS® AMOS v. 24.0.0 (IBM Corporation 2016).

C. Overview of Following Chapters

With intraguild predation theory and the current understanding of ecological and trophic interactions within the soil microarthropod community as a foundation, I will evaluate how the results of my experiment confirm, or fail to support, hypotheses related to basal resource enhancement, IGP, and decomposition. These results and statistical analyses, their interpretation, and discussion of their implications, are presented in the next three chapters. In chapter 2, I describe how the soil microarthropod community changes when basal resources are augmented through artificial enhancement over two years. I evaluate direct and indirect interactions between IG-predators, IG-prey, and their shared

fungivore resources in Chapter 3. Chapter 4 evaluates the effect of these interactions on the ecosystem process of cellulose decomposition. This research is unique in that there has been no previous *in situ* research on a highly complex community, such as the microarthropod community of the soil food web, that investigates the effects of bottom-up and top-down limitation through IGP dynamics at the sampling intensity and replication done here. These findings have the potential to better inform models of community dynamics examining how variation in the rate of basal-resource input affects the strength and pattern of interactions within the IGP module, and IGP as a structuring force in a pervasive type of detritus-based food web.

II. INVESTIGATION OF THE COMPOSITION OF THE SOIL MICROARTHROPOD COMMUNITY IN RESPONSE TO ARTIFICIAL DETRITAL ENHANCEMENT

A. Results

From the 689 litter samples and 689 soil cores used for this analysis, 60,355 microarthropods and other invertebrates were collected in 104 taxonomic groups. These are listed in Table XXVI of Appendix C. The most abundant taxonomic group overall was the mite family Tydeidae in the suborder Prostigmata. Tydeids are minute, piercing-sucking fungivores that inhabit litter and humic soil on the forest floor (Walter et al. 2009). The details on relative abundances for common-taxa and uncommon-taxa groups are presented as ranked abundance distribution (RAD) plots in Appendix A (Figures 25-32).

This analysis was approached from the perspective that there are two characteristic groups of taxa collected during this experiment, common and uncommon, and that litter and soil layers are often comprised of communities with differing taxa. The first group is the more abundant taxa, or "common" taxa, which I hypothesized would either respond more strongly to the treatment and/or whose responses would be easier to detect upon statistical analyses due to their higher abundances. This group consisted of taxa collected in a plot at least once, on average, every time samples were collected, or > 690 individuals. A second "uncommon" group (< 690 individuals collected) consisted of taxa that may not have been abundant from the outset, did not respond strongly to treatment, and/or were so rare that responses would have been difficult to detect statistically because of many zeroes in the sample. Furthermore, their relative rarity may reflect a combination of behavioral and life history characteristics that might lead them to respond differently from abundant taxa.

1. Soil Environmental Parameters

Means and 95% confidence intervals presented in Figure 6 show little difference between enhancement treatments for soil organic material (SOM) and gravimetric soil moisture (GSM). At both end-of-year determinations of litter depth, No enhancement and Reference controls have higher litter depth than, specifically, High-level enhancement plot determinations. There is no difference between

litter depths at the beginnings of both years (Figure 6). SOM, unsurprisingly, does not change much over the course of this experiment. However, GSM is much higher in July 2014 (before the start of the experiment) and April 2015 (beginning of year 2) than the ends of these years. Average rainfall per day for the months that included the two weeks before microarthropod collection took place: July 2014 (mean = 0.38 cm+/- CL 0.39), September 2014 (mean = 0.26 cm +/- CL 0.22), April 2015 (mean = 1.4 cm +/- CL 2.1), and August 2015 (mean = 0.42 cm +/- CL 0.32). Average daily temperatures were characteristic for these collection periods (July 2014 mean = 26.3 °C, September 2014 mean = 23.4°C, April 2015 mean = 16.7 °C, August 2015 mean = 27.0 °C).

2. Evaluation of Effect of Detrital Enhancement for the Common Taxa Community

Structural differences between the communities in Reference and No treatment plots were analyzed over the entire experiment to see if the aluminum fencing altered community structure. If fencing had an effect, then effects of the detrital treatments would have to be interpreted in the context of this perturbation of the system. A PERMANOVA revealed no effect of fencing on community structure in the absence of detrital additions (P(Fencing Treatment x Date) = 0.36, and P(Fencing Treatment) = 0.66; Table I). The three fenced treatments, High, Low, and No treatment (control) were used for the rest of this analysis

To investigate the possibility that changes in the microarthropod community in response to detrital supplementation were influenced by Block, I did a PERMANOVA investigating the interaction between Treatment, Sampling date, and Block. There was no evidence that Block was a factor in the dynamics of the microarthropod community during the experiment (Table II); therefore, this analysis was continued ignoring Block.

3. Differences in the Structure of Common-Taxa Community at the End of Year 1

Detrital addition clearly affected community structure during the first year, with the effect being stronger (i.e. more differentiation between the three treatment levels) in the soil layer (Figure 7, Tables III and IV). In a comparison of treatment groups, litter communities receiving any detrital

enhancement were significantly different from those that did not with the largest difference being between High-level and No enhancement community samples (Table VA). In the soil community, High-level enhancement samples were different from both Low-level and No enhancement samples (PERMANOVA, Table VB).

Community samples from soil clustered differently in ordination space based on enhancement treatment. Soil communities that received High-level enhancement became more similar in dispersion in ordination space than samples from other treatments in the soil layer (Figure 8; PERMDISP, Table VIB). Litter community samples from all treatments had the same level of community dispersion in all treatments (PERMDISP, Table VIA).

A canonical analysis of principle coordinates (CAP) (Figure 9) was used to investigate taxa that responded the most to enhancement and, therefore, influenced overall community structure the most. In litter communities, two fungivores, Tarsonemidae (Prostigmata) and Isotomidae (Collembola), and one predatory mite family, Parasitidae (Mesostigmata), increased due to High-level enhancement. Tarsonemidae was almost 5x more abundant than in Low-level enhancement samples (Figure 10B) and around 9x more abundant on average than in No enhancement samples. Tarsonemidae also replaced Tydeidae (Prostigmata) as the most abundant and dominant taxon at the end of year 1 (Figure 11; Appendix A, Figure 26). Parasitidae were 15x more abundant in High-level enhancement samples compared to No treatment (Figure 10A). Isotomidae were 7x more abundant in High-level enhancement samples than in No enhancement. In the soil community samples, Onychiuridae, also fungivorous Collembola, were 2.5x more abundant in High-level versus No enhancement samples (Figure 10A).

4. Differences in the Structure of Common Taxa Community at the End of Year 2

A large difference in community structure was found between the beginning of year 2 (April 2015) and the end of year 2 (August 2015), with soil communities differentiating at all levels of enhancement treatment. The community analysis at the beginning of year 1 (April 2015) revealed no residual effect of treatment from the year before in either the litter (PERMANOVA, Table IIIC) or soil layers (PERMANOVA, Table IVC). The PCOs for April confirm this visually (Figure 7 and Figure 8).

In August 2015, the largest change in community structure was observed in the soil community as they experienced more differentiation due to enhancement treatment than litter communities. Samples from High-level enhancement litter communities differed from the other treatments (PERMANOVA, Table VIIA), while all treatments were different from each other in the soil layer (PERMANOVA, Table VIIB). In the soil layer, community samples that received enhancement shared the same level of community dispersion in the PCO ordination (PERMDISP, Table VIF). In litter, High-level and Low-level treatment communities were significantly different in their level of dispersion similarity (PERMDISP, Table VIE).

Fungivore families Tarsonemidae (Prostigmata) and Isotomidae (Collembola), and predator Parasitidae (Mesostigmata), are the most affected taxa in the litter layer (CAP, Figure 9). In the soil layer, Isotomidae and Parasitidae increased the most in abundance (CAP, Figure 9). Isotomidae were over 4x more abundant in High-level enhancement soil samples than litter on average (Figure 10). Parasitidae were over 6x more abundant in High-level enhancement samples from the soil layer than in the litter layer (Figure 10). Litter Tarsonemidae and Parasitidae were collected the most in High-level enhancement plots. Isotomidae showed the most differentiation in abundance due to enhancement (Figure 10B) in both layers. Parasitidae were significantly more abundant in the High-level treatment soil community, but not litter, at the end of year 2 (Figure 10A). Clearly, large predators were highly abundant this time of year and appear to respond to different prey items in each layer of the soil horizon in High-level enhancement communities; Isotomidae in the soil layer and Tarsonemidae in the litter layer.

5. Evaluation of Effect of Experimental Design for the Uncommon Taxa Community

Using a PERMANOVA to compare fenced (No treatment) and un-fenced (Reference) control plots, I found there was no difference between fenced and unfenced control communities (Table VIII). I also investigated the possibility of a Block effect and found no evidence this (PERMANOVA, Table IX). The rest of the analysis was conducted without consideration of Block.

6. Differences in the Structure of Uncommon Taxa Community at the End of Year 1

The uncommon taxa community responded very little to treatment at the end of year 1. There is no evidence of any change due to enhancement in the litter community (Figure 12; PERMANOVA, Table XB, and Table XIA). The overall soil community was marginally different due to treatment (Figure 13; PERMANOVA, Table XIIB). This was the result of community responses to High-level treatment (Table XIB). Litter communities for different treatment groups were homogeneous in dispersion relative to each other in ordination space (PERMDISP, Table XIII).

The uncommon taxa that responded to treatment at the end of year 1 were mostly predators (CAP, Figure 14; Figure 15). The only predator that responded positively due to enhancement was Trombidiidae (Prostigmata) (Figure 15A). The small predator Ascidae (Mesostigmata) declined in abundance at the end of year 1 (Figure 15A). Alycidae (Endeostigmata) was negatively affected by enhancement (Figure 15A). The sole fungivore revealed by the CAP to be affected by enhancement is the detritus-burrowing fungivore Phthiracaridae (Oribatida). This response was similar to all other treatments (Figure 15B).

7. Differences in the Structure of Uncommon Taxa Community at the End of Year 2

There was a stronger response to enhancement by uncommon taxa in August 2015 compared to year 1. The litter layer community was less affected by enhancement than the soil layer community (Table X and Table XII). Litter and soil communities both responded to High-level enhancement the most (Table XIV). A PERMDISP revealed that High-level enhancement and No enhancement litter layer communities has different dispersions in ordination space from each other (Table XIIIE). In the soil layer community the largest structural differences were observed between Low enhancement and No enhancement groups (Table XIIIF).

Uncommon taxa showed very little positive response or a larger negative response to enhancement at the end of year 2. Only litter Hypogastruridae (Collembola) and Trombidiidae (Prostigmata) had a positive response to enhancement (Figure 14 and Figure 15B). There was no difference between treatments in the abundance of soil Neelidae, Phthiracaridae, or Alycidae (Figure 15B).

B. Discussion

The goal of the analysis in this chapter was to investigate how detrital enhancement altered community structure by changing abundances of different taxa in the layers of the soil horizon over the course of this experiment. Equally important, I presented information regarding taxa that did not respond, or responded negatively, to detrital enhancement treatment. It is clear that bottom-up pressure caused a very large increase in a small number of common prey taxa at the end of years 1 and 2, with coinciding, but not as large, increase in some ubiquitous predator taxa. In this discussion I will address the first few hypotheses I put forth in the introduction, discuss some implications regarding bottom-up and top-down forces, including what can be discerned from the patterns in uncommon taxa, and discuss differences in response strength between litter and soil communities.

1. Bottom-up Forces Affect Prey and Their Predators in the Common Taxa

The detrital enhancement treatment that was intended to directly affect abundances in the fungivore community did do so. This was expected as both Chen and Wise (1999) and Lawrence and Wise (submitted) saw similar abundance increases in some families of fungivorous Collembola, such as Isotomidae. As I hypothesized prior to my experiment, large increases in the abundance of minute, quickly reproducing fungivores, such as Isotomidae and Tarsonemidae were observed at the end of year 1, and again at the end of year 2. With regard to Isotomidae, this is not a surprising result, as individuals are known to increase in size and reproductive maturity quickly in the field under typical spring and summer temperature conditions (Joose and Veltkamp 1970). Growth is also known to continue for isotomids, though at a reduced rate, during the winter months and this may have allowed them to take advantage of the enhancement dispersed in the previous year to make it the common responding fungivore at the end of year 2 in both soil and litter.

One finding that is intensely interesting is the reduction in the abundance and dominance of the prostigmatid family Tydeidae at the end of both years in High enhancement litter communities by the prostigmatid family Tarsonemidae (Figure 11). Both of these families consist of small-sized (90-400 μm),

piercing-sucking fungivores in temperate forests, through they are known in tropical (Walter and O'Dowd 1995) and desert locations (Santos et al. 1981) to have phytophagous and predatory tendencies. Phytophagous genera of this family are known to appear quickly as pests in greenhouses (Walter et al. 2009) and to have acarine behavioral traits linked to the ability to make quick use of ephemeral resources, such as phoresy (the use of other arthropods as transportation) and wind dispersal. One primary difference between these two families is that tarsonemids are incapable of feeding on thickened cell walls (Jeppson et al. 1975), as would be characteristic of mature plant and fungal cell walls. Their increased abundance in High-level enhancement plots, therefore, points directly to the presence of new saprophytic fungal growth that was caused by the enhancement treatment. Though fungal growth and abundance was not directly assessed in this research, fungal density is known to increase with this enhancement (Lawrence and Wise, submitted). This particular finding provides additional support for the efficacy of the detrital enhancement treatment in the growth of the saprophytic fungal community. This change in familial dominance also signals that there may typically be competition between these two very similar fungivorous taxa. It is also a signal that High-level enhancement created a niche for individuals in the Tarsonemidae to grab a reproductive "foothold".

My results point to a large influence of basal resource enhancement on the fungivore community leading to increases in abundance in the population densities of both IGP-related predator communities. The mite predator that had the largest positive correlation to fungivore prey population increases was the family Parasitidae (Mesostigmata) in the soil layers in August 2015. This is a common generalist predatory mite in detrital and soil systems (Lindquist et al. 2009). In the soil microarthropod community, this family very much fits the definition of an IG-predator in the IGP vernacular (Polis et al. 1989) as well as the definition of a coupling predator in other work (Moore and de Ruiter 1991, Rooney et al. 2008). Because of their relatively large size and mobility, they can respond to an increased abundance of prey, such as microarthropod fungivores. The increase in abundance of Parasitidae at the end of both years provides evidence that for ubiquitous, mobile predators, bottom-up limitation exists in the soil food web.

2. Uncommon Taxa and Non-Response to Enhancement

One prediction regarding outcomes of this experiment that did not occur was a larger response by slower-developing fungivores at the end of year 2. These taxa, such as Phthiracaridae, did not appear to respond to treatment. In fact, these appeared to be negatively affected by enhancement and were considered uncommon taxa, as the ranked abundance distributions for uncommon taxa show many slow-maturing Oribatida did not increase in abundance (Appendix A, Figure 30 and Figure 32). Many of the microbi-detritivore oribatids that were placed into the uncommon category are not necessarily tied to leaf litter as their main habitat. A number of these (Phthiracaridae, Liacaridae, Peloppiidae, and Astegistidae, among others) are endophagous in small branches, pine needles, and other decaying pieces of wood (Aoki 1967, Norton and Behan-Pelletier 2009). These taxa may not have responded because they did not have the same exposure to changes in the microbial community stemming from enhancement.

Some trophic tendencies of the less-abundant predator taxa may make them less responsive to the indirect effects of resource enhancement. Less-abundant predators present in a system studied by Klarner et al. (2013) were shown to be more reliant on litter-feeding fauna as a prey source whereas more abundant predators appear to be more reliant on root-feeding fauna, like nematodes. If the most-consumed litter-feeding prey sources are not increased by enhancement, there would not be an indirect response to treatment. Other taxa, such as Alycidae, are thought to be mainly nematophagous, although they have been known to pierce plant roots and fungi (Walter 2009). So, while this enhancement increased microarthropod prey, this may not have increased other prey types.

Finally, the observation of low or declining abundance of these taxa due to enhancement may be a sign of heavy predation by the common predators that increased in abundance over the course of the experiment. This would be indistinguishable from non-response to enhancement and could be a major contributor to reduced abundance in uncommon taxa. This issue will be addressed further in Chapter 3, the intraguild predation chapter.

3. Effects of Enhancement on Microarthropods in Litter and Humic Soil Layers

My data show overall there are more differences in community structure between the three treatments in the soil community than in the litter community, both at the end of year 1 and year 2. Although there was an increase in fungivores at the end of both years, litter fungivores were observed to have the largest population increase in October of year 1 while soil fungivores were observed to have the largest increase in August of year 2. This is a counterintuitive result since the enhancement was dispersed directly to the litter layer and not mixed into the ambient detritus already present.

The patterns I found regarding patterns of taxa that responded in different layers have been observed before. Hutson and Veitch (1987) found in an investigation of differences in soil mite and Collembola communities across layers of the soil horizon and season that the largest differences had to do with layer, with Prostigmata and Onychiuridae observed to have the most difference (Prostigmata being mostly present in the litter and Onychiuridae mostly present in the soil). They also found the most abundant Collembolan in their samples was Isotomidae. The fungivores that responded in each layer to enhancement in my experiment confirm these previous findings regarding typical abundance and location of these families, as Onychiuridae are considered euedaphic (inhabiting upper mineral soil layers/humus layer) and Tarsonemidae and Isotomidae were the most abundant fungivores.

The distinctive environmental characteristics of soil and litter layers make them more typical habitat for some taxa than others and it is why certain taxa were impacted. Reasons for the particular response by fauna collected in the soil layer may be because humic soil is an environment with more consistent moisture and temperature conditions making it more favorable (though individual species are known to vary on this point (Verhoef and van Selm 1983)), due in great part to the environmental buffering and protective qualities of the litter layer (Sayer 2005). This makes humic soil the typical place for oviposition by soil taxa and refuge from drought, etc. However, the diversity of food resources in the litter layer can compete with humus and mineral soil as a favorable habitat at times as temperature and, especially, moisture conditions can cause rapid increased in microbial and algal growth.

It is also possible the addition of enhancement treatment during this experiment may have altered the typical location of some taxa. Chauvat et al. (2014) observed in a microcosm experiment that Collembola will travel farther into soil environments with a larger diversity of available resources, thereby changing their exploratory foraging behavior. I suggest that this could cause Collembola to traverse the soil-detritus interface by changing the total density of fungi, which can be changed by this same enhancement combination (Lawrence and Wise, submitted). Thus, the extent of structural change over time to communities in humic soil speaks to, not only movement of prey, but also reproduction by these prey in the soil layer, and the movement of predators to this increasing resource.

4. Changes in Chewing Versus Piercing-Sucking Fungivores

At the ends of both years, I observed an increase in piercing-sucking fungivores in litter communities that received High-level enhancement compared to soil communities and litter communities receiving other treatments, in which I observed increases in fungivores with chewing mouthparts at the end of both years 1 and 2 (Figure 8). This increase was due to enhancement. Taxa with these feeding types appear to be typical of these layers of the soil horizon as judged by their overall abundance in the ranked abundance distributions (Appendix A). Though there is no previous mention of this observation specifically in the literature, it is known that the succession of saprophytic fungal taxa proceeds rapidly in new litter as it decomposes (Voriskova and Baldrian 2013), so there is a continually renewing community of younger hyphae better suited for some piercing and sucking fungivores. The addition of detritus amplified fungal and fungivore responses and made them detectable. There is movement and reproduction of fungivores naturally in response to localized increases in ephemeral resources, such as that mentioned by Verhoef and Nagelkerke (1977) with Collembola. Because these may be extremely localized and fleeting in nutritional content, it is understandable that this is not a widely written about phenomenon in the literature in reference to minute, fungivorous mites.

5. Comparison with Previous Literature

I found at the ends of both years that these large-sized mite predators reacted positively to the increase in prey abundance, specifically in High enhancement plots. Though Lawrence and Wise

(submitted) examined other predators besides the predatory mite taxa in their experiment, my finding runs counter to their general conclusion that there is little evidence of bottom-up limitation in the secondary consumer/predator guild. They suggested their conclusions may have been affected by lower rainfall than is typical in their in experimental site during their period of data collection. Raub et al. (2014) corroborated this finding in their work in tropical systems, although tropical systems are not comparable in their diversity of microbes and level of ecosystem processing, as a temperate forest, so may, in general, not be a viable comparison to use. However, Chen and Wise (1999) did conclude that predator taxa were bottom-up limited in soil food webs in a site very close in character and geographic location to that of Lawrence and Wise's. Though Chen and Wise (1999) did not assess the abundance or composition of separate soil mite taxa or trophic guilds in their work, they arrived as their conclusion from their analysis of predatory taxa they did evaluate, including spiders and centipedes.

6. Seasonality and Fluctuation of the Soil Microarthropods Community

The final topic of discussion for contextualizing the responses by the community of soil microarthropods I observed during this experiment is the known seasonal fluctuation of these taxa throughout the year, as these could affect the level of response. Even without any resource manipulation, soil mites and, especially, Collembola are known to have large increases in density due to seasonal variation in temperature, soil moisture, and resource availability. Commonly in the colder climates of the U.S., peaks in density occur in spring and fall with a reduction in abundance during summer (Christiansen 1964). My results show that, overall, taxa that were most responsive to enhancement showed the strongest response at the end of years 1 (fall) and 2 (summer). I observed community structure in April 2015 to be similarity across all treatments (Figure 7 and Figure 8). This, of course, has something to do with the lack of enhancement dispersed over winter. It reveals that the impact of the detrital supplement has worn off over the winter through utilization by fungi and fauna, but also that conditions "relaxed" back to a situation where other factors are influencing faunal abundances.

C. Conclusions

This research did show the existence of simultaneous increases in predators and prey due to artificial detrital enhancement and a clear pattern of bottom-up control at all trophic levels. The results presented here speak to the influence of enhancement on overall abundances due to detrital enhancement in soil and litter layer communities, and in communities divided based on frequency of collection. However, this work does not investigate interactions between trophic groups to any impact of higher trophic levels on fungivores and, therefore, cannot address top-down control. Therefore, the next chapter addresses the interactions between trophic guilds, specifically those hypothesized to be involved in omnivorous IGP interactions in both soil and litter.

III. INVESTIGATION INTO INTRAGUILD PREDATION AS A STRUCTURING FORCE IN THE DETRITAL MICROARTHROPOD COMMUNITY

The following results address hypotheses regarding the strength of IGP interactions in structuring the microarthropod community. The best-fitting models were path analyses that reduced the taxonomic resolution to groupings into the three main trophic groups in an IGP module: IG predators, IG prey and a common prey resource, fungivores (for the taxa that comprise these groups see Appendix C, Table XXV). These are the groups Polis et al (1989) and Polis and Holt (1992) used to define the IGP interaction, and their analysis of factors contributing to coexistence of IG predators and IG prey. The fact that the model fitting with my data yielded a combination of taxa in each IGP group was expected, as explained by Attayade and Hansson (2001), who found that a coarse taxonomic resolution resulted in clearer interaction pathways. The minimization of variables is also a necessity in developing a good-fitting SEM, as it is recommended that there be ten samples in a data set for every variable in an SEM (Grace 2006).

In analyzing the interactions between IGP trophic groups in data from 2014 and 2015, two models were found to be good fits to the end-of-year data. Although percent soil organic material (SOM), gravimetric soil moisture (GSM) and litter depth were all utilized separately as environmental variables, due to ill model fit for models with SOM, only models including GSM and litter depth were investigated further. The GSM model fit the data for October 2014, but it was the lesser-fitting of the models (litter depth model AIC = 53.998, GSM model AIC = 54.958). For August 2015, two interaction pathways were not significant for any of the treatments when GSM was included. Therefore, the GSM model is presented in the Appendix B (Figure 37). The model that included litter depth was the best fitting (Figure 16) as shown by goodness-of-fit statistics when performed on the full October 2014 (df = 2, $\chi^2 = 0.211$, $P = 0.900$, CFI = 1.0, PCFI = 0.333, RMSEA = 0.0, AIC = 16.221) and August 2015 (df = 2, $\chi^2 = 1.041$, $P = 0.594$, CFI = 1.0, PCFI = 0.333, RMSEA = 0.0; AIC = 17.042) data sets with no treatment group comparisons. The litter depth variable was the environmental parameter that changed the most due to

enhancement treatment (Figure 6). This is the model presented in this chapter and is the one from which conclusions regarding IGP interaction hypotheses are drawn.

A. Results

1. Abundances of IGP Trophic Guilds

In general, fungivores, IG-prey, and IG-predators are more abundant in High-enhancement plots than all other treatments at the ends of both years. At the end of year 1, fungivores in High-enhancement samples increased to over 2.5x that of the average abundance prior to the beginning of the experiment, and were 2.4x more abundant than the No enhancement control (Figure 17). At the beginning of year 2 (April 2015), average abundances in High-enhancement samples returned to those of initial condition-levels and rose again at the end of year 2 (August 2015). Fungivores averaged 1.8x more in No enhancement control samples than High-level treatment and 1.2x more in High-level than Low-level enhancement samples (Figure 17). This shows the fungal community changed in abundance due to High-level enhancement and then relaxed back to the levels observed at the beginning of year 2.

Both groups of predators were affected positively by High-level enhancement in year 1. IG-prey and IG-predator individuals were collected in similar averages in year 1. At the end of year 2, IG-prey average abundance in High-level samples dropped to 43% of the previous year average (Figure 17). IG-predators increased 1.3x on average from year 1 to year 2 in High-level samples. This coincides with decreases in abundance of small predators such as Ascidae and Alycidae (Figure 15A). The average abundances of IG-predators at the end of years 1 and 2 were 3x and 4.3x more than the No enhancement control averages for those years, respectively. Overall, abundance peaked for IG-prey at the end of year 1, while abundance peaked for IG-predators at the end of year 2.

2. Evidence of Intraguild Predation at the Beginning of Year 1 (Initial Conditions)

The model that I found to be the best fitting for both end-of-year data sets was not a good model for either IGP interactions at initial conditions of the experiment or for April 2015, the beginning of year 2, for different reasons (Figure 18 and Figure 19). The model evaluated with initial condition data was a poor fit for the data. It shows the strongest interaction is between fungivores and IG-prey with some

evidence of IGP (Figure 18). When run as a multigroup model (a model with samples designated by their treatment group), we see that this is because of weak IGP interactions across all treatments and no role of leaf litter depth (Figure 19). At the beginning of year 2, the IGP model shows that there is little evidence for the existence of these interactions (Figures 18 and 19).

3. Interactions with Litter Depth at the End of Both Years

At the end of year 1, litter depth, the major substrate for fungal growth, played a more significant role in communities that did not receive enhancement treatments (Figure 20). Litter is thicker in these plots as well (Figure 6). These interaction pathway estimates were found to be invariant between enhanced and non-enhanced communities (Table XVA) with no difference in regression slopes between communities observed using a Student's t-test on regression estimates (Table XVI). A further evaluation of path estimates for all treatments confirms there is no difference between effect sizes for each treatment group (Table XVII).

At the end of year 2, litter depth affected fungivores significantly in plots receiving detrital enhancement, whereas no interaction was observed in No enhancement control samples. This is the reverse of what was observed at the end of year 1 (Figure 20). This interaction was not invariant across enhancement versus no-enhancement treatments (Table XV) or all treatments (Table XVIIIB), but had a significantly larger positive effect on fungivores in High-level compared to No enhancement communities (Table XXB).

4. Evidence of Intraguild Predation at the End of Year 1 (October 2014)

There appeared to be strong effects on the IGP trophic groups overall at the end of year 1 due to High-level enhancement. All three IGP trophic groups were significantly higher in abundance in samples from High enhancement plots in October 2014 (Figure 17). Fungivores, the common prey source shared between IG-predator and IG-prey groups, had significant positive effects on both predator groups regardless of whether or not they received enhancement (Figure 20). They had the largest direct effect on IG-prey, followed by IG-predators (Figure 20). In Low-level treatment communities, fungivores only influence IG-predators indirectly through their consumption of fungivores (Figure 21).

The effect of IG-prey on IG-predators was significant at the end of year 1 in communities that received detrital enhancement compared to those that did not, with the largest direct effect being seen in samples from Low treatment communities (Figure 21). The coefficient estimate was significantly variant (Table XV) between communities that received enhancement and those that did not, and a Student's t-test of regression estimates revealed a much higher effect of IG-prey on IG-predators in plots that received enhancement (Table XVI). A further analysis of the three treatments revealed that the regression estimate for the IGP interaction was significantly larger for Low enhancement treatment than either High-level or No enhancement estimates separately (Figure 21 and Table XVIIIA).

5. Evidence of Intraguild Predation at the End of Year 2 (August 2015)

At the end of year 2, detrital enhancement affected IGP interactions, as all path strengths were different between samples from communities that received enhancement and those that did not (Figure 20, Table XVB). IG-prey were affected significantly by fungivores at the end of year 2, regardless of enhancement, whereas IG-predators showed a stronger indirect effect of fungivores by way of IG-prey in enhancement plots (Figure 20). The effect of fungivores on IG-prey was variant between samples from plots that received enhancement and those that did not (Table XVB) with the effect on IG-prey being significantly stronger in communities not receiving enhancement, as seen by Student's t-test (Table XIX).

In contrast to the results after year 1, IG-predators were affected only indirectly by fungivores through the consumption of IG-prey, revealing IGP to be the strongest interaction in communities receiving either enhancement treatment. I observed a large increase in abundance in the IG-predator population in year 2 relative to the end of year 1 in High-level enhancement samples (Figure 17), suggesting a noticeable amount of consumption by IG-predators. Additionally, I observed IG-prey in High-level plots to have an abundance similar to other treatments at the end of year 2 compared to year 1, suggesting this is a consequence of the larger IGP interaction strength observed for this treatment group (Figure 21). However, a test of invariance between the three treatment groups did show invariance in this path and this was confirmed in a Student's t-test of regression estimates (Table XX).

B. Discussion

The goal of this analysis was to evaluate the strength of top-down and bottom-up control on the detritus-based soil microarthropod food web using IGP as a framework for these concepts. By analyzing static "snapshots" of community structure, I investigated predictions regarding hypothesized dynamics of the system. I examined the effects of basal resources on fungivores, whether fungivorous prey affected one or both of the predator groups, and whether responses by predators include intraguild predation, or the consumption of predators by other predators with whom there is a shared common resource. IGP theory suggests that along an increasing gradient of productivity, the impact of predation becomes more evident (Polis et al. 1989) and, in general, I found this to be the case. In the following, I will discuss results in regards of the original hypotheses I developed for the soil microarthropod community and link them to IGP theories of interaction. Additionally, I will bring to bear known life history information in an effort to elucidate possible ecological phenomena or mechanisms that influence interactions in the soil microarthropod community

1. Bottom-Up Limitation in the Soil Microarthropod Community

One of my predictions (Hypothesis 1) was that, initially, fungivorous prey would increase in abundance leading to an increase in IG-prey (small adult and juvenile predatory mites) due to their close proximity to the origination point of juvenile fungivores (deeper soil) (Figure 2A). I found this to be the case as large abundances of fungivores were observed at the end of year 1 and to a lesser extent in year 2. The second prediction I made (Hypothesis 2, Figure 2B) was that the IG-predators would also increase in abundance, but not as much as, and later than, the IG-prey. In October 2014, there is a large increase in fungivores, which correlated with a large increase in IG-prey and a smaller increase in IG-predators (Figure 17) indicative of bottom-up limitation (McQueen et al. 1986). The strongest positive direct interaction is also between fungivores and IG-prey in the end of year 1. This supports my Hypotheses 1 and 2, and is the situation indicative of bottom-up limitation within the food web with increases in abundance observed at all trophic levels, but with smaller increases at higher trophic levels (Figures 4 and 5).

2. Intraguild Predation and Top-Down Limitation

The third hypothesis I put forth was that after long-term enhancement, IG-prey would be negatively affected by IG-predators or, in other words, the system would be subject to top-down control (Figures 2C, 4 and 5B). At the end of year 1, I observed an increase of IG-predators that was less than that of IG-prey (Figure 17) and there is a large indirect effect of fungivores, by way of consumption of IG-prey by IG-predators, in Low enhancement communities. I found this interaction was also significant in High-level enhancement samples, but the interaction was not as strong (Figure 21).

At the end of year 2, I observed a large increase in the population of IG-predators but a smaller abundance of IG-prey in High-level enhancement communities (Figure 17). High-level enhancement plots also had the largest strength positive IGP interaction, that of small predators (IG-prey) on large predators (IG-predators). In Low-level treatment communities, the IGP interaction is the only interaction of significance. This is likely because the lesser level of enhancement increased the fungivore prey resource in an inadequate amount to sustain the increased population size of the IG-predator guild. This is a situation mentioned specifically by Polis et al. (1989) to be a common IGP scenario that encourages large predators to diversify the prey types in their diet to include small predators. It is reasonable, then, to interpret the seeming lack of response to High-level enhancement on the part of small predators (IG-prey) as indicative of top-down limitation by large predators (IG-predators) as shown in Figure 4 and 5). Though it is difficult to provide definitive support in this analysis for a difference between this and a general lack of response to enhancement, the conclusion that there is little response by IG-prey to increased abundance of fungivores in August 2015 is inconsistent considering the very large positive response to enhancement observed in October 2014 (Figure 17). Therefore, I suggest that lack of response by IG-prey is an unlikely scenario and that this smaller abundance in IG-prey and very large increase in IG-predators at the end of year 2 is support for my third hypothesis, IG-prey are reduced by IG-predators.

3. Caveats

Though SEM is a meaningful way to analyze the direction and magnitude of interaction strengths between variables, it has drawbacks. SEM provides an overall regression coefficient for each

pathway based on, in this case, abundances that are the result of responses to treatments. McQueen et al (1986) concluded that regression coefficient variability in a bottom-up interaction in their results could always be explained by top-down limitation. As I demonstrated, there are both bottom-up and top-down forces playing a role in the system used for this research. What we observe in our results is a modulated effect size in the direction of the largest effect. With this method, I am unable to determine magnitudes of separate positive and negative interaction strengths that comprise one pathway. This is a general limitation of SEM, which makes additional statistical approaches necessary in interpreting data.

In evaluating interaction strengths between IGP trophic guilds it is clear none of the interaction effects are very large. This outcome was likely, as mentioned in the introduction of this dissertation, because there are many generalist predators in the soil food web that utilize multiple common prey items (Klarner et al. 2013, Walter and Proctor 2013) and there is a frequent occurrence of feeding redundancy due to prey switching (Siepel 1994, Levin et al. 2001). Additionally, there are multiple species in each predatory group in the IGP module, and this can sustain the IGP interaction (Polis et al. 1989). As the IGP interaction is generally of weak strength, IGP will likely continue (Mylius et al. 2001) as will the coexistence of the IGP predatory groups.

Also contributing to the observed weak interaction is that there may be prey in the system that I did not evaluate. Mite predators can utilize prey resources that are not microarthropods, which would not be reflected in my original data set. Nematodes can contribute to the diet of mesostigmatid predators (Klarner et al. 2013, Heidemann et al. 2014), and even some oribatids (Schneider et al. 2004), which are typically considered to be fungivores. Evaluating the nematode community would close some of this gap in knowledge in future work.

C. Conclusions

There is evidence that both bottom-up and top-down control influenced the soil microarthropod community during this experiment, mostly bottom-up in year 1 and bottom-up and top-down in year 2. This agrees with previous literature that systems are subject to some level of both types of control (Wardle 2002, Bardgett and Wardle 2010, Moore and de Ruiter 2012). Though these interactions have

been previously investigated in models, microcosm experiments, and simple three-species modules, this is the first time, to my knowledge, that IGP has been investigated in an experiment with a fully realized, complex system under otherwise typical forest conditions. The addition of other analyses, such as molecular gut-content analyses of predators and suspected mutual predators, would help assess the level top-down control of prey through consumption, which cannot be determined simultaneously with positive effects through SEM. The next chapter presents analyses that seek to include microbial activity as a variable affecting fungivores as well as a variable dependent upon fungivore consumption.

IV. CHANGES IN THE RATE OF CELLULOSE DECOMPOSITION DUE TO DETRITAL ENHANCEMENT AND ALTERED INTERACTIONS WITHIN THE IGP MODULE

To answer questions relating to how detrital enhancement, and changes in the IGP module due to detrital enhancement, may have affected the activity of microbes as measured by rates of cellulose decomposition, cotton strip tensile-strength loss (CSTL) was measured at three times in year 2 (July 2015, August 2015, and September 2015). Results for August 2015 were also incorporated into an SEM model of IGP interactions. Poor fitting and less well fitting models that were examined are presented in Appendix C (Figures 38-44).

A. Results

Mean tensile strength loss and the mean daily rate of loss, i.e. the "rotting rate" (Correll et al. 1997), which corrects for the time strips were buried in plots, were both higher in High enhancement plots in July and August (Figure 22). Rates in the Low enhancement treatment were intermediate between those in High and No-enhancement plots (Figure 22). Neither variable differed among treatments in September 2015, but the overall very low rates suggest that environmental conditions severely limited decomposition in September. Rates were highest in all treatments in August, which prompted me to use the August data for the SEM. The number of samples in the data set for August 2015 was n = 93.

1. Differences in Effects of Predators and Fungivores on Loss of Tensile Strength

In evaluating the effect of fungivores on CSTL in plots receiving enhancement versus no enhancement, there was no evidence of a difference between the two (Figure 23). The model separating samples by treatment did show a small negative effect of fungivores on CSTL in the Low-level enhancement plots in August. This is linked with the inhibition of fungal activity. Details on model results are presented in Appendix C.

B. Discussion

The evidence provided here for the effect of changes in the IGP microarthropod community on a proxy for microbial activity and growth is clear, but needs to be unpacked further because, I suggest, three

distinct dynamics scenarios are occurring in treatment groups, warranting special consideration in the top-down/bottom-up control discussion. In High-level enhancement communities, fungivores do not strongly inhibit fungal activity, though they have a positive effect on IG-prey and have a positive indirect effect on IG-predators through IGP, supporting strong bottom-up limitation (McQueen et al. 1986, Mittelbach et al. 1988). All signs point to microbial growth being highest in these plots as revealed by increase in tensile strength loss (Figure 22) and the relatively large abundance of fungivores that are restricted to new fungal and algal growth (Figures 10 and 11). In this scenario, fungivores are abundant prey for predators as well as do a small amount of damage, or inhibit, microbes (Hanlon and Anderson 1979, Parkinson et al. 1979, Seastedt 1984). Additionally, there is evidence from the previous analysis for control of fungivores by predators (a reduction in overall fungivore abundance (Figure 17) and increased positive effect of fungivores on IG-prey (Figure 24)). So, this reduces any effect of fungivores on CSTL.

In No-enhancement communities, fungivores have a strong positive effect on IG-prey and indirectly affect IG-predators through IGP, revealing bottom-up limitation in the system. Microbial abundance in these plots is at ambient levels and unaltered by enhancement (Figure 22). There was not a large increase in fungivore abundance, so this scenario represents the typical, ambient activity of this abundance of fungivores.

In communities receiving Low-level enhancement, something distinctive is happening. In my experiment CSTL was affected the most negatively (Figure 24) by an average abundance of fungivores that is no different from control plot abundances (Figure 17). I suggest that fungivore abundance in Low-level enhancement plots increased to some extent by the presence of detrital enhancement. Fungivores were able to consume a great deal of the fungi produced increasing their numbers overall. Predators, then, increased in abundance due to increased prey (Figure 17), but this increase may have been over the carrying capacity for fungivore prey, so the larger IG-predators expanded to consume the smaller IG-prey. This may have relieved some of the top-down control on fungivores, placing it on IG-prey, and perhaps causing some fungal activity inhibition due increase consumption of fungivores. This is the type of situation predicted in Polis et al. (1989) and Holt and Polis (1997) when the common resource decreases.

It appears that fungivores are not affecting IG-prey or IG-predators, directly or indirectly. This is clearly not true regarding what we know about the IGP community module from Chapter 3, as IGP interactions were the strongest in Low-level enhancement communities when all 200 samples are analyzed. However, a reduced data set was used for this SEM analysis (n = 93; 97 - 4 samples removed as statistical outliers) due to the sampling design of the cotton strip assay (see Chapter I, Introduction), which may change these particular results.

A further point to address here is that change in the abundances of taxa of certain feeding types may affect soil processes differently. These fauna could have different impacts on the density and enzymatic activity of their fungal resources, a top-down effect. A large abundance of chewing and piercing-sucking fungivores were observed in High-level enhancement plots at the end of year 2, whereas comparatively more piercing-sucking fungivores (Tarsonemidae and Tydeidae) were in Low-level enhancement communities (Figures 11 and 17). This could have caused the larger negative effect of fungivores on CSTL. In research evaluating chewing (browsing) versus piercing-sucking (grazing) fungivorous Oribatida, Siepel and Maaskamp (1994) suggested that chewing mites were more likely to damage hyphal cell walls causing a compensatory growth reaction on the part of the fungus. Piercing-sucking feeders are able to access fungal cell contents with little damage to the cell wall and this results in a general inhibition in activity of the fungus with little to no observed compensatory growth compared to damage from chewing "browsers" (Siepel and Maaskamp 1994). This phenomenon has good support in the microarthropod-microbe literature as an influential force regulating fungal activity and decomposition (Van der Drift and Jansen 1977, Hanlon and Anderson 1979, Hanlon 1981, Bengtsson and Rundgren 1983) and could account for this result.

C. Conclusions

Though the dynamics suggested by these results are the product of an evaluation of a "snapshot" of one state of this community in time, there are some reasonable inferences to make regarding community dynamics. The analysis and results presented here do not discount the role of predator-prey interactions in regulating ecosystem processes. As basal resources increase, decomposition increases as

do abundances of fungivores. At an intermediate level of resource increase, there is evidence that fungivores can inhibit the activity of fungi, reducing decomposition. Though this appears to be independent of bottom-up or top-down limitation in the system, this is likely not true, but based on the limitation of the SEM technique to present only one path coefficient. Additionally, understanding the composition of fungi that increased and decreased in density during the experiment would help me understand which fungal groups were most responsive to enhancement, and also the palatability of these to fungivores in the soil food web.

V. FINAL CONCLUSIONS AND FUTURE WORK

A. Conclusions

In this experiment, I investigated the strength of bottom-up and top-down limitation as community structuring forces through the examination of the IGP interaction during a basal-resource supplementation experiment. Guided by intraguild predation theory and the current understanding of ecological and trophic interactions within the soil microarthropod community, I sought to answer 1) how does enhanced detrital input affect soil microarthropod community abundance and family composition over a multi-season period? and 2) how do changes in abundance and trophic and family composition of microarthropod fungivores affect decomposition? In this dissertation, I evaluated effects on the overall structure of the soil microarthropod community, how enhancement changed abundances within IGP trophic groups and the strength the IGP interaction, and how enhancement and changes in fungivore abundance affected microbial activity related to decomposition. I have concluded:

- The soil microarthropod community is both bottom-up and top-down limited when there is a large increase in basal resources over two years.
- The intraguild predation interaction is strongest when there is a large increase in the abundance of large predators over more than one season.
- High-level of enhancement increased decomposition, but increasing fungivore density had a small impact on decomposition.
- Communities subjected to enhancement perturbation appear to quickly "relax" back to conditions where typical soil environmental factors are a larger influence on community structure.

B. Further Work

This work confirmed some previously held theories regarding the existence and strength of bottom-up and top-down limitation in food webs. Further research would broaden the general conclusions and further test theories regarding bottom-up and top-down control. One aspect that I did not examine was the composition of fungal hyphae in plots subject to different enhancement treatments. As Hunter

and Price (1992) suggest, not all plants are of similar palatability to herbivores and that this can affect the dominance of bottom-up or top-down control. The same goes for fungi and fungivores (Schneider and Maraun 2005, Schneider et al. 2005). Understanding which fungi increased in density may help explain the increase of some fungivores and not others. Additionally, understanding how ambient diversity and patchiness of fungal hyphae on the forest floor compares to the level I affected in plots would assist in the understanding the mechanisms by which bottom-up and top-down limitation are more likely to occur.

This research supports the Fretwell-Oksanen theoretical model of patterns of trophic limitation over a relatively small community module, IGP. Expanding this model to five (or six) trophic-levels, a common level food web of complexity in temperate forest soil systems, would tell me how the model of alternating trophic levels subject to top-down/bottom-up limitation holds for large food webs subjected to disturbance, how strengths of these interactions change with increasing trophic level, and the circumstances in which a trophic level switches from being subject to bottom-up control to a dependent variable subject to top-down control.

Another aspect tied to this research, which needs to be investigated further, is the level to which this system was subjected to rapid change in structure and then "relaxed" to no noticeable effect of enhancement by the beginning of the next year. This experiment was run under typical temperature and rainfall conditions for the seasons, but these conditions are predicted to change with climate warming. Though researchers investigating changes to forests and forest soils subjected experimentally to climate change conditions are finding that predicted increases in primary productivity are relatively short-lived, there is little information on how interactions between soil fauna change or how long changes last. Given that my research revealed some effect of fungivores on decomposition at a small resource increase, the question of whether these interaction strengths change with increased drought conditions or increased rainfall should be pursued if this new information is to be synthesized for use in future food web and ecosystem research.

TABLES

TABLE I

PERMANOVA RESULTS EVALUATING DIFFERENCES BETWEEN COMMON TAXA NO TREATMENT (FENCED) COMMUNITIES AND REFERENCE (UNFENCED) COMMUNITIES OVER TIME[a]

Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Treat	1	1305	1305	0.75213	0.6623	9922	0.6569
Date	3	235550	78518	45.252	0.0001	9901	0.0001
Treat x Date	2	3741.6	1870.8	1.0782	0.3617	9916	0.3571
Residuals	327	558710	1735.1				
Total	328	812680					

[a] Performed under a reduced model with results from Monte Carlo tests using Bray-Curtis dissimilarity.

TABLE II

PERMANOVA RESULTS EVALUATING DIFFERENCES IN TREATMENT AND BLOCK OVER TIME FOR COMMON TAXA COMMUNITIES[a]

Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Treat	3	17382	5793.9	3.7261	0.0001	9893	0.0001
Date	3	587400	195800	125.92	0.0001	9908	0.0001
Block	4	56289	14072	9.05	0.0001	9874	0.0001
Treat x Date	8	18996	2374.5	1.5271	0.0015	9817	0.0018
Treat x Date x Block[b]	32	47343	1479.5	0.95152	0.7196	9675	0.7174
Pooled Residuals	638	992060	1555				
Total	688	173740					

[a] Performed under a reduced model with results from Monte Carlo tests using Bray-Curtis dissimilarity.

[b] Treat x Block and Date x Block interactions were pooled.

TABLE III

PERMANOVA RESULTS FROM A TEST OF EFFECTS OF TREATMENT AND BLOCK INTERACTION OVER TIME FOR HIGH, LOW, AND NO TREATMENT COMMON-TAXA LITTER COMMUNITIES USING BRAY-CURTIS DISSIMILARITY

	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
A. July 2014							
Treat	2	2191.4	1095.7	0.65547	0.7859	9930	0.7827
Block	4	24839	6209.8	3.7149	0.0001	9880	0.0001
Treat x Block	8	10894	1361.8	0.81466	0.81	9860	0.7983
Residuals	135	225670	1617.6				
Total	149	263590					
B. October 2014							
Treat	2	9502	4751	3.0034	0.0004	9931	0.0002
Block	4	18169	4542.2	2.8714	0.001	9896	0.0001
Treat x Block	8	10164	1270.5	0.8429	0.8429	9866	0.8296
Residuals	135	213550	1581.9				
Total	149	251390					
C. April 2015							
Treat	2	1462.4	731.22	0.74622	0.6653	9932	0.6572
Block	4	5334.6	1333.7	1.361	0.1514	9909	0.1632
Treat x Block	8	6643.5	830.44	0.84747	0.713	9889	0.7034
Residuals	75	74493	979.91				
Total	89	86934					
D. August 2015							
Treat	2	13056	6528.2	3.9043	0.0001	9915	0.0001
Block	4	21003	5250.7	3.1402	0.0001	9883	0.0001
Treat x Block	8	15131	1891.3	1.1311	0.2488	9859	0.2501
Residuals	134	24060	1672.1				
Total	148	73440					

TABLE IV

PERMANOVA RESULTS FROM A TEST OF EFFECTS OF TREATMENT AND BLOCK INTERACTION OVER TIME FOR HIGH, LOW, AND NO TREATMENT COMMON TAXA SOIL COMMUNITIES USING BRAY-CURTIS DISSIMILARITY

	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
A. July 2014							
Treat	2	3896.5	1948.3	0.61369	0.835	9914	0.8319
Block	4	31907	7976.7	2.5126	0.0001	9895	0.0004
Treat x Block	8	34372	4296.5	1.3534	0.0556	9876	0.0572
Residuals	135	428580	3174.7				
Total	149	498760					
B. October 2014							
Treat	2	10457	5228.7	2.2965	0.0033	9937	0.0039
Block	4	24779	6194.6	2.7208	0.0001	9904	0.0001
Treat x Block	8	23035	2879.4	1.2647	0.0100	9874	0.1062
Residuals	135	307370	2276.8				
Total	149	365640					
C. April 2015							
Treat	2	2570.8	1285.4	1.0555	0.3918	9942	0.3877
Block	4	6407.1	1601.8	1.3152	0.1927	9915	0.2049
Treat x Block	8	11048	1381	1.1339	0.3003	9891	0.3037
Residuals	75	91339	1217.9				
Total	89	111360					
D. August 2015							
Treat	2	14508	7254.1	6.1935	0.0001	9934	0.0001
Block	4	14350	3587.4	3.0629	0.0001	9907	0.0001
Treat x Block	8	10941	1367.7	1.1677	0.2069	9832	0.2185
Residuals	134	156950	1171.2				
Total	148	196330					

TABLE V

PERMANOVA RESULTS OF A PAIR-WISE TEST OF STRUCTURAL DIFFERENCES IN THE COMMON MICROARTHROPOD A. LITTER COMMUNITY AND B. SOIL COMMUNITY IN OCTOBER 2014 BY TREATMENT USING BRAY-CURTIS DISSIMILARITY[a]

Groups	*t*	P (perm)	Unique perms	P (MC)
A. Litter				
High, Low	1.2375	0.156	9949	0.1656
High, No	2.1586	0.0001	9941	0.0002
Low, No	1.6555	0.011	9951	0.0131
B. Soil				
High, Low	1.4097	0.052	9942	0.0631
High, No	2.025	0.0002	9938	0.0001
Low, No	0.96936	0.4836	9938	0.4804

[a] Performed under a reduced model using type III sum of squares. 9999 permutations.

TABLE VI

PERMDISP RESULTS SHOWING DIFFERENCES IN HOMOGENEITY OF MULTIVARIATE DISPERSIONS BETWEEN TREATMENTS IN THE COMMON TAXA COMMUNITY BY DATE USING BRAY-CURTIS DISSIMILARITY

October 2014	df	F	P (perm)	Groups	*t*	P (perm)
A. Litter	2.147	1.724	0.2581	High, Low	0.57989	0.5947
				High, No	1.7089	0.1302
				Low, No	1.2595	0.2647
B. Soil	2, 147	11.057	0.0006	High, Low	3.3334	0.0042
				High, No	4.5516	0.0001
				Low, No	1.2211	0.273
April 2015						
C. Litter	2, 87	3.7382	0.0551	High, Low	1.57	0.177
				High, No	1.1347	0.3001
				Low, No	2.5791	0.0256
D. Soil	2, 87	0.62026	0.6689	High, Low	0.12222	0.9238
				High, No	0.97432	0.4207
				Low, No	0.99713	0.4159
August 2015						
E. Litter	2, 146	3.1856	0.0761	High, Low	2.3459	0.0375
				High, No	1.5985	0.1562
				Low, No	0.71658	0.526
F. Soil	2, 146	11.986	0.0003	High, Low	1.971	0.0688
				High, No	4.7778	0.0001
				Low, No	2.8317	0.0106

TABLE VII

PERMANOVA RESULTS OF A PAIR-WISE TEST OF COMMON MICROARTHROPOD COMMUNITY DIFFERENCES IN AUGUST 2015 BY TREATMENT USING BRAY-CURTIS DISSIMILARITY[a]

Groups	t	P (perm)	Unique perms	P (MC)
A. Litter				
High, Low	2.167	0.0001	9945	0.0002
High, No	2.3651	0.0001	9945	0.0001
Low, No	0.94517	0.509	9943	0.4946
B. Soil				
High, Low	1.6848	0.0068	9944	0.0111
High, No	3.2641	0.0001	9959	0.0001
Low, No	2.0195	0.0003	9949	0.0011

[a] Performed under a reduced model using type III sum of squares. 9999 permutations.

TABLE VIII

PERMANOVA RESULTS EVALUATING DIFFERENCES BETWEEN NO TREATMENT (FENCED) COMMUNITIES AND REFERENCE (UNFENCED) COMMUNITIES OVER TIME FOR UNCOMMON TAXA[a]

Source	df	SS	MS	Pseudo-F	*P* (perm)	Unique perms	*P* (MC)
Treat	1	4410.1	4410.1	1.233	0.2247	9899	0.2377
Date	3	110740	36913	10.32	0.0001	9864	0.0001
Treat x Date	2	8185.4	4092.7	1.1443	0.255	9893	0.2568
Residuals	327	1151700	3576.7				
Total	328	1280700					

[a] Performed under a reduced model using Bray-Curtis dissimilarity. Monte Carlo tests are included for 9999 permutations.

TABLE IX

PERMANOVA RESULTS EVALUATING DIFFERENCES IN TREATMENT AND BLOCK OVER TIME UNDER A REDUCED MODEL[a]

Source	df	SS	MS	Pseudo-F	*P* (perm)	Unique perms	*P* (MC)
Treat	3	19231	6410.2	1.8517	0.0001	9833	0.0002
Date	3	249090	83031	23.985	0.0001	9863	0.0001
Block	4	85432	21358	6.1695	0.0001	9833	0.0001
Treat x Date	8	34044	4255.5	1.2293	0.0273	9731	0.0298
Treat x Date x Block[b]	32	111550	3485.9	1.0069	0.4473	9553	0.4511
Pooled Residuals	638	2208600	3461.8				
Total	688	2719100					

[a] Performed using Bray-Curtis dissimilarity Monte Carlo tests are included for 9999 permutations.

[b] Treat x Block and Date x Block interactions were pooled.

TABLE X

PERMANOVA RESULTS FROM A TEST OF EFFECTS OF TREATMENT AND BLOCK INTERACTION OVER TIME FOR HIGH, LOW, AND NO-TREATMENT UNCOMMON-TAXA LITTER COMMUNITIES FOR EACH SAMPLING DATE USING BRAY-CURTIS DISSIMILARITY

	df	SS	MS	Pseudo-F	*P* (perm)	Unique perms	*P* (MC)
A. July 2014							
Treat	2	4683.5	2341.8	0.7593	0.8194	9896	0.7884
Block	4	39712	9928.1	2.9929	0.0001	9884	0.0001
Treat x Block	8	27840	3479.9	1.049	0.3582	9835	0.3724
Residuals	135	447830	3317.2				
Total	149	520060					
B. October 2014							
Treat	2	7832.6	3916.3	1.2408	0.2166	9907	0.2261
Block	4	33074	8268.5	2.6198	0.0001	9885	0.0001
Treat x Block	8	26995	3374.4	1.0691	0.3341	9849	0.3313
Residuals	135	426080	3156.2				
Total	149	493990					
C. April 2015							
Treat	2	5915.7	2957.9	0.9604	0.5137	9916	0.5064
Block	4	24452	6113.1	1.9849	0.0006	9869	0.0011
Treat x Block	8	23351	2918.9	0.94776	0.607	9827	0.596
Residuals	75	230990	3079.8				
Total	89	284710					
D. August 2015							
Treat	2	13917	6958.7	1.9354	0.0103	9913	0.0143
Block	4	30683	7670.7	2.1334	0.0009	9871	0.0005
Treat x Block	8	27411	3426.4	0.95297	0.5842	9810	0.5792
Residuals	134	481790	3595.5				
Total	148	553960					

TABLE XI

PERMANOVA RESULTS FROM A TEST OF EFFECTS OF TREATMENT AND BLOCK INTERACTION OVER TIME FOR UNCOMMON-TAXA SOIL COMMUNITIES FOR EACH SAMPLING DATE USING BRAY-CURTIS DISSIMILARITY

	df	SS	MS	Pseudo-F	*P* (perm)	Unique perms	*P* (MC)
A. July 2014							
Treat	2	5341	2670.5	0.77146	0.7106	9930	0.6992
Block	4	26110	6527.4	1.8857	0.0057	9909	0.0065
Treat x Block	8	20569	2571.2	0.74277	0.9307	9845	0.9238
Residuals	135	467320	3461.6				
Total	149	519340					
B. October 2014							
Treat	2	11894	5947.1	1.7046	0.0435	9902	0.0412
Block	4	27094	6773.5	1.9414	0.0013	9872	0.0029
Treat x Block	8	27812	3476.5	0.99644	0.4822	9839	0.4828
Residuals	135	471010	3488.9				
Total	149	537810					
C. April 2015							
Treat	2	3158.9	1593	0.60111	0.8625	9935	0.8465
Block	4	15148	3786.9	1.429	0.0724	9921	0.0851
Treat x Block	8	28429	3553.7	1.341	0.0561	9853	0.068
Residuals	75	198750	2650				
Total	89	245510					
D. August 2015							
Treat	2	16008	8003.8	2.3833	0.0028	9909	0.0046
Block	4	24707	6178.7	1.8392	0.0041	9885	0.0057
Treat x Block	8	35668	4458.5	1.3276	0.0526	9824	0.0583
Residuals	134	450010	3358.3				
Total	148	526300					

TABLE XII

PERMANOVA RESULTS OF A PAIR-WISE TEST OF UNCOMMON MICROARTHROPOD COMMUNITY DIFFERENCES IN OCTOBER 2014 BY TREATMENT USING BRAY-CURTIS DISSIMILARITY[a]

Groups	t	*P* (perm)	Unique perms	*P* (MC)
A. Litter				
High, Low	1.0518	0.356	9930	0.3545
High, No	1.3056	0.0827	9939	0.0901
Low, No	0.94617	0.5192	9930	0.5189
B. Soil				
High, Low	1.5815	0.0131	9938	0.0135
High, No	1.3789	0.0509	9929	0.0566
Low, No	0.84334	0.6741	9941	0.6652

[a] Performed under a reduced model using type III sum of squares. 9999 permutations.

TABLE XIII

PERMDISP RESULTS SHOWING DIFFERENCES IN HOMOGENEITY OF MULTIVARIATE DISPERSIONS BETWEEN TREATMENTS IN THE UNCOMMON TAXA COMMUNITY BY DATE USING BRAY-CURTIS DISSIMILARITY

October 2014	df	F	P (perm)	Groups	t	*P* (perm)
A. Litter	2.147	0.43327	0.7087	High, Low	0.75303	0.51146
				High, No	0.87557	0.43359
				Low, No	0.10254	0.92834
B. Soil	2, 147	0.69255	0.548	High, Low	1.1478	0.2682
				High, No	0.94417	0.3974
				Low, No	0.12752	0.9053
April 2015						
C. Litter	2, 87	0.51983	0.6633	High, Low	0.49843	0.6646
				High, No	0.54441	0.6329
				Low, No	0.97352	0.4045
D. Soil	2, 87	1.6956	0.2758	High, Low	0.82962	0.4698
				High, No	1.8361	0.1172
				Low, No	1.022	0.3648
August 2015						
E. Litter	2, 146	2.4934	0.105	High, Low	0.66946	0.52
				High, No	2.0608	0.0473
				Low, No	1.4584	0.1697
F. Soil	2, 146	1.8169	0.1914	High, Low	1.3034	0.2165
				High, No	0.45747	0.6758
				Low, No	2.1856	0.0276

TABLE XIV

PERMANOVA RESULTS OF A PAIR-WISE TEST OF UNCOMMON MICROARTHROPOD COMMUNITY DIFFERENCES IN AUGUST 2015 BY TREATMENT USING BRAY-CURTIS DISSIMILARITY[a]

Groups	t	*P* (perm)	Unique perms	*P* (MC)
A. Litter				
High, Low	1.3806	0.042	9932	0.04422
High, No	1.7115	0.0038	9935	0.005
Low, No	0.97547	0.4745	9929	0.4743
B. Soil				
High, Low	1.3815	0.0546	9931	0.0569
High, No	2.0125	0.0003	9946	0.0007
Low, No	1.0521	0.357	9949	0.3494

[a] Performed under a reduced model using type III sum of squares. 9999 permutations.

TABLE XV

RESULTS OF MULTIGROUP INVARIANCE TESTS FOR PATH ESTIMATES COMPARING COMMUNITIES THAT RECEIVED DETRITAL ENHANCEMENT TO COMMUNITIES RECEIVING NO ENHANCEMENT IN A. OCTOBER 2014 AND B. AUGUST 2015[a]

A. October 2014		df	χ^2	*P*	CFI	df	$\Delta\chi^2$	P_{diff}	ΔCFI
Unconstrained		4	1.894	0.76	1.00	4	6.178	0.186	0.01
Constrained		8	8.072	0.43	0.99				

SEM path[b]		df	χ^2	*P*
Fungivores	← Litter depth	5	1.922	0.86
IGprey	← Fungivores	5	2.091	0.84
IGpredator	← Fungivores	5	2.894	0.72
IGpredator	← IGprey*[c]	5	7.831	0.17

B. August 2015*		df	χ^2	*P*	CFI	df	$\Delta\chi^2$	P_{diff}	ΔCFI
Unconstrained		4	1.147	0.89	1.00	4	8.992	0.061	0.048
Constrained		8	10.139	0.23	0.952				

SEM path		df	χ^2	*P*
Fungivores	← Litter depth	5	3.058	0.69
IGprey	← Fungivores*	5	4.406	0.49
IGpredator	← Fungivores	5	1.894	0.86
IGpredator	← IGprey	5	3.050	0.69

[a] χ^2 = Chi-squared; RMSEA = root-mean-squared error of approximation; and CFI = comparative fit index are included. $\Delta\chi^2$ and ΔCFI are the differences in χ^2 and CFI, respectively, for the unconstrained and fully constrained models.

[b] SEM paths describe causal relationships, with variables in the first column being affected by the variable in the second column.

[c] Asterisks (*) denote model or path invariance between groups.

TABLE XVI

RESULTS FOR TEST OF DIFFERENCE IN REGRESSION ESTIMATES BETWEEN ENHANCEMENT AND NO ENHANCEMENT COMMUNITIES IN OCTOBER 2014[a]

SEM Path[b]		Treatment (n)	Estimate	S.E.	*t*	*P*
Fungivores	← **Litter Depth**	Enhancement (100)	0.088	0.061	0.171	0.864
		No Enhancement (100)	0.101	0.046		
IGprey	← **Fungivores**	Enhancement (100)	0.391	0.074	0.449	0.654
		No Enhancement (100)	0.443	0.090		
IGpredator	← **Fungivores**	Enhancement (100)	0.148	0.073	1.007	0.316
		No Enhancement (100)	0.260	0.085		
IGpredator	← **IGprey**	Enhancement (100)	0.439	0.087	2.471	0.014
		No Enhancement (100)	0.140	0.085		

[a] Unstandardized path coefficients (Estimate), standard error of regression (S.E.), the calculated t statistic (*t*), and the two-tailed probability value (*P*) are included.

[b] SEM paths describe a causal relationship, with variables in the first column being affected by the variable in the second column.

TABLE XVII

RESULTS FOR TEST OF DIFFERENCE IN REGRESSION SLOPES BETWEEN ALL TREATMENT GROUPS IN OCTOBER 2014[a]

SEM Path[b]		Treatment (n)	Estimate	S.E.	*t*	*P*
A.						
Fungivores	← **Litter Depth**	High (50)	0.138	0.089	0.925	0.357
		Low (50)	0.029	0.079		
IGprey	← **Fungivores**	High (50)	0.432	0.111	0.958	0.340
		Low (50)	0.289	0.102		
IGpredator	← **Fungivores**	High (50)	0.198	0.095	1.153	0.252
		Low (50)	0.038	0.103		
IGpredator	← **IGprey**	High (50)	0.262	0.107	2.274	0.025
		Low (50)	0.648	0.134		
B.						
Fungivores	← **Litter Depth**	High (50)	0.138	0.089	0.412	0.681
		No (100)	0.101	0.046		
IGprey	← **Fungivores**	High (50)	0.432	0.111	0.074	0.941
		No (100)	0.443	0.090		
IGpredator	← **Fungivores**	High (50)	0.198	0.095	0.453	0.651
		No (100)	0.260	0.085		
IGpredator	← **IGprey**	High (50)	0.262	0.107	0.864	0.389
		No (100)	0.140	0.085		
C.						
Fungivores	← **Litter Depth**	Low (50)	0.029	0.079	0.846	0.399
		No (100)	0.101	0.046		
IGprey	← **Fungivores**	Low (50)	0.289	0.102	1.059	0.291
		No (100)	0.443	0.090		
IGpredator	← **Fungivores**	Low (50)	0.038	0.103	1.589	0.114
		No (100)	0.260	0.085		
IGpredator	← **IGprey**	Low (50)	0.648	0.134	3.343	0.001
		No (100)	0.140	0.085		

[a] Unstandardized path coefficients (Estimate), standard error of regression (S.E.), the calculated t statistic (*t*), and the two-tailed probability value (*P*) are included.

[b] SEM paths describe a causal relationship, with variables in the first column being affected by the variable in the second column.

TABLE XVIII

RESULTS OF MULTIGROUP INVARIANCE TESTS FOR PATH ESTIMATES COMPARING ALL TREATMENT GROUPS FOR A. OCTOBER 2014 AND B. AUGUST 2015[a]

A. October 2014		df	χ^2	*P*	CFI	df	$\Delta\chi^2$	P_{diff}	ΔCFI
Unconstrained		6	5.998	0.423	1.00	8	12.289	0.139	0.045
Constrained		14	18.287	0.194	0.955				
SEM path[b]		df	χ^2	*P*					
Fungivores	← Litter depth	8	6.939	0.543					
IGprey	← Fungivores	8	7.451	0.489					
IGpredator	← Fungivores	8	8.772	0.362					
IGpredator	← IGprey*[c]	8	15.697	0.047					
B. August 2015		df	χ^2	*P*	CFI	df	$\Delta\chi^2$	P_{diff}	ΔCFI
Unconstrained		6	4.117	0.661	1.00	8	11.003	0.202	0.026
Constrained		14	15.120	0.370	0.974				
SEM path		df	χ^2	*P*					
Fungivores	← Litter depth	8	8.612	0.376					
IGprey	← Fungivores	8	7.649	0.469					
IGpredator	← Fungivores	8	4.690	0.790					
IGpredator	← IGprey	8	5.566	0.696					

[a] χ^2 = Chi-squared; RMSEA = root-mean-squared error of approximation; and CFI = comparative fit index are included. $\Delta\chi^2$ and ΔCFI are the differences in χ^2 and CFI, respectively, for the unconstrained and fully constrained models.

[b] SEM paths describe causal relationships, with variables in the first column being affected by the variable in the second column.

[c] Asterisks (*) denote model or path invariance between groups.

TABLE XIX

RESULTS FOR TEST OF DIFFERENCE IN REGRESSION ESTIMATES BETWEEN ENHANCEMENT AND NO ENHANCEMENT COMMUNITIES IN AUGUST 2015[a]

SEM Path[b]		Treatment (n)	Estimate	S.E.	*t*	*P*
Fungivores	← **Litter Depth**	Enhancement (100)	0.159	0.067	1.575	0.117
		No Enhancement (99)	0.038	0.056		
IGprey	← **Fungivores**	Enhancement (100)	0.204	0.076	1.816	0.071
		No Enhancement (99)	0.425	0.96		
IGpredator	← **Fungivores**	Enhancement (100)	0.142	0.084	0.874	0.383
		No Enhancement (99)	0.035	0.090		
IGpredator	← **IGprey**	Enhancement (100)	0.382	0.108	1.397	0.164
		No Enhancement (99)	0.191	0.087		

[a] Unstandardized path coefficients (Estimate), standard error of regression (S.E.), the calculated t statistic (*t*), and the two-tailed probability value (*P*) are included.

[b] SEM paths describe a causal relationship, with variables in the first column being affected by the variable in the second column.

TABLE XX

RESULTS FOR TEST OF DIFFERENCE IN REGRESSION SLOPES BETWEEN ALL TREATMENT GROUPS IN AUGUST 2015[a]

SEM Path[b]		Treatment (n)	Estimate	S.E.	*t*	*P*
A.						
Fungivores	**← Litter Depth**	High (50)	0.271	0.094	1.504	0.136
		Low (50)	0.072	0.095		
IGprey	**← Fungivores**	High (50)	0.213	0.090	0.249	0.804
		Low (50)	0.175	0.125		
IGpredator	**← Fungivores**	High (50)	0.144	0.112	0.427	0.670
		Low (50)	0.077	0.112		
IGpredator	**← IGprey**	High (50)	0.408	0.168	0.555	0.580
		Low (50)	0.293	0.125		
B.						
Fungivores	**← Litter Depth**	High (50)	0.271	0.094	2.273	0.024
		No (99)	0.038	0.056		
IGprey	**← Fungivores**	High (50)	0.213	0.090	1.426	0.156
		No (99)	0.425	0.096		
IGpredator	**← Fungivores**	High (50)	0.144	0.112	0.733	0.465
		No (99)	0.035	0.090		
IGpredator	**← IGprey**	High (50)	0.408	0.168	1.280	0.203
		No (99)	0.191	0.087		
C.						
Fungivores	**← Litter Depth**	Low (50)	0.072	0.095	0.330	0.742
		No (99)	0.038	0.056		
IGprey	**← Fungivores**	Low (50)	0.175	0.125	1.556	0.122
		No (99)	0.425	0.096		
IGpredator	**← Fungivores**	Low (50)	0.077	0.112	0.283	0.778
		No (99)	0.035	0.090		
IGpredator	**← IGprey**	Low (50)	0.293	0.125	0.679	0.498
		No (99)	0.191	0.087		

[a] Unstandardized path coefficients (Estimate), standard error of regression (S.E.), the calculated t statistic (*t*), and the two-tailed probability value (*P*) are included.

[b] SEM paths describe a causal relationship, with variables in the first column being affected by the variable in the second column.

FIGURES

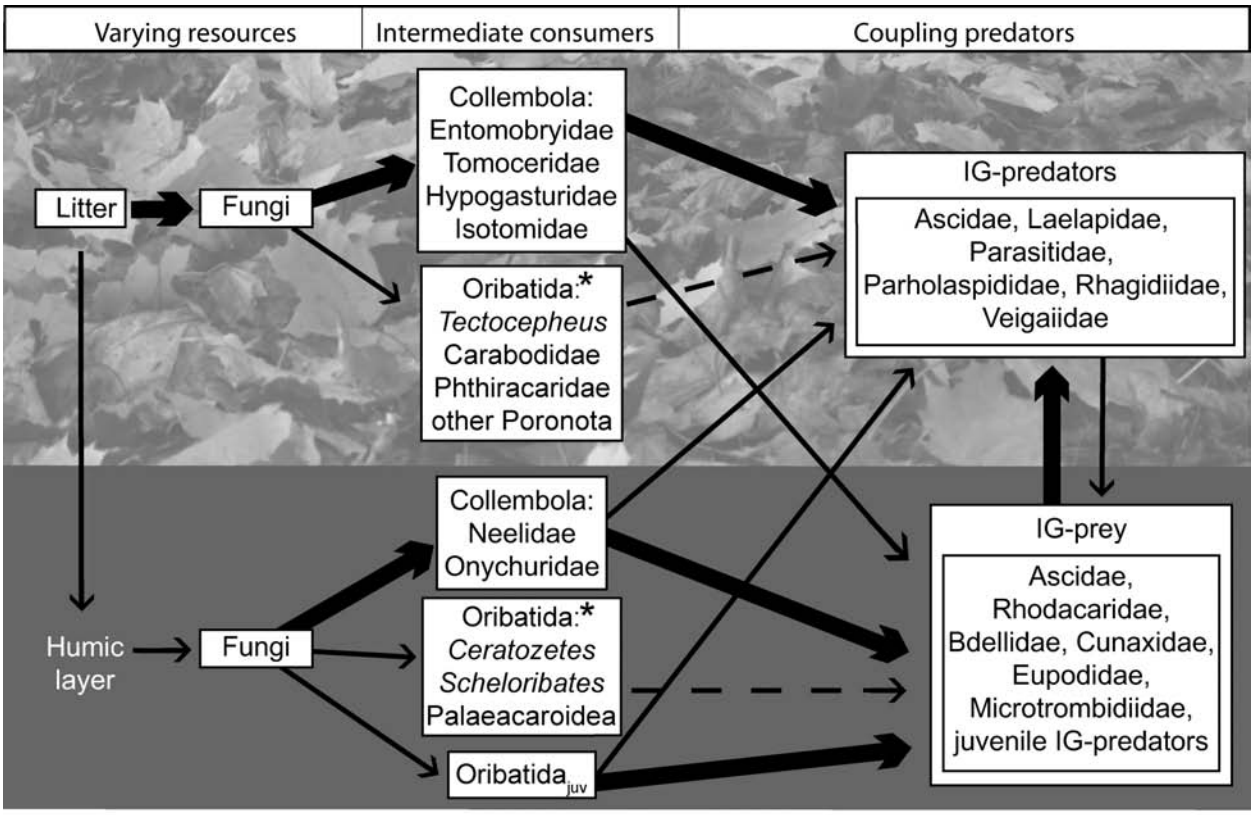

Figure 1. Food web diagram of interactions and hypothesized strengths (darker arrows are hypothesized to be stronger, dashed lines are weakest) between consumers and resources in the detrital food web based on Mitchell (1978), Rooney et al. (2008), Krantz and Walter (2009), and The OSU Acarology Summer Program Manual. *Oribatida are noted as prey for other organisms, but few predatory soil mites (Lindquist et al. 2009).

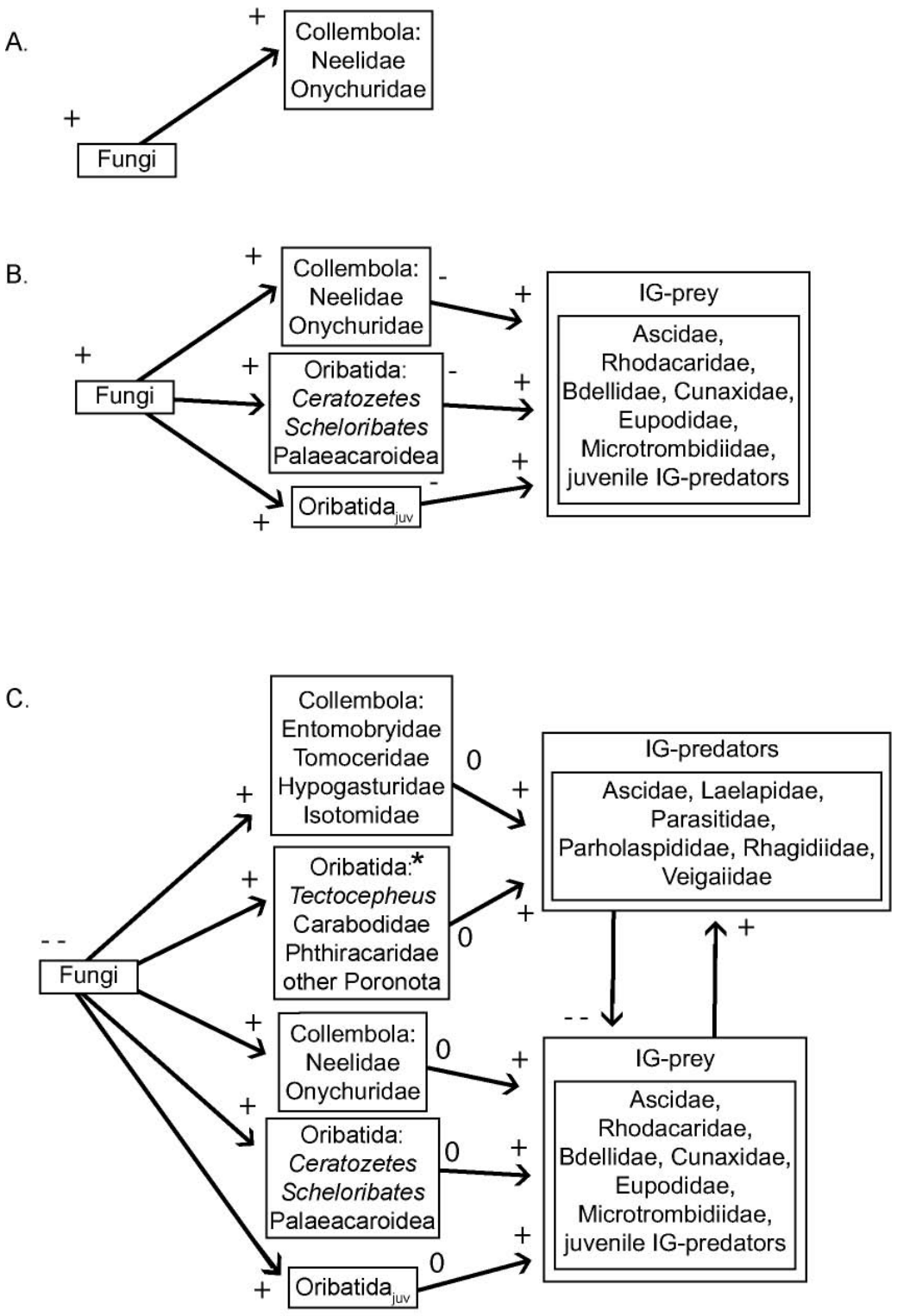

Figure 2. Diagrams of hypothesized interaction strengths. Arrows designate the direction of energy flow. Signs (+) and (-) designate the direction of effect (increase or decrease in abundance) over A. three-month time span, nine-month timespan, and C. 13-month time span.

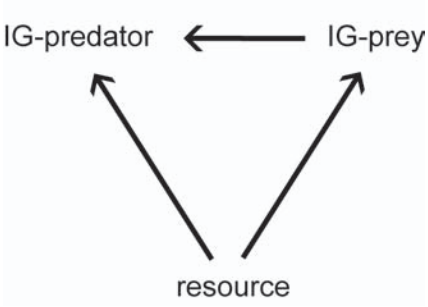

Figure 3. Diagram of the intraguild predation interaction (after Polis et al. 1989).

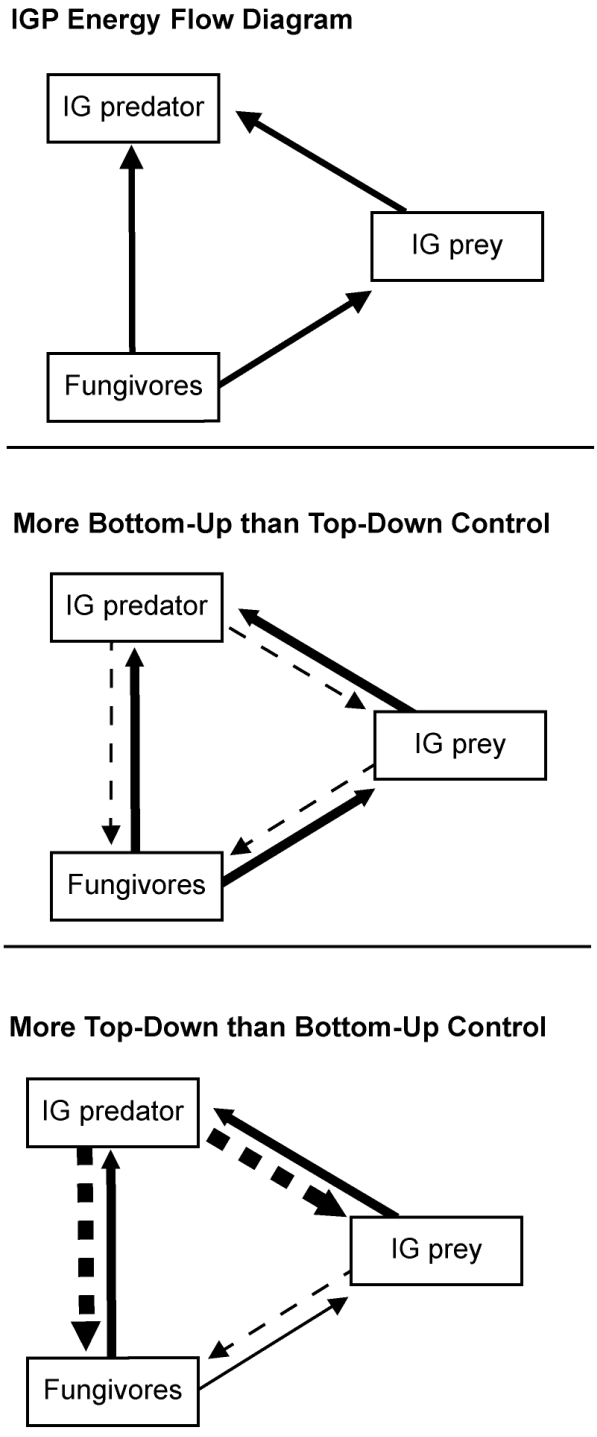

Figure 4. The dynamics of the IGP module. The trophic dynamics (change in energy flow) of the IGP module change in direction and strength based on whether the system experiences more bottom-up or top-down control. Thick lines represent stronger interactions than thin. Dashed lines represent negative interactions (negative effects).

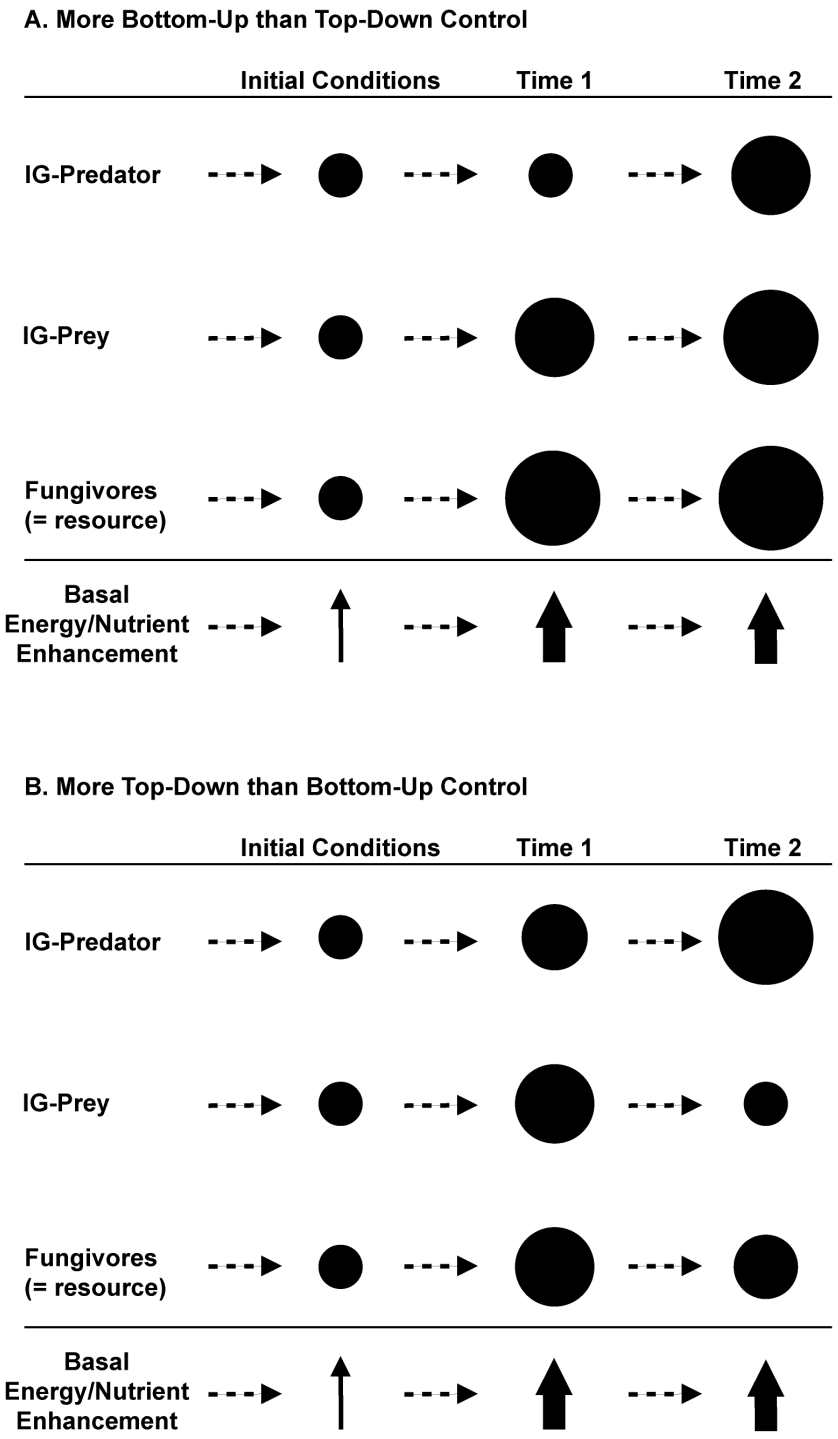

Figure 5. Diagram of predictions of relative abundances of the three IGP trophic guilds during a basal-resource enhancement augmentation based on hypothesized dynamics of A. a system under more bottom-up than top-down control and B. a system under more top-down control than bottom-up control. Changes in the areas of the circles for each trophic level indicate changes over time in abundance, or biomass, of that trophic level.

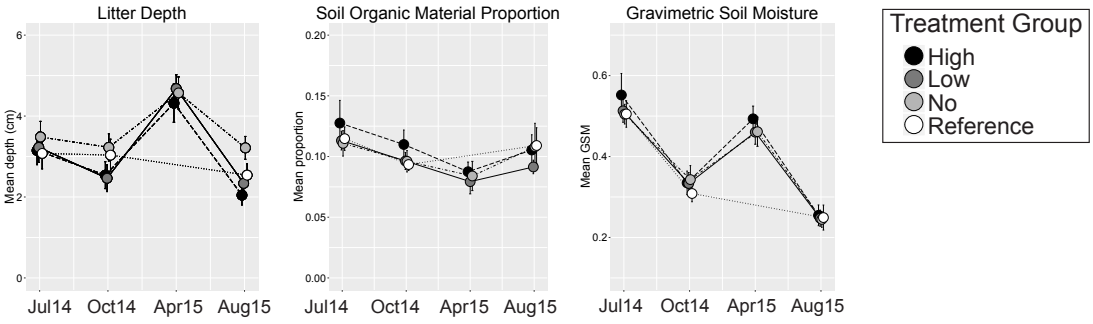

Figure 6. The means and 95% confidence intervals for soil parameters litter depth (LD), proportion of soil organic material (SOM), and gravimetric soil moisture (GSM) in plots during the experiment.

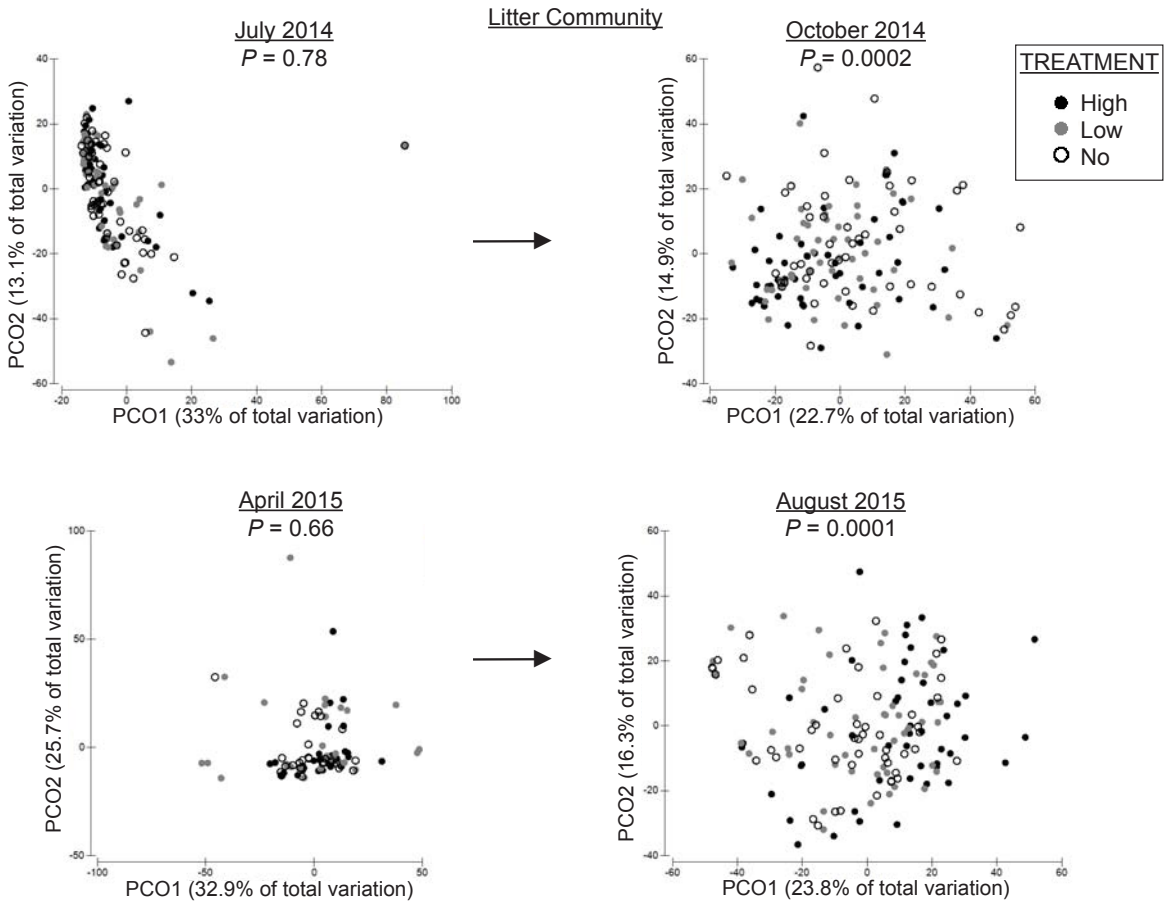

Figure 7. Ordination from principle coordinates analyses of common-taxa litter communities at all sampling time periods. P-values from PERMANOVAs evaluating differences in community structure based on treatment are included.

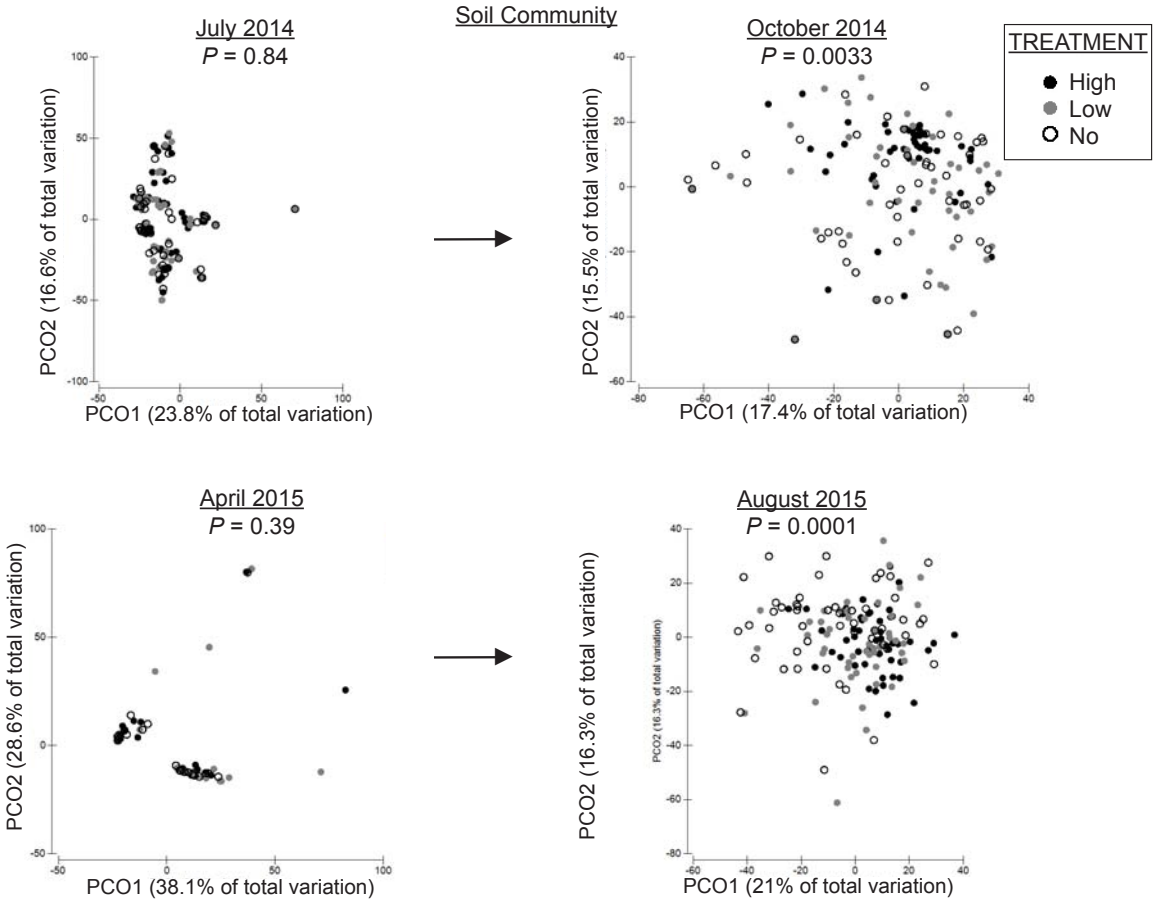

Figure 8. Ordination from principle coordinates analyses of common-taxa soil communities at all sampling time periods. P-values from PERMANOVAs evaluating differences in community structure based on treatment are included.

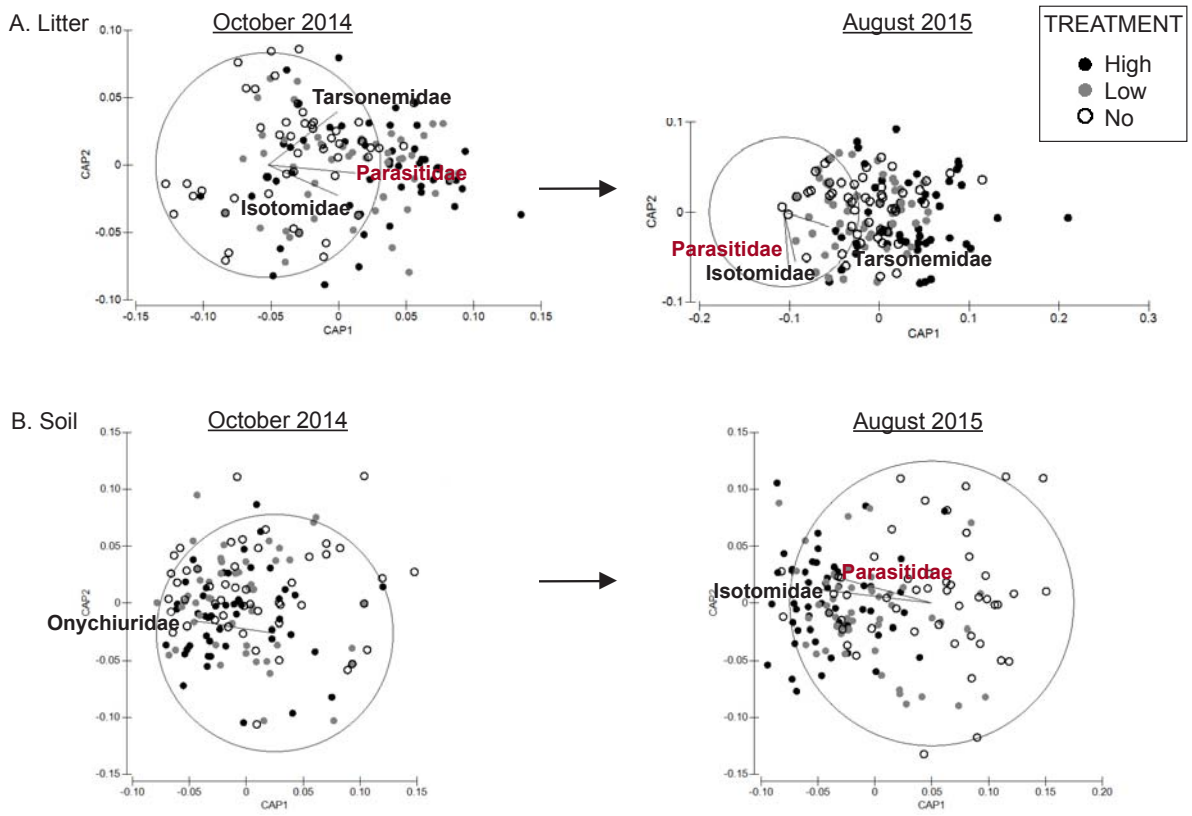

Figure 9. Ordinations from a canonical analysis of principle coordinates (CAPs) for common litter and soil microarthropod communities in October 2014 (end of year 1) and August 2015 (end of year 2). Vectors are shown for taxa with a Pearson correlation coefficient of 0.6 or greater. Taxa in black lettering are fungivorous. Taxa in red lettering are predatory mites.

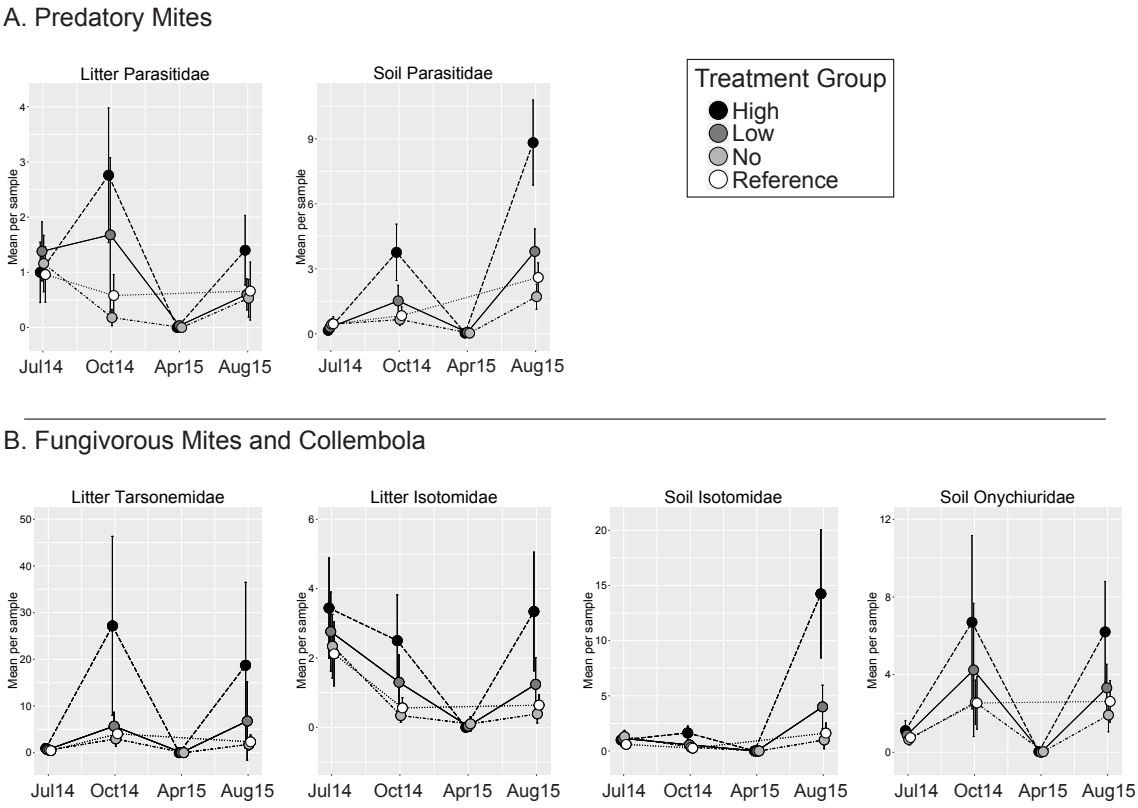

Figure 10. Means and 95% confidence intervals at each sampling period for common A. predator and B. fungivorous prey taxa that were the most influenced by treatment as shown by canonical analysis of principle coordinates (CAP).

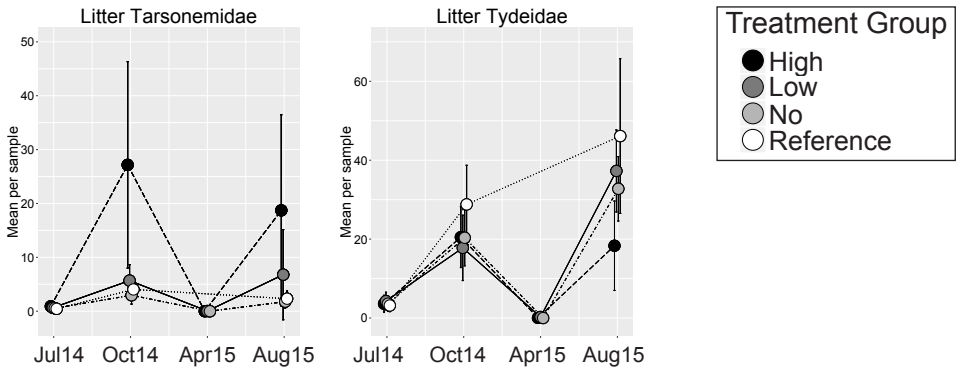

Figure 11. The means and 95% confidence intervals for litter Tarsonemidae and litter Tydeidae abundances per sample.

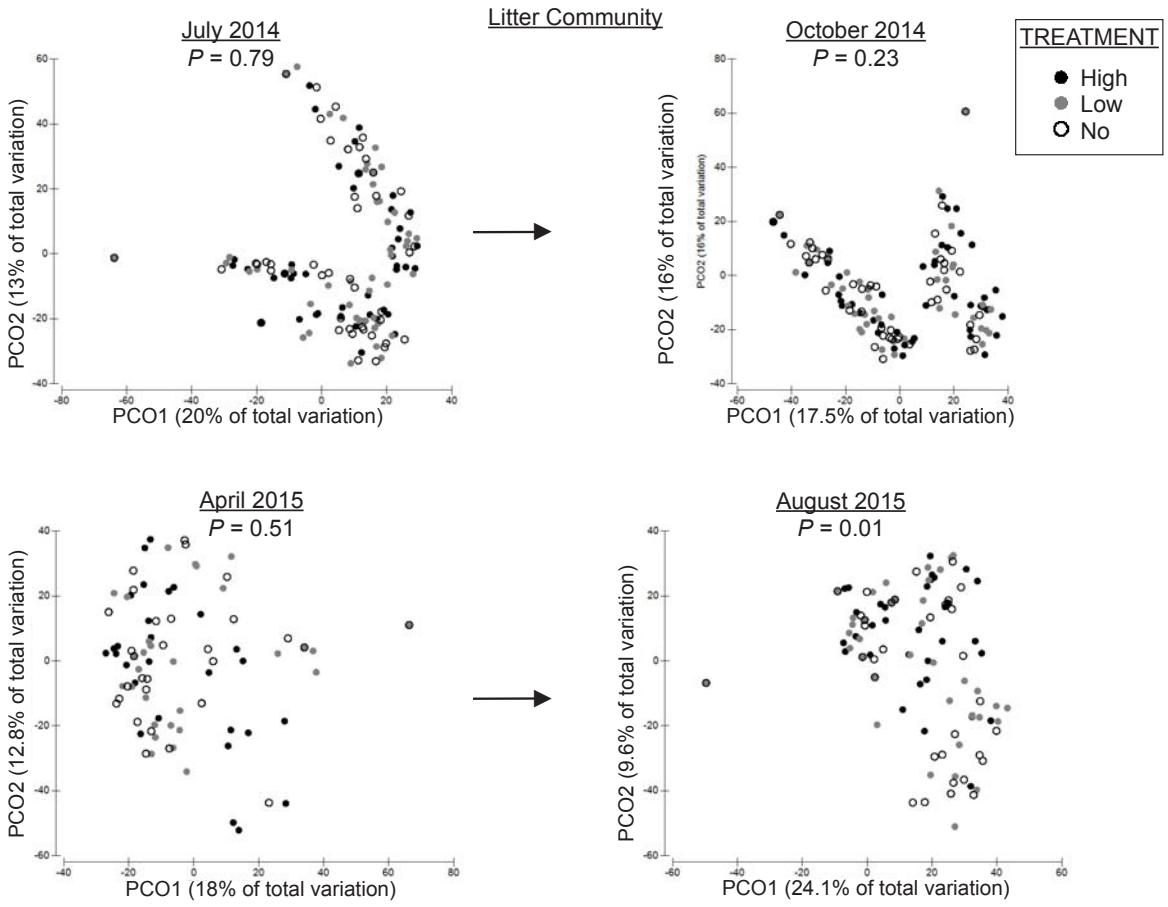

Figure 12. Ordination from principle coordinates analyses of uncommon-taxa litter communities at all sampling time periods. P-values from PERMANOVAs evaluating differences in community structure based on treatment are included.

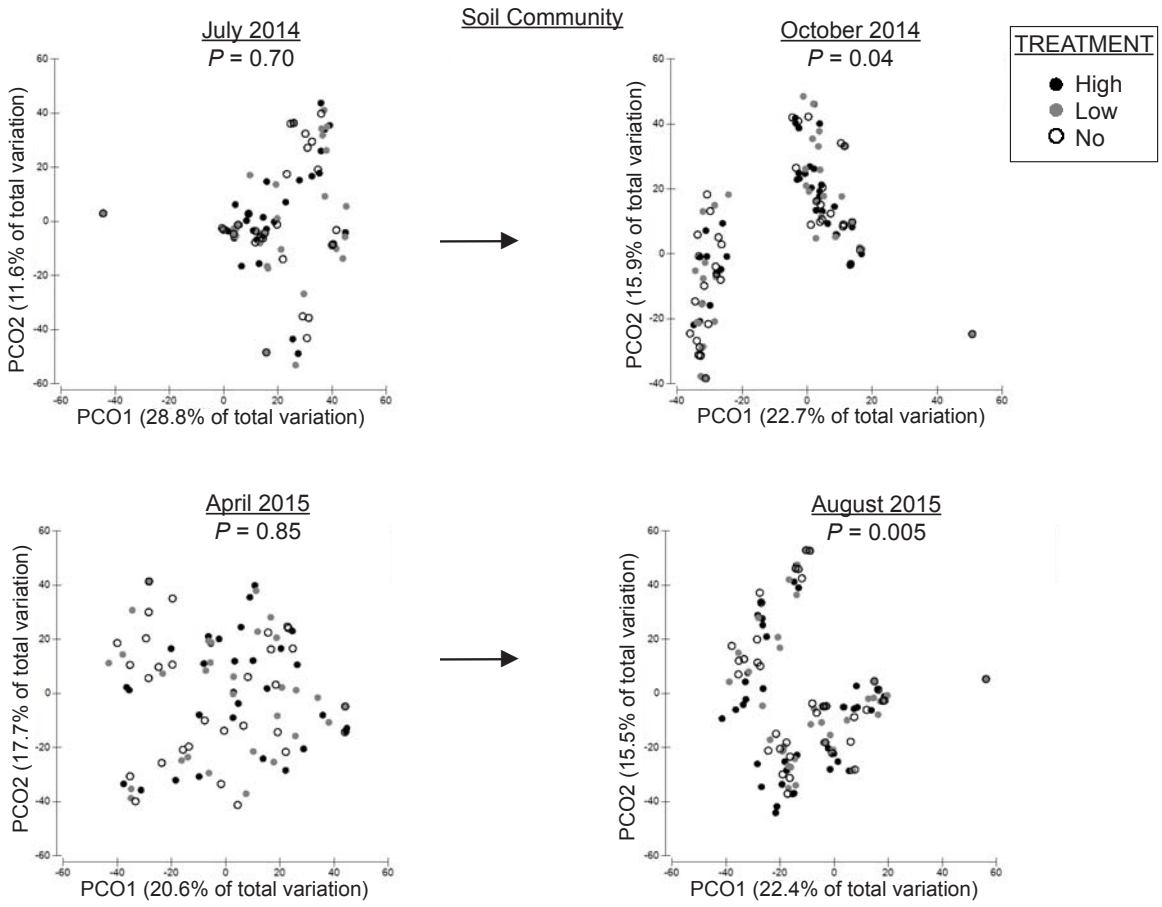

Figure 13. Ordination from principle coordinates analyses of uncommon-taxa soil communities at all sampling time periods. P-values from PERMANOVAs evaluating differences in community structure based on treatment are included.

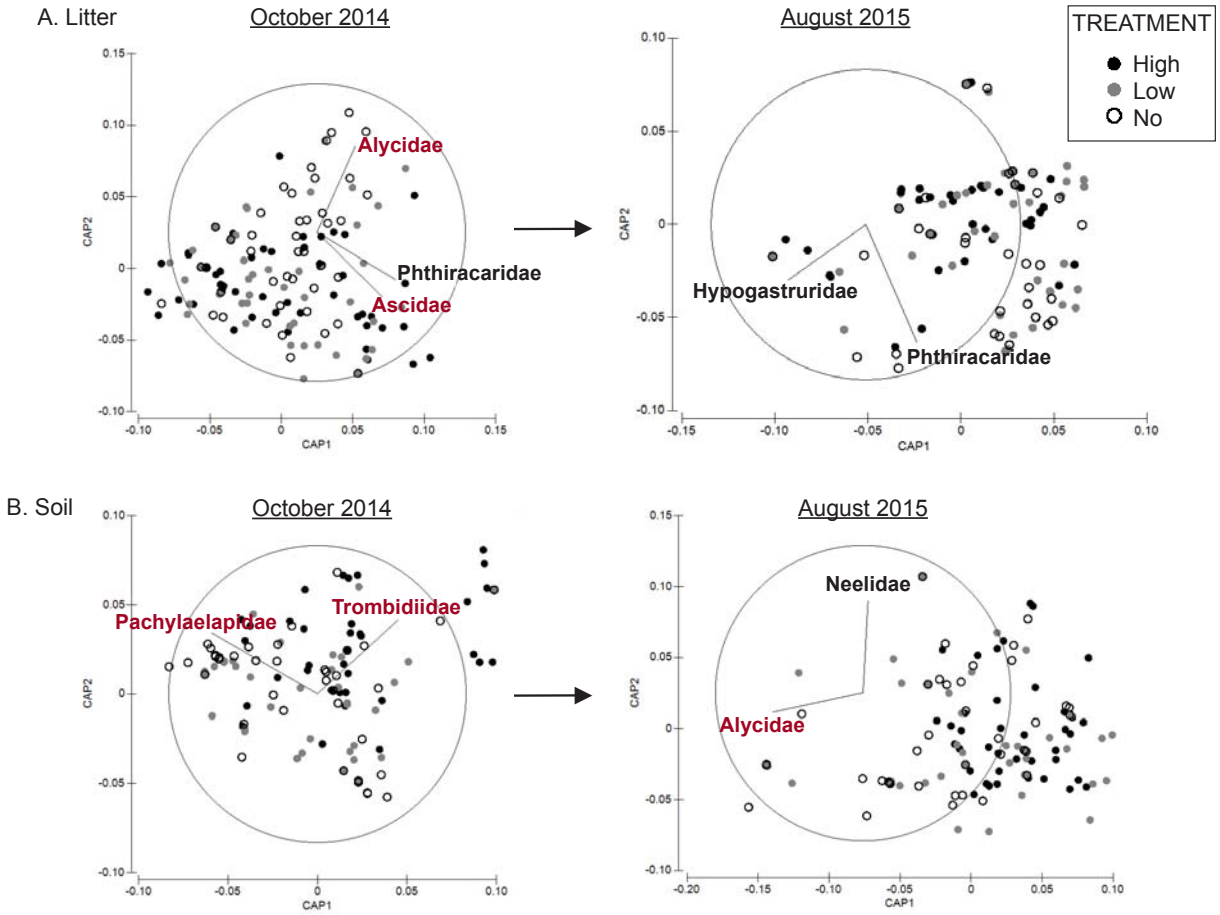

Figure 14. Ordinations from a canonical analysis of principle coordinates (CAPs) for uncommon litter and soil microarthropod communities in October 2014 (end of year 1) and August 2015 (end of year 2). Vectors are shown for taxa with a Pearson correlation coefficient of 0.6 or greater. Taxa in black lettering are fungivorous. Taxa in red lettering are predatory mites.

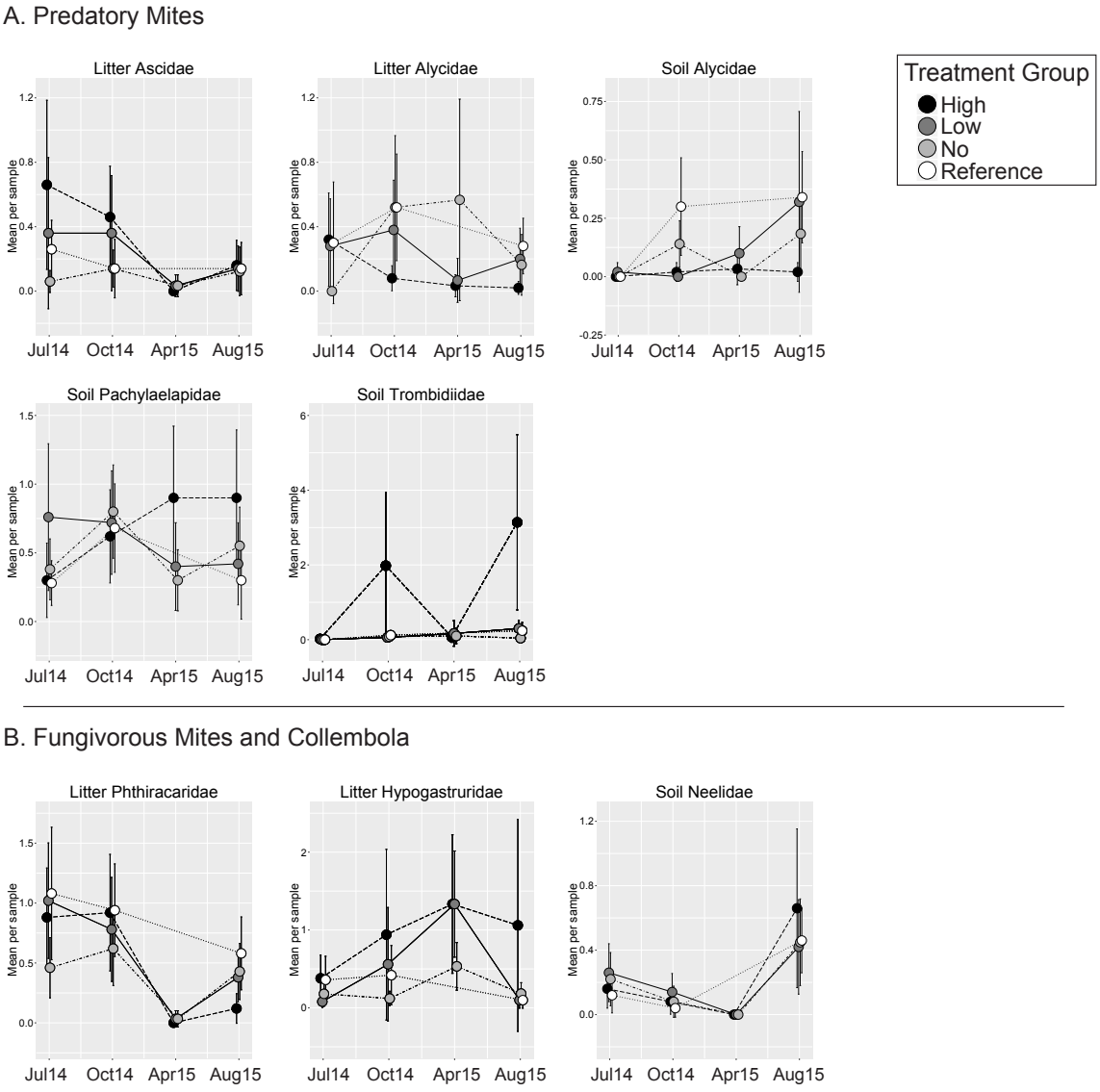

Figure 15. Means and 95% confidence intervals at each sampling period for uncommon taxa that were the most influenced by treatment as shown by canonical analysis of principle coordinates (CAP).

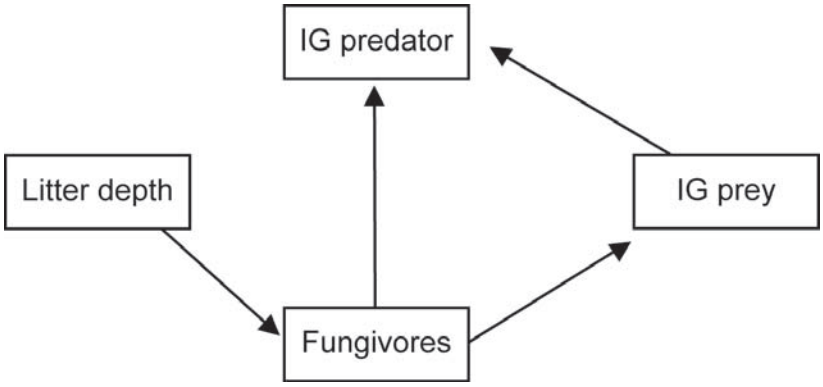

Figure 16. General intraguild predation model used for path analysis model fit to data from October 2014 and August 2015.

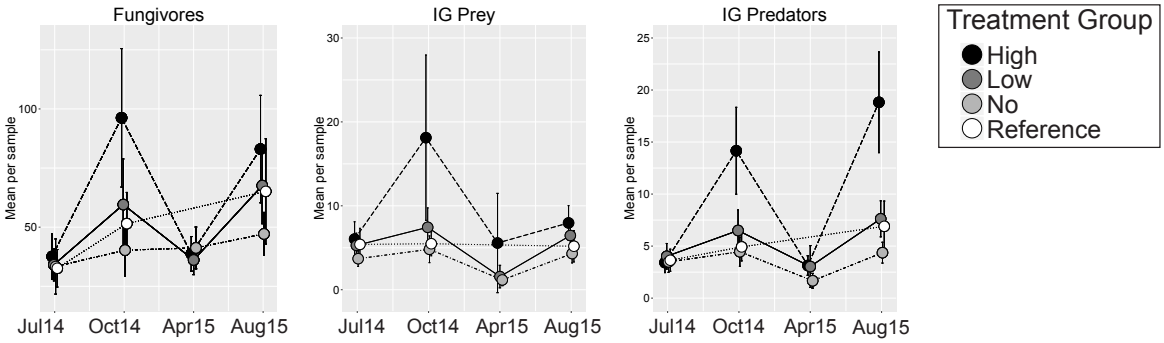

Figure 17. Means and 95% confidence intervals at each sampling period for the three intraguild predation trophic groups.

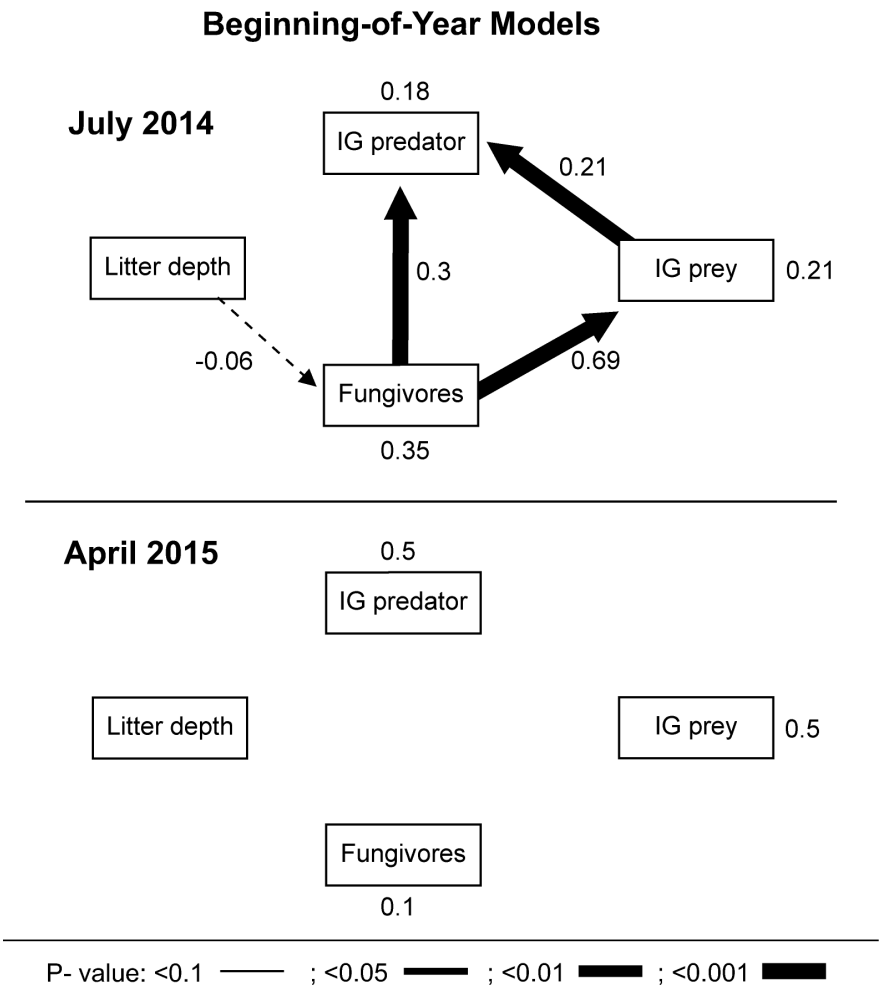

Figure 18. July 2014 and April 2015 structural equation models. Unstandardized coefficients are shown. Solid lines denote positive interaction strengths. Dashed lines represent negative interaction strengths. Paths with no arrows have *P*-values > 0.10. The July 2014 model shows high significance of interactions in an overall model except that the goodness-of-fit statistics show this is a poor model. Goodness-of-fit statistics: $\chi^2 = 9.769$, df = 2, $P = 0.008$, CFI = 0.96, PCFI = 0.32, RMSEA = 0.14. The April 2015 model was poor-fitting because none of the pathways were significant given the data. Goodness of fit statistics: $\chi^2 = 0.631$, df –=2, $P = 0.730$, CFI could not be calculated, PCFI could not be calculated, RMSEA = 0.00.

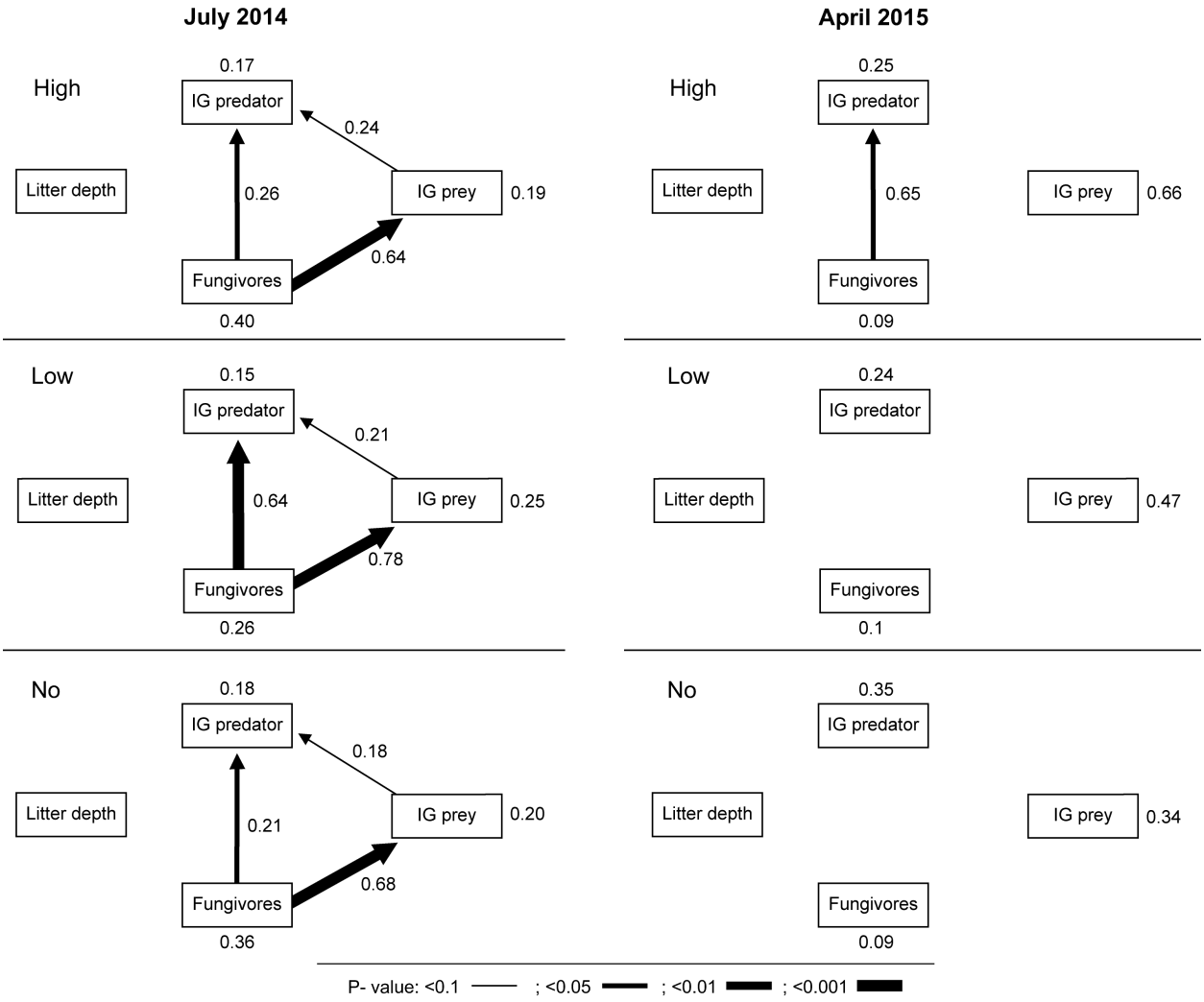

Figure 19. Structural equation models by treatment for July 2014 (initial conditions) and April 2015 (beginning of year 2) communities. Unstandardized coefficients are shown. Solid lines denote positive interaction strengths. Dashed lines represent negative interaction strengths. Paths with no arrows have *P*-values > 0.10. Both of these models were poor-fitting to the data. July 2014 goodness-of-fit statistics: χ^2 = 12.968, df = 6, *P* = 0.044, CFI = 0.965, RMSEA = 0.077. April 2015 goodness-of-fit statistics: χ^2 = 10.547, df = 6, *P* = 0.103, CFI = 0.00, RMSEA = 0.093.

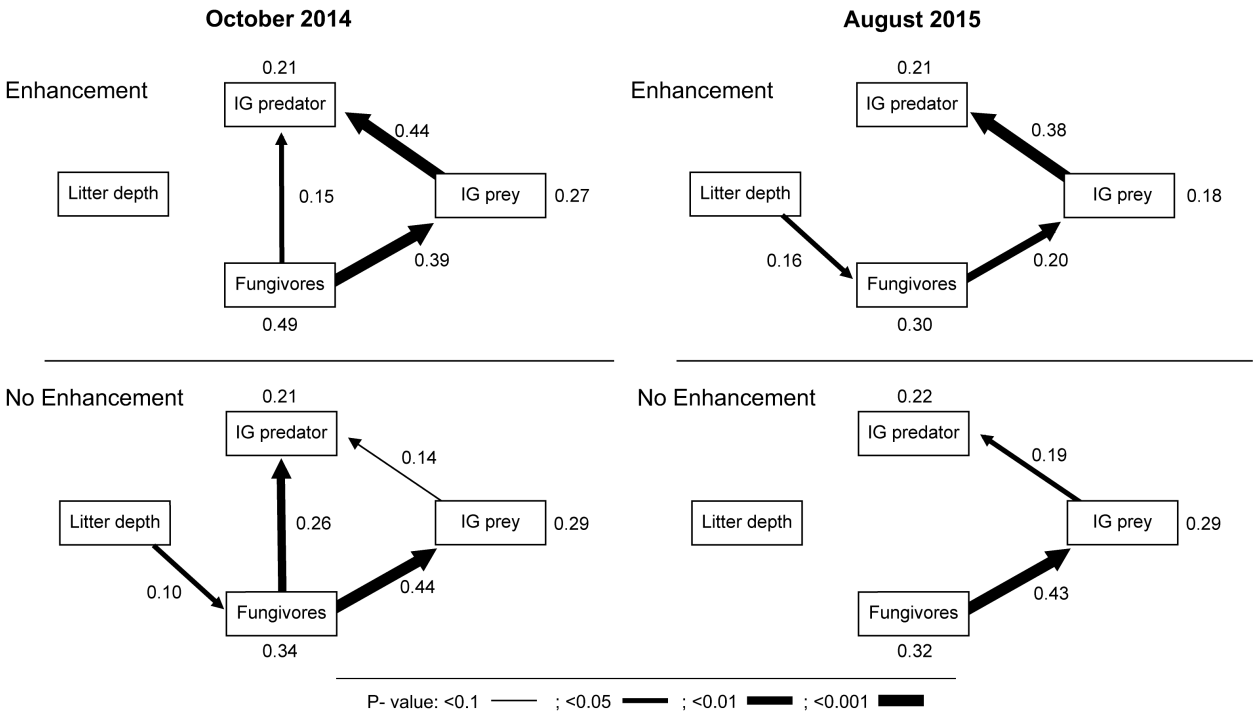

Figure 20. Estimates from IGP community path analysis for October 2014 communities that received detrital enhancement (High and Low treatment together) and October 2014 communities not receiving enhancement (No treatment and Reference together). Unstandardized coefficients are shown. Paths with no arrows have *P*-values > 0.10. Solid lines denote positive interaction strengths. Dashed lines represent negative interaction strengths. Goodness-of-fit statistics for October 2014: df = 4, χ^2 = 1.894, *P* = 0.76, RMSEA = 0.00, CFI = 1.00, PCFI = 0.333. August 2015 communities that received detrital enhancement (High and Low treatment together) and August 2015 communities not receiving enhancement (No treatment and Reference together). Goodness-of-fit statistics for August 2015: df = 4, χ^2 = 1.147, *P* = 0.89, RMSEA = 0.00, CFI = 1.00, PCFI = 0.333.

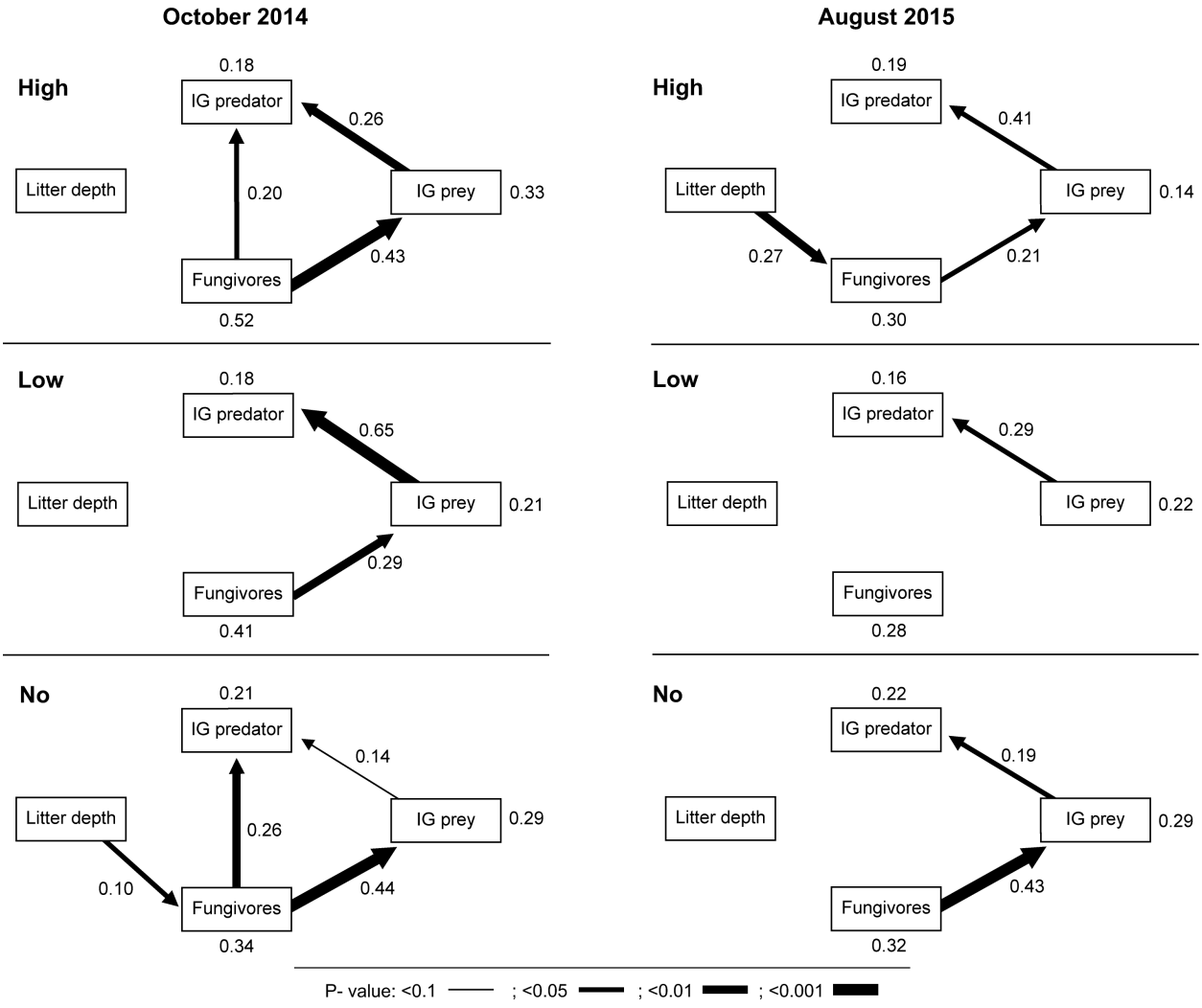

Figure 21. Results for October 2014 and August 2015. IGP community path analyses. Unstandardized coefficients are shown. Paths with no arrows have *P*-values > 0.10. Solid lines denote positive interaction strengths. Dashed lines represent negative interaction strengths. October 2014 goodness-of-fit statistics: df = 6, $\chi^2 = 5.998$, $P = 0.423$, RMSEA = 0.00, CFI = 1.00, PCFI = 0.333. August 2015 High, Low, and No treatment groups. August 2015 goodness-of-fit statistics: df = 6, $\chi^2 = 4.117$, $P = 0.661$, RMSEA = 0.00, CFI = 1.00, PCFI = 0.333.

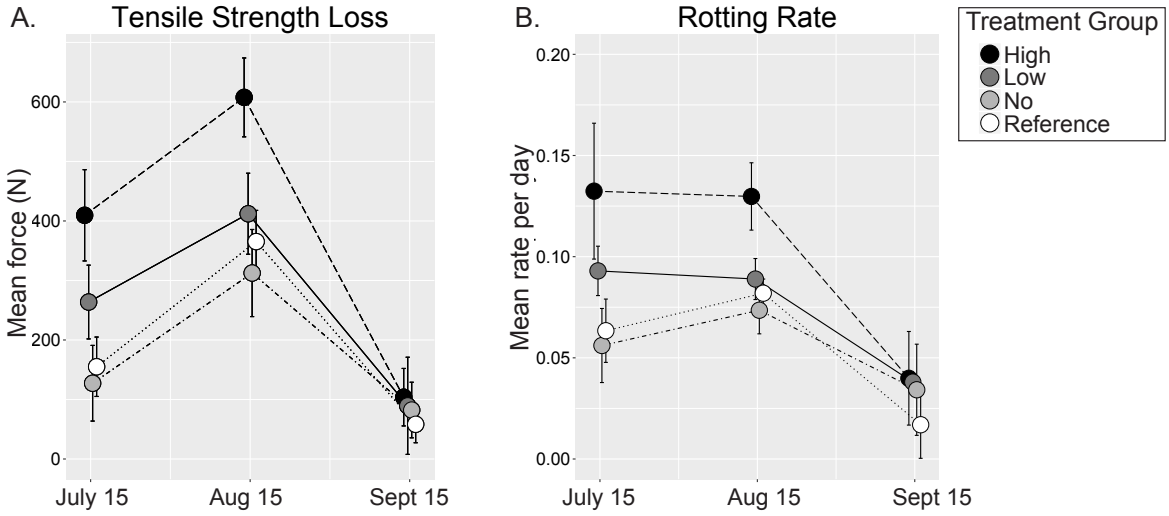

Figure 22. These plots show the means and 95% confidence intervals for A. tensile strength loss of cotton strips (N) and B. Correll's "rotting rate" (Correll et al. 1997) for treatments over three time periods in 2015. July 2015 strips were buried for 8 days, August 2015 strips were buried for 11 days, and late September strips were out for 5 days.

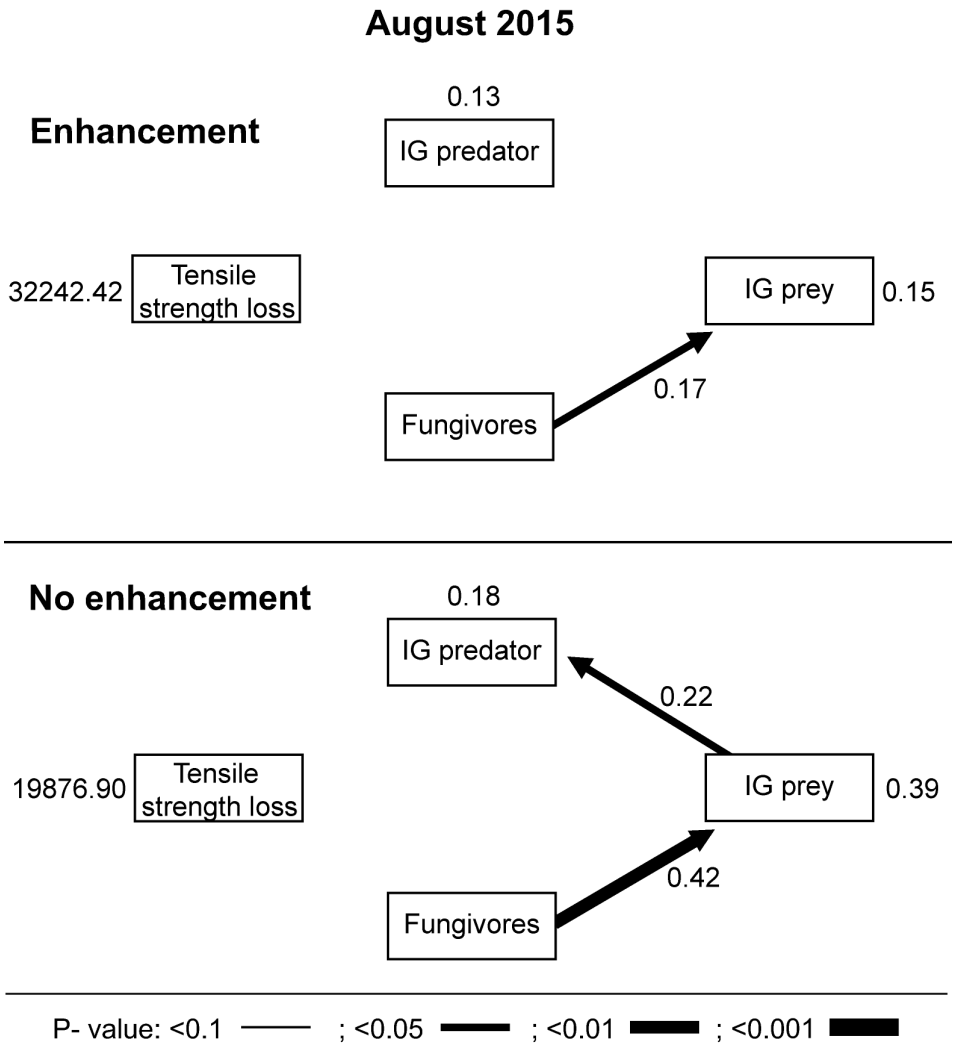

Figure 23. Results for the August 2015 path analysis of IGP community interaction effects on cotton tensile strength loss for communities receiving enhancement and communities not receiving enhancement. Unstandardized coefficients are shown. Paths with no arrows have *P*-values > 0.10. Solid lines denote positive interaction strengths. Dashed lines represent negative interaction strengths. Goodness-of-fit statistics: $\chi^2 = 5.961$, df = 6, $P = 0.428$, RMSEA = 0.00, CFI = 1.00, AIC = 33.961.

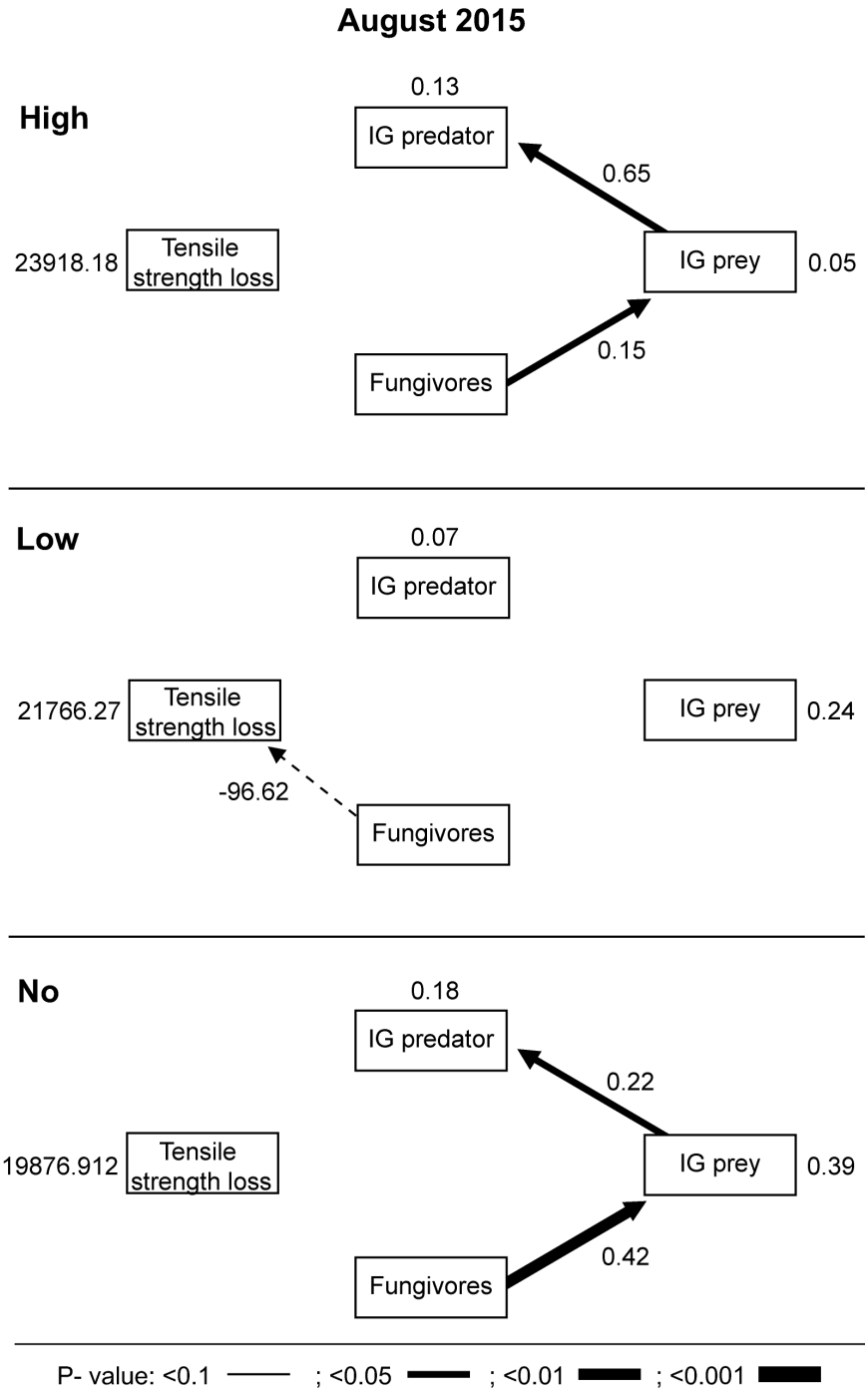

Figure 24. Results for the August 2015 path analysis of IGP community interaction effects on cotton tensile strength loss for High, Low, and No treatment groups. Unstandardized coefficients are shown. Paths with no arrows have *P*-values > 0.10. Solid lines denote positive interaction strengths. Dashed lines represent negative interaction strengths. Goodness-of-fit statistics: $\chi^2 = 8.129$, df = 9, $P = 0.521$, RMSEA = 0.00, CFI = 1.00, AIC = 50.129.

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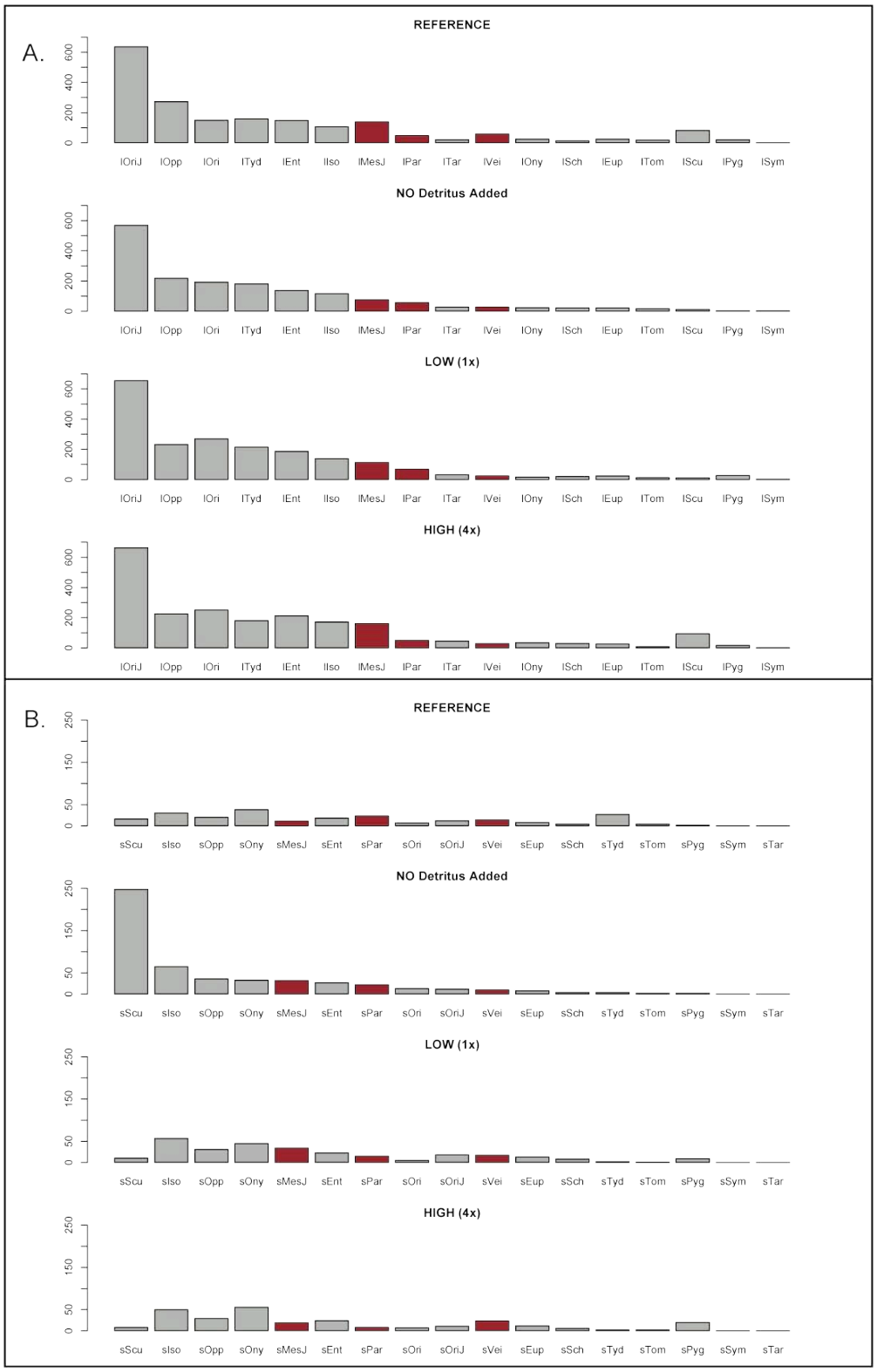
APPENDICES

APPENDIX A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HIGH (4x)
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200
400
600
lOriJ
lOpp
lOri
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lEnt
lIso
lMesJ
lPar
lTar
lVei
lOny
lSch
lEup
lTom
lScu
lPyg
lSym
B.
REFERENCE
NO Detritus Added
LOW (1x)
HIGH (4x)
0
50
150
250
sScu
sIso
sOpp
sOny
sMesJ
sEnt
sPar
sOri
sOriJ
sVei
sEup
sSch
sTyd
sTom
sPyg
sSym
sTar

Figure 25. Ranked abundance distribution of common taxa in July 2014 in the A. litter community and B. soil community. Taxa are designated by layer code, l (litter) or s (soil) and a three-letter taxa code. A. lOriJ = Oribatida juvenile, lOpp = Oppiidae, lOri = Oribatulidae, lTyp = Tydeidae, lEnt = Entomobryidae, lIso = Isotomidae, lMesJ = Mesostigmata juvenile, lPar = Parasitidae, lTar = Tarsonemidae, lVei = Veigaiidae, lOny = Onychiuridae, lSch = Scheloribatidae, lEup = Eupodidae, lTom = Tomoceridae, lScu = Scutacaridae, lPyg = Pygmephoridae, lSym = Symphyla. B. sScu = Scutacaridae, sIso = Isotomidae, sOpp = Oppiidae, sOny = Onychiuridae, sMesJ = Mesostigmata juvenile, sEnt = Entomobryidae, sPar = Parasitidae, sOri = Oribatulidae, sOriJ = Oribatida juvenile, sVei = Veigaiidae, sEup = Eupodidae, sSch = Scheloribatidae, sTyd = Tydeidae, sTom = Tomoceridae, sPyg = Pygmephoridae, sSym = Symphyla, sTar = Tarsonemidae. Patterns shown are relative to the No detritus added treatment. Fungivorous taxa are represented by gray bars and predatory taxa by red bars.

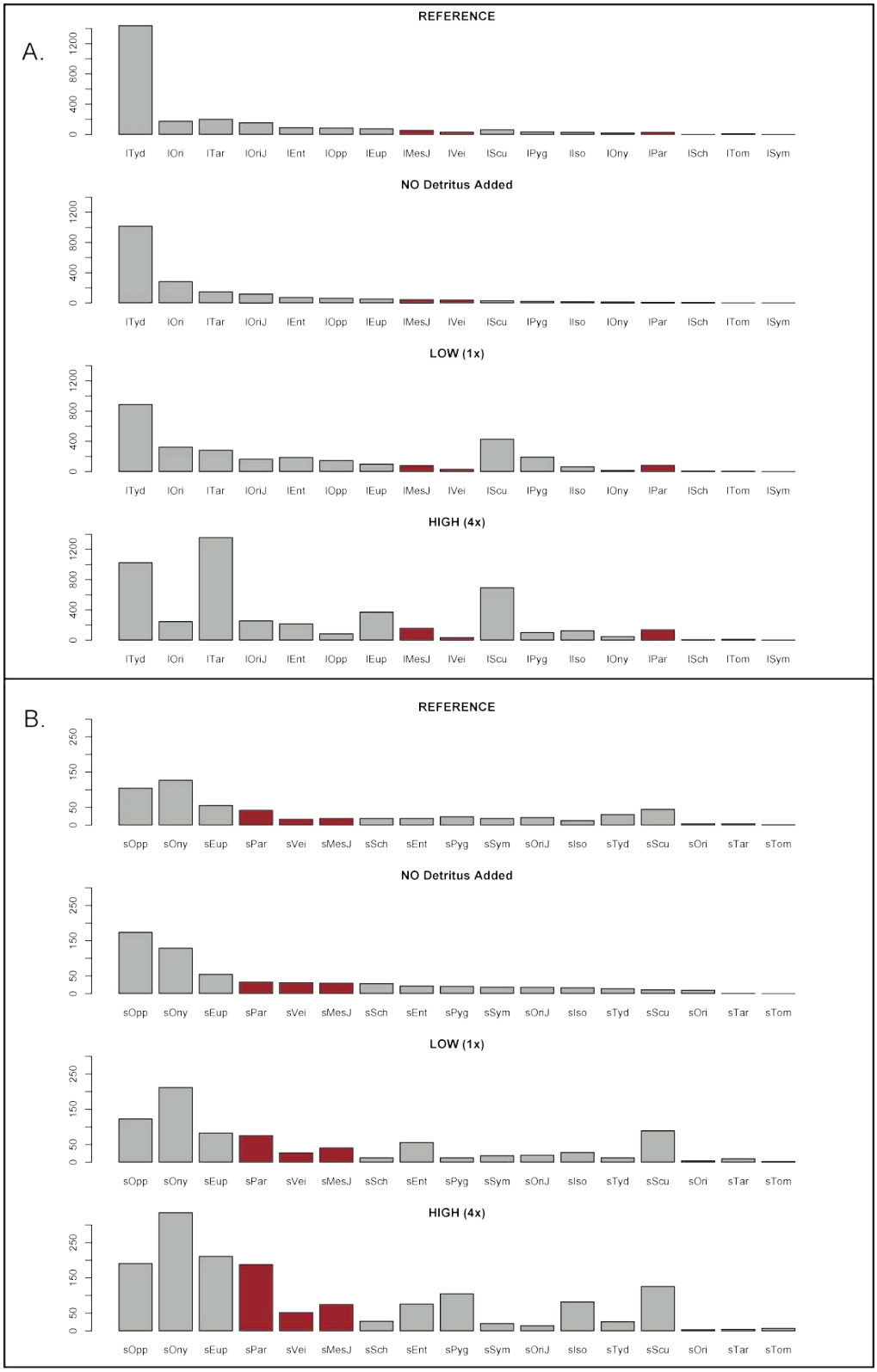

A.
REFERENCE
NO Detritus Added
LOW (1x)
HIGH (4x)
0
400
800
1200
lTyd
lOri
lTar
lOriJ
lEnt
lOpp
lEup
lMesJ
lVei
lScu
lPyg
lIso
lOny
lPar
lSch
lTom
lSym
B.
REFERENCE
NO Detritus Added
LOW (1x)
HIGH (4x)
0
50
150
250
sOpp
sOny
sEup
sPar
sVei
sMesJ
sSch
sEnt
sPyg
sSym
sOriJ
sIso
sTyd
sScu
sOri
sTar
sTom

Figure 26. Ranked abundance distribution of common taxa in October 2014 in the A. litter community and B. soil community. Taxa are designated by layer code, l (litter) or s (soil) and a three-letter taxa code. A. lTyp = Tydeidae, lOri = Oribatulidae, lTar = Tarsonemidae, lOriJ = Oribatida juvenile, lEnt = Entomobryidae, lOpp = Oppiidae, lEup = Eupodidae, lMesJ = Mesostigmata juvenile, lVei = Veigaiidae, lScu = Scutacaridae, lPyg = Pygmephoridae, lIso = Isotomidae, lOny = Onychiuridae, lPar = Parasitidae, lSch = Scheloribatidae, lTom = Tomoceridae, lSym = Symphyla. B. sOpp = Oppiidae, sOny = Onychiuridae, sEup = Eupodidae, sPar = Parasitidae, sVei = Veigaiidae, sMesJ = Mesostigmata juvenile, sSch = Scheloribatidae, sEnt = Entomobryidae, sPyg = Pygmephoridae, sSym = Symphyla, sOriJ = Oribatida juvenile, sIso = Isotomidae, sTyd = Tydeidae, sScu = Scutacaridae, sOri = Oribatulidae, sTar = Tarsonemidae, sTom = Tomoceridae. Patterns shown are relative to the No detritus added treatment. Fungivorous taxa are represented by gray bars and predatory taxa by red bars.

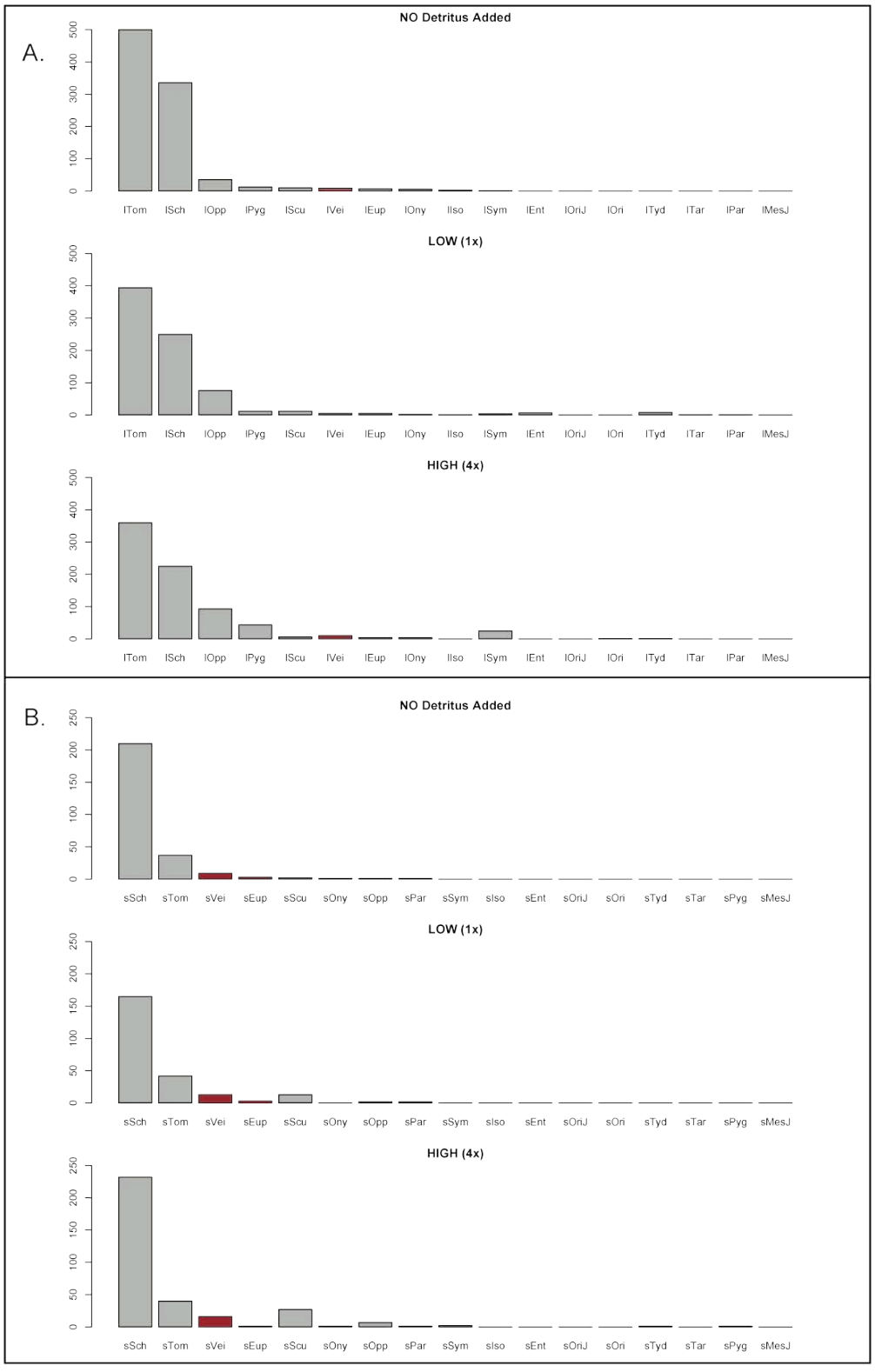
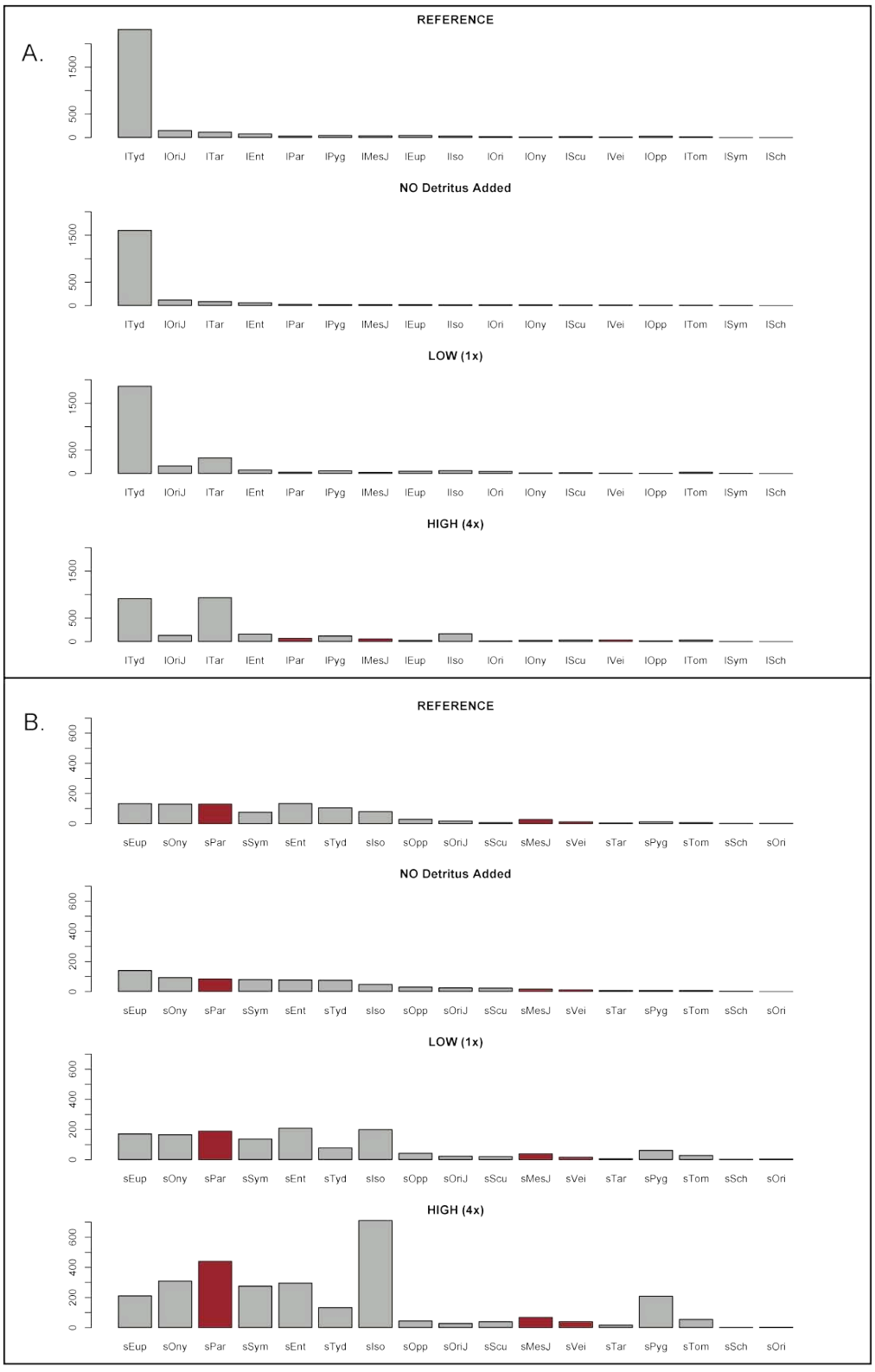

A.
NO Detritus Added
0
100
200
300
400
500
lTom lSch lOpp lPyg lScu lVei lEup lOny lIso lSym lEnt lOriJ lOri lTyd lTar lPar lMesJ
LOW (1x)
0
100
200
300
400
500
lTom lSch lOpp lPyg lScu lVei lEup lOny lIso lSym lEnt lOriJ lOri lTyd lTar lPar lMesJ
HIGH (4x)
0
100
200
300
400
500
lTom lSch lOpp lPyg lScu lVei lEup lOny lIso lSym lEnt lOriJ lOri lTyd lTar lPar lMesJ
B.
NO Detritus Added
0
50
100
150
200
250
sSch sTom sVei sEup sScu sOny sOpp sPar sSym sIso sEnt sOriJ sOri sTyd sTar sPyg sMesJ
LOW (1x)
0
50
100
150
200
250
sSch sTom sVei sEup sScu sOny sOpp sPar sSym sIso sEnt sOriJ sOri sTyd sTar sPyg sMesJ
HIGH (4x)
0
50
100
150
200
250
sSch sTom sVei sEup sScu sOny sOpp sPar sSym sIso sEnt sOriJ sOri sTyd sTar sPyg sMesJ

Figure 27. Ranked abundance distribution of common taxa in April 2015 in the A. litter community and B. soil community. Taxa are designated by layer code, l (litter) or s (soil) and a three-letter taxa code. A. lTom = Tomoceridae, lSch = Scheloribatidae, lOpp = Oppiidae, lPyg = Pygmephoridae, lScu = Scutacaridae, lVei = Veigaiidae, sEup = Eupodidae, lOny = Onychiuridae, sIso = Isotomidae, lSym = Symphyla, lEnt = Entomobryidae, lOriJ = Oribatida juvenile, lOri = Oribatulidae, lTyd = Tydeidae, lTar =Tarsonemidae, lPar = Parasitidae, lMesJ = Mesostigmata juvenile. B. sSch = Scheloribatidae, sTom = Tomoceridae, sVei = Veigaiidae, sEup = Eupodidae, sScu = Scutacaridae, sOny = Onychiuridae, sOpp = Oppiidae, sPar = Parasitidae, sSym = Symphyla, sIso = Isotomidae, sEnt = Entomobryidae, sOriJ = Oribatida juvenile, sOri = Oribatulidae, sTyd = Tydeidae, sTar =Tarsonemidae, sPyg = Pygmephoridae, sMesJ = Mesostigmata juvenile. Patterns shown are relative to the No detritus added treatment. Fungivorous taxa are represented by gray bars and predatory taxa by red bars.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HIGH (4x)
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500
1500
lTyd lOriJ lTar lEnt lPar lPyg lMesJ lEup lIso lOri lOny lScu lVei lOpp lTom lSym lSch
B.
REFERENCE
NO Detritus Added
LOW (1x)
HIGH (4x)
0
200
400
600
sEup sOny sPar sSym sEnt sTyd sIso sOpp sOriJ sScu sMesJ sVei sTar sPyg sTom sSch sOri

Figure 28. Ranked abundance distribution of common taxa in August 2015 in the A. litter community and B. soil community. Taxa are designated by layer code, l (litter) or s (soil) and a three-letter taxa code. A. lTyp = Tydeidae, lOriJ = Oribatida juvenile, lTar = Tarsonemidae, lEnt = Entomobryidae, lPar = Parasitidae, lPyg = Pygmephoridae, lMesJ = Mesostigmata juvenile, lEup = Eupodidae, lIso = Isotomidae, lOri = Oribatulidae, lOny = Onychiuridae, lScu = Scutacaridae, lVei = Veigaiidae, lOpp = Oppiidae, lTom = Tomoceridae, lSym = Symphyla, lSch = Scheloribatidae. B. sEup = Eupodidae, sOny = Onychiuridae, sPar = Parasitidae, sSym = Symphyla, sEnt = Entomobryidae, sTyd = Tydeidae, sIso = Isotomidae, sOpp = Oppiidae, sOriJ = Oribatida juvenile, sScu = Scutacaridae, sMesJ = Mesostigmata juvenile, sVei = Veigaiidae, sTar = Tarsonemidae, sPyg = Pygmephoridae, sTom = Tomoceridae. sSch = Scheloribatidae, sOri = Oribatulidae. Patterns shown are relative to the No detritus added treatment. Fungivorous taxa are represented by gray bars and predatory taxa by red bars.

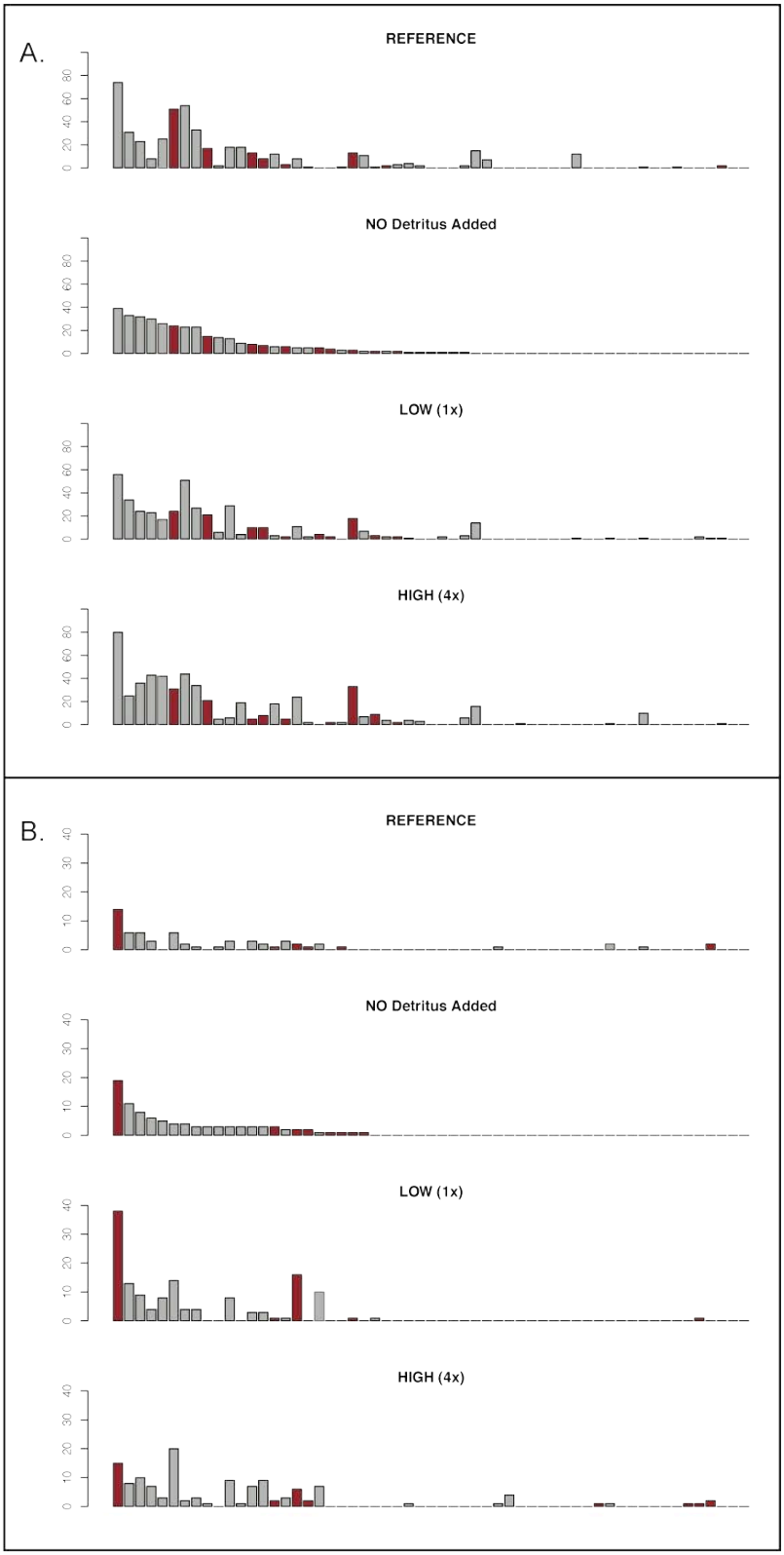
A.
REFERENCE
NO Detritus Added
LOW (1x)
HIGH (4x)
B.
REFERENCE
NO Detritus Added
LOW (1x)
HIGH (4x)

Figure 29. Ranked abundance distribution of uncommon taxa in July 2014 in the A. litter community and B. soil community. Patterns shown are relative to the No detritus added treatment. Fungivorous taxa are represented by gray bars and predatory taxa by red bars.

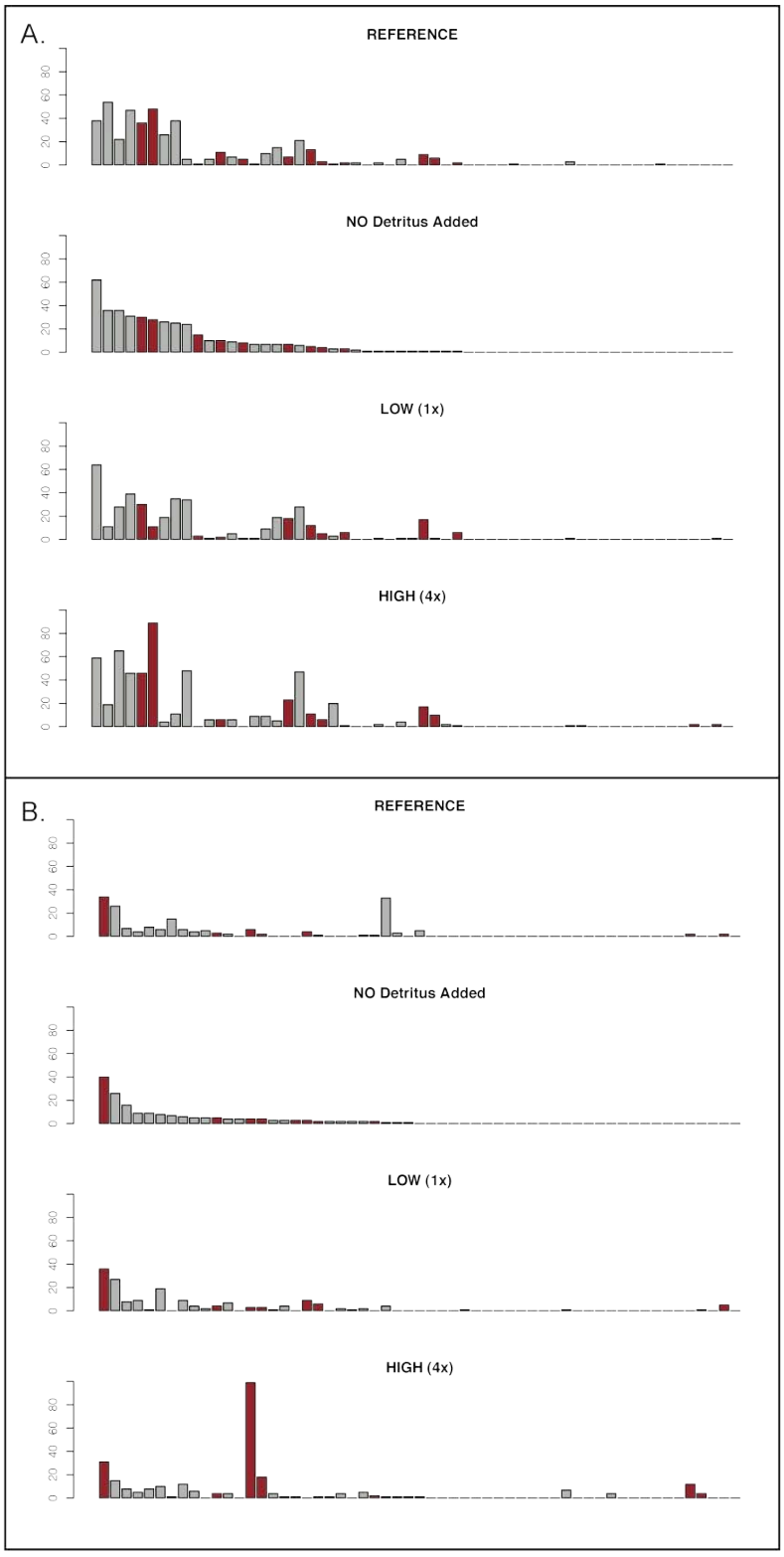
A.
REFERENCE
NO Detritus Added
LOW (1x)
HIGH (4x)
B.
REFERENCE
NO Detritus Added
LOW (1x)
HIGH (4x)

Figure 30. Ranked abundance distribution of uncommon taxa in October 2014 in the A. litter community and B. soil community. Patterns shown are relative to the No detritus added treatment. Fungivorous taxa are represented by gray bars and predatory taxa by red bars.

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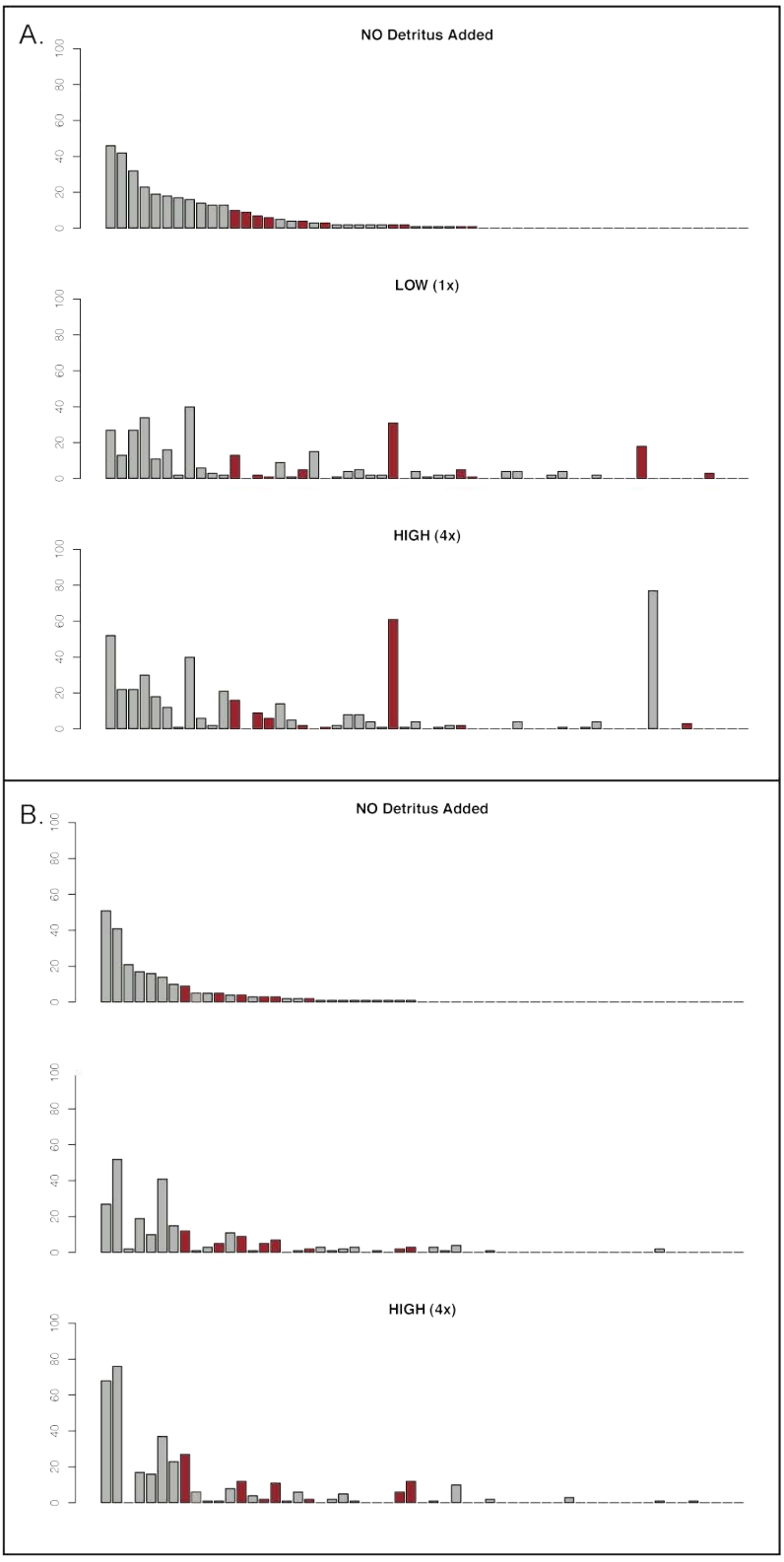
A.
NO Detritus Added
LOW (1x)
HIGH (4x)
B.
NO Detritus Added
HIGH (4x)

Figure 31. Ranked abundance distribution of uncommon taxa in April 2015 in the A. litter community and B. soil community. Patterns shown are relative to the No detritus added treatment. Fungivorous taxa are represented by gray bars and predatory taxa by red bars.

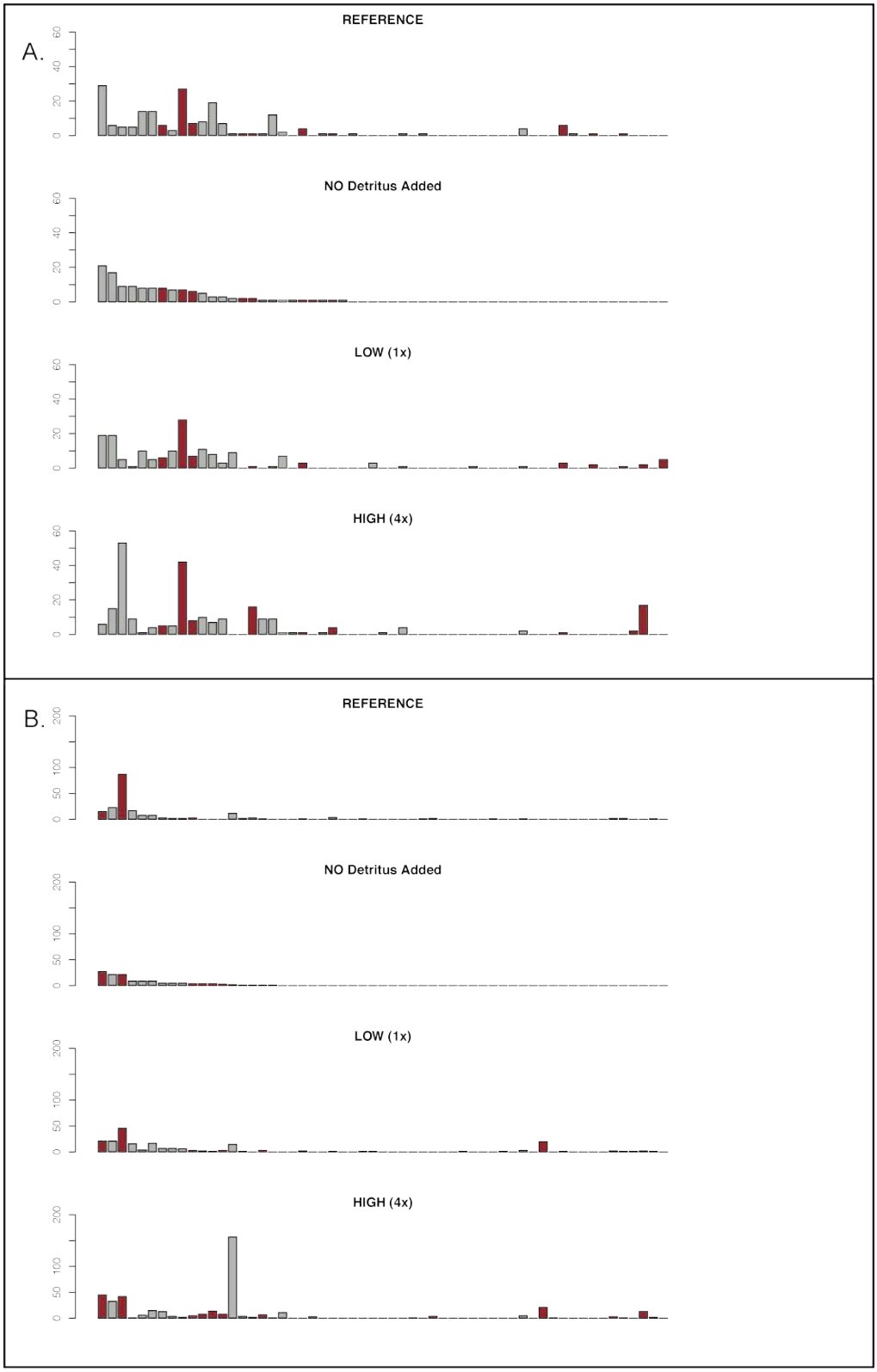
A.
REFERENCE
NO Detritus Added
LOW (1x)
HIGH (4x)
B.
REFERENCE
NO Detritus Added
LOW (1x)
HIGH (4x)

Figure 32. Ranked abundance distribution of uncommon taxa in August 2015 in the A. litter community and B. soil community. Patterns shown are relative to the No detritus added treatment. Fungivorous taxa are represented by gray bars and predatory taxa by red bars.

APPENDIX B

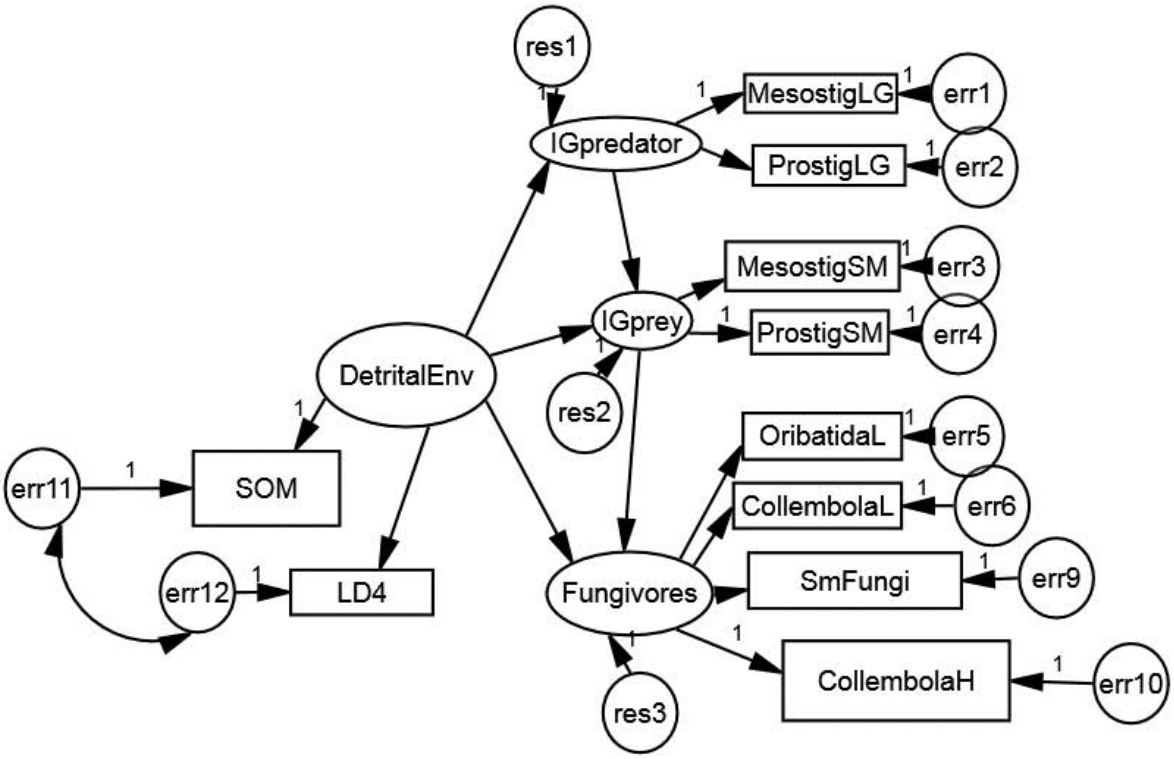

Figure 33. Originally proposed structural equation model. In the running of this model, the iteration limit for calculating estimates was reached. Therefore, this model is incorrect.

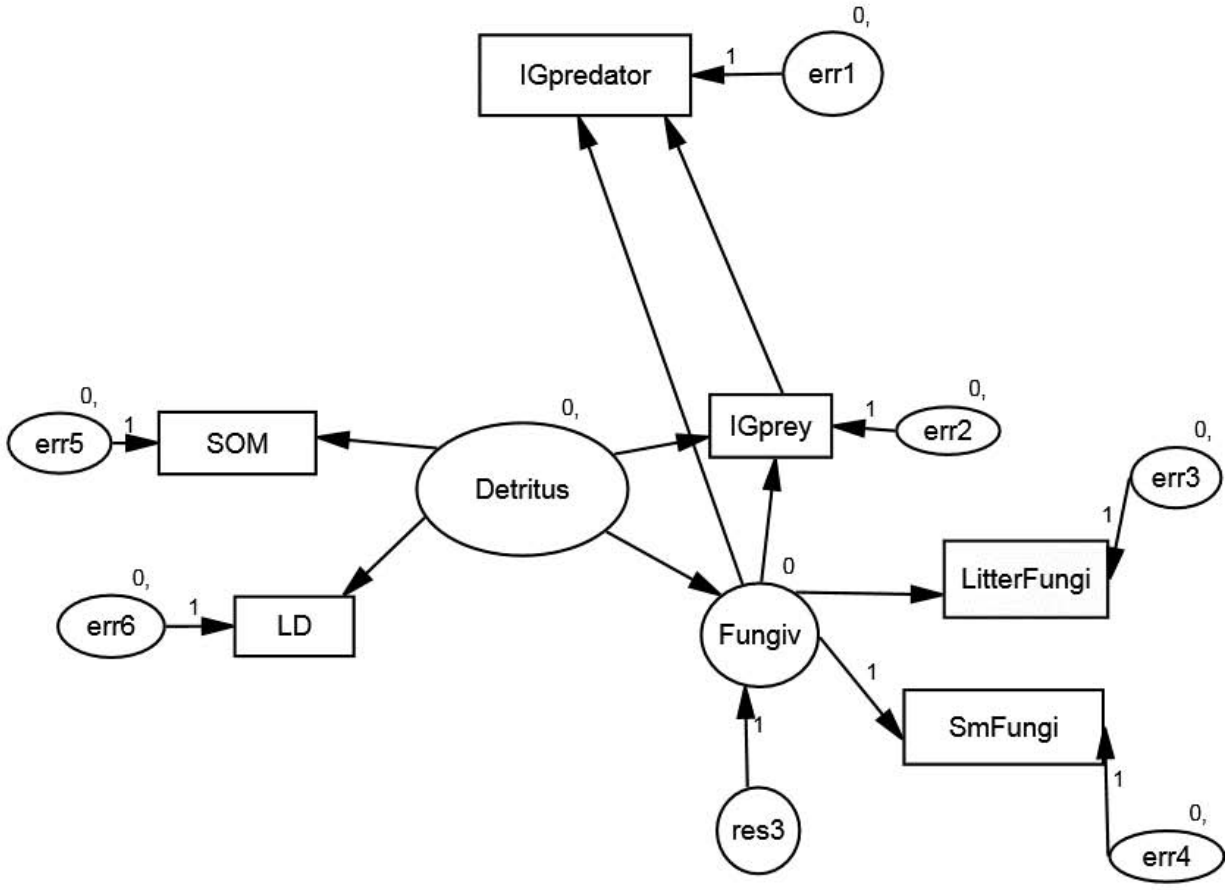

Figure 34. Modified structural equation model with small and large fungivores as separate variables contributing to the latent variable "Fungiv". and also included soil organic matter (SOM) and litter depth (LD) was unidentified for all my datasets. This means there were not enough degrees of freedom to estimate the regression. The program Amos, suggested reducing estimated parameters by 3.

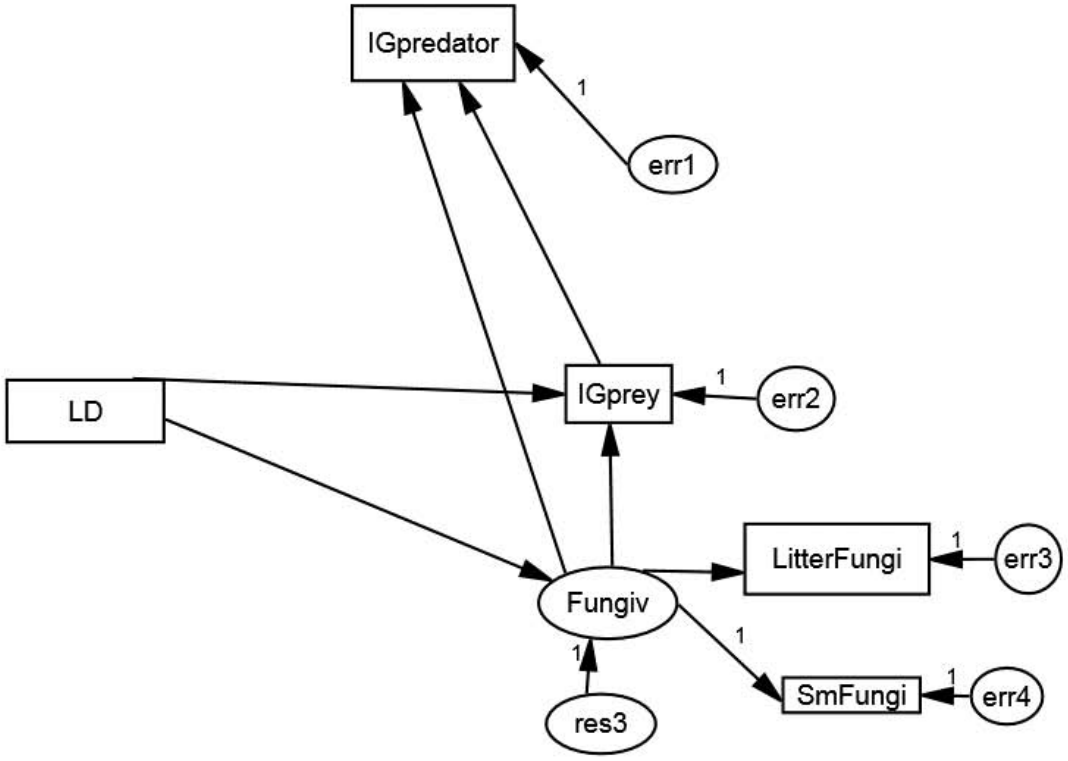

Figure 35. Modified structural equation model with small and large fungivores as separate variables contributing to the latent variable "Fungiv". This model fit well on first evaluation, except that the multivariate critical ratio, which is Mardia's normalized estimate of multivariate kurtosis, is larger than 5 (C.R. = 6.664) in High treatment data. Typically, one would adjust outliers in any individual variable with a very large kurtosis to fix this issue, by there is no such offending variable. For all treatments, the path between the latent variable for fungivores (Fungiv) and litter depth (LD) was not significant to this model. Additionally, the path between "IGprey" and "LD" was not significant for any of the treatment groups either. Therefore, I chose to eliminate the IGprey to LD path, and change fungivores from a latent variable to two observed variables.

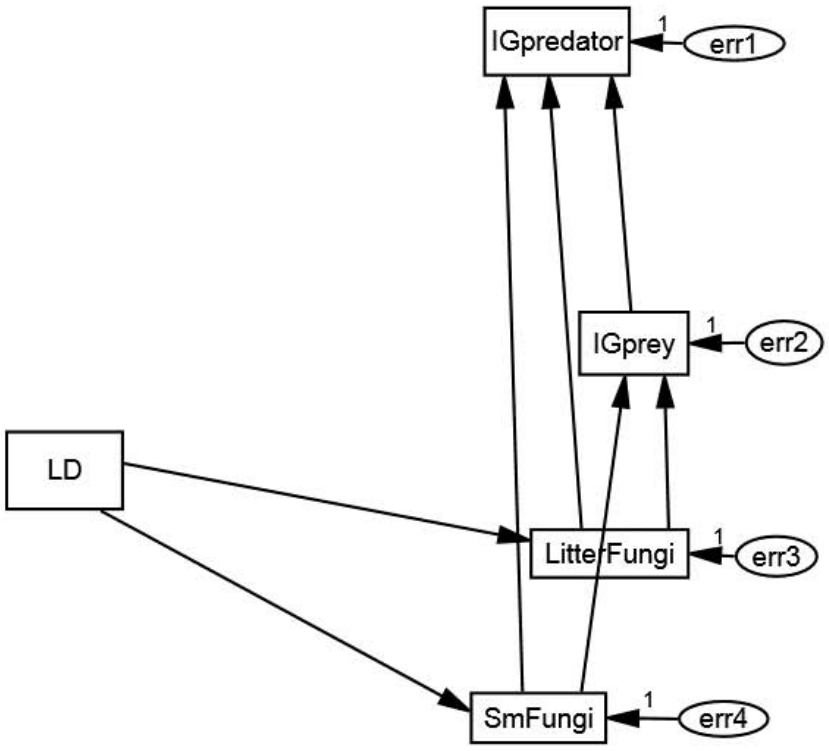

Figure 36. Structural equation model integrating fungivores as observed variables only. This is a poorly fitting model. Goodness of fit statistics: $\chi^2 = 22.412$, df = 9, $P = 0.008$, CFI = 0.889, RMSEA = 0.087. I decided to reduce more paths that were not significant. This brought me to the conclusion that small fungivores (SmFungi) were not significant to this model on their own, so I combined them into the current "Fungivores" variable used in the current model.

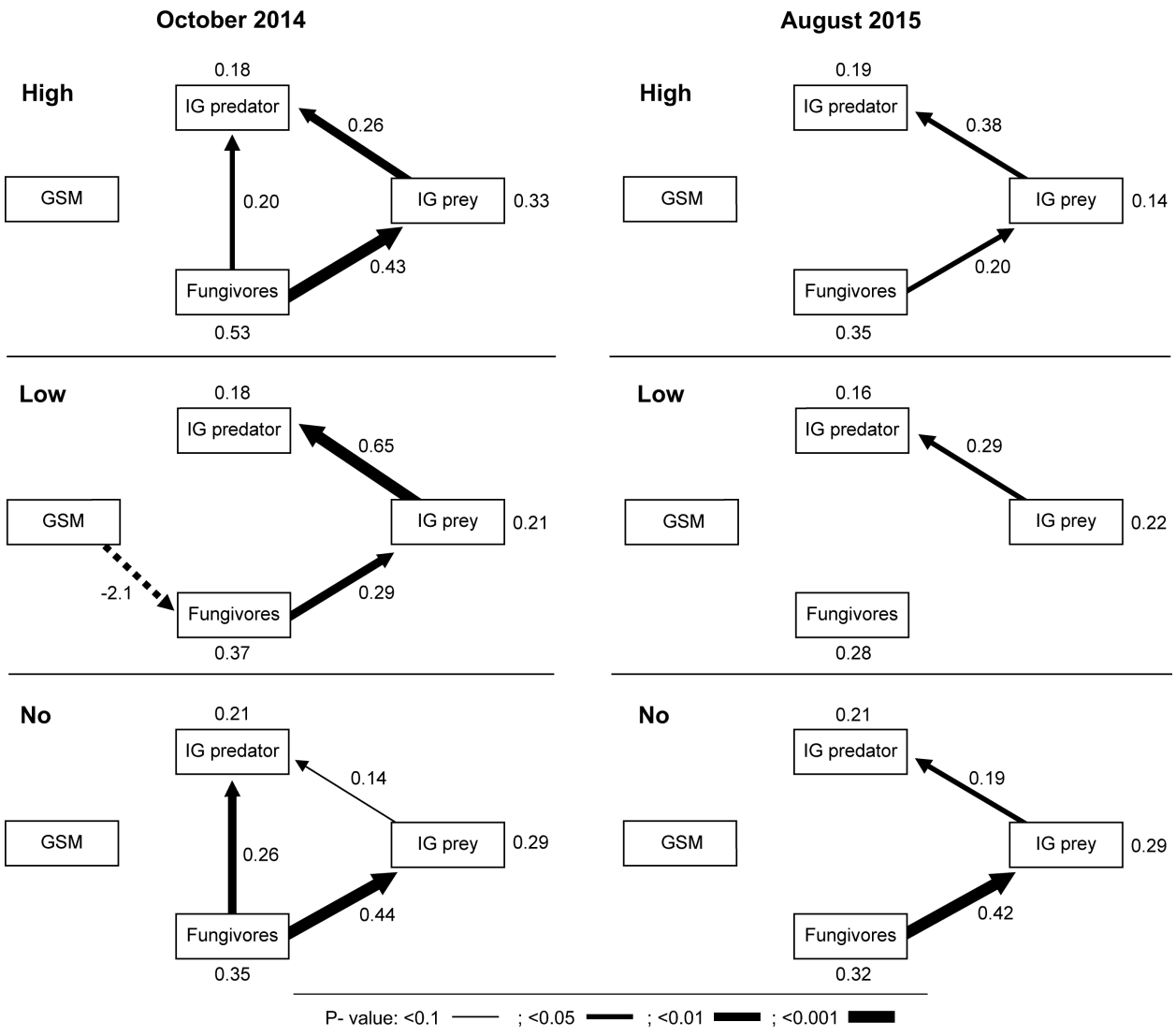

Figure 37. Structural equation model using gravimetric soil moisture (GSM) as the environmental variable for October 2014 and August 2015. Unstandardized coefficients are shown. Solid lines denote positive interaction strengths. Dashed lines represent negative interaction strengths. Paths with no arrows have *P*-values > 0.10. For October 2014, this was a good-fitting model. Goodness of fit statistics: χ^2 = 6.958, df = 6, *P* = 0.325, CFI = 0.99, RMSEA = 0.028, AIC = 54.958. For August 2015, two data were removed, along with a fourth-root transformation, to make the data multivariate normal. This is a poor-fitting model because the GSM-fungivore and fungivore-IG-predator interactions are not significant for any treatment group in the model. Goodness of fit statistics: χ^2 = 5.792, df = 6, *P* = 0.447, CFI = 1.0, RMSEA = 0.00, AIC = 53.792.

APPENDIX C

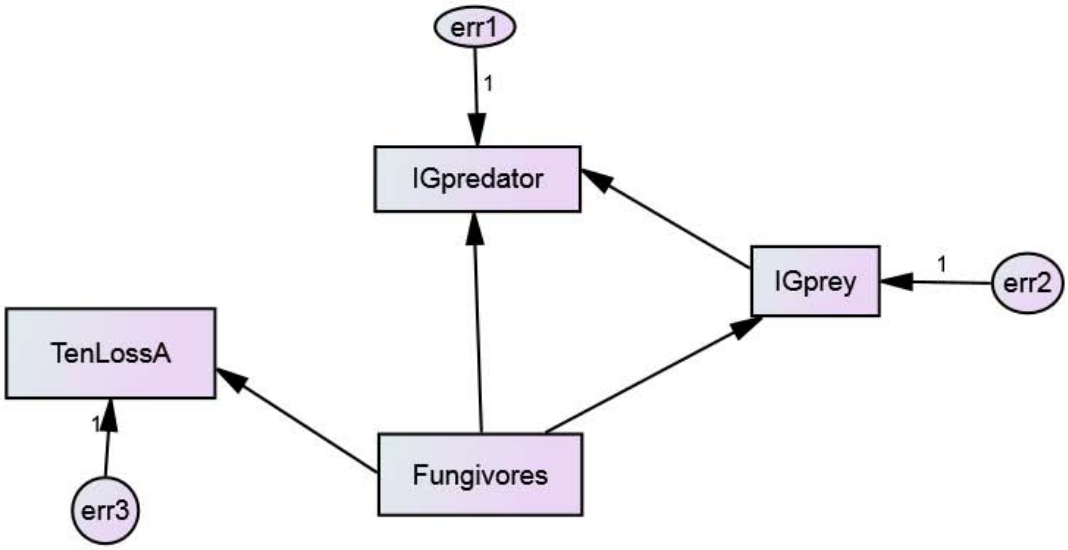

Figure 38. Structural equation model evaluated in the investigation of how IGP interactions within the microarthropod community affects cotton strip tensile loss (TenLossA) in August 2015 that includes an interaction between Fungivores and IG-predators. This model fit well, but the interaction between fungivores and IG-predators was not significant for any of the treatment groups (High unstand. estimate = 0.139, $P = 0.209$; Low unstand. estimate = -0.012, $P = 0.906$; No unstand. estimate = 0.012, $P = 0.921$. Goodness-of-fit statistics: $\chi^2 = 6.58$, df = 6, $P = 0.361$, CFI = 0.963, RMSEA = 0.033, AIC = 54.58.

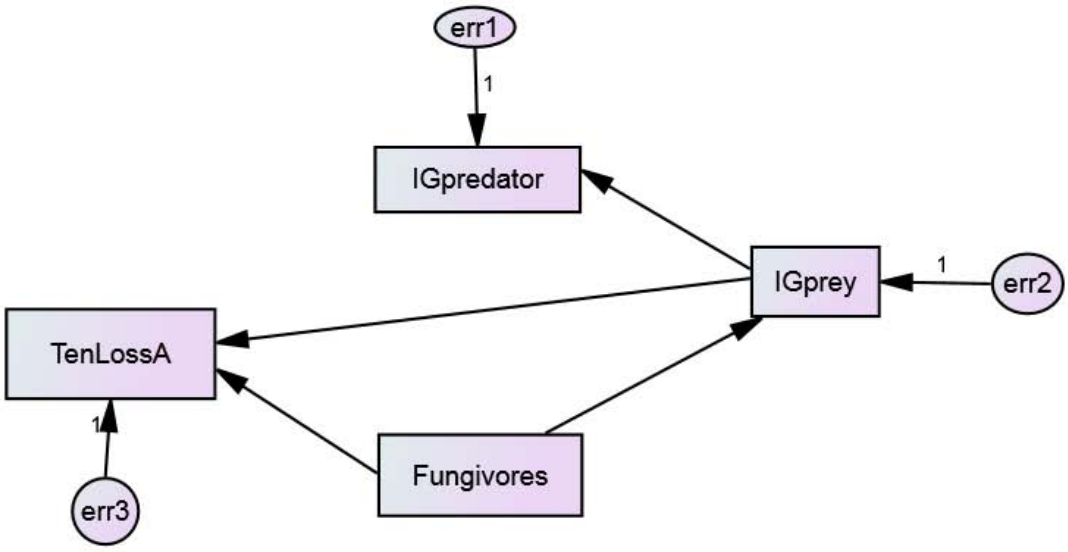

Figure 39. Structural equation model attempted in the investigation of how IGP interactions within the microarthropod community affects cotton strip tensile loss (TenLossA) in August 2015 that includes a n interation between IG-prey and TenLossA. This model fit well, but the interaction between IG prey and tensile strength loss was not significant for any of the treatment groups (High unstand. estimate = 178.621, $P = 0.20$; Low unstand. estimate = -57.644, $P = 0.350$; No unstand. estimate = 8.315, $P = 0.806$. Goodness-of-fit statistics: $\chi^2 = 5.63$, df = 6, $P = 0.466$, CFI = 1.0, RMSEA = 0.00, AIC = 53.630.

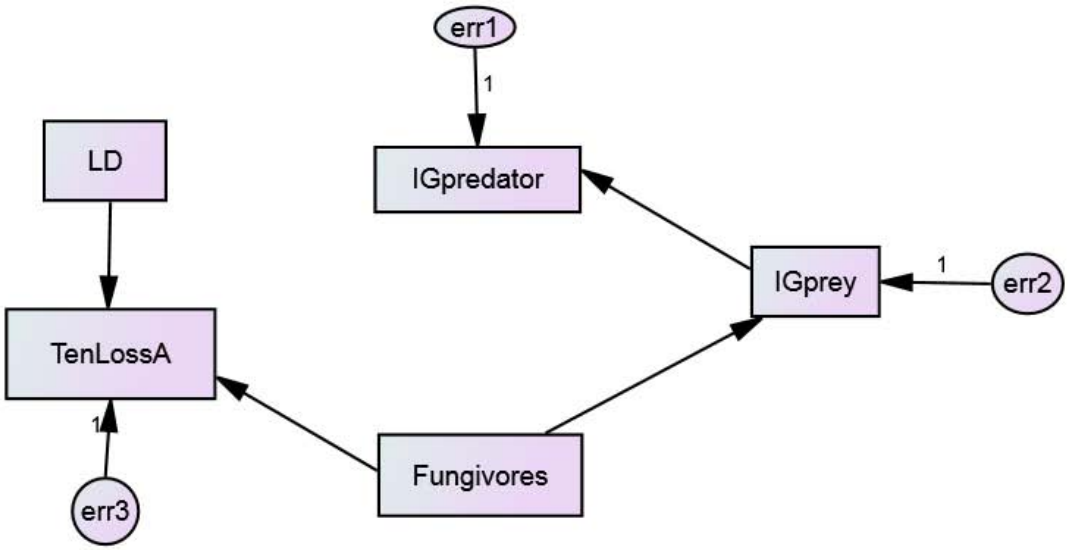

Figure 40. Structural equation model attempted in the investigation of how IGP interactions within the microarthropod community affects cotton strip tensile loss (TenLossA) in August 2015 that includes an interaction between litter depth (LD) and TenLossA. Litter depth (LD) and fungivores are highly correlated, therefore, this model was not run.

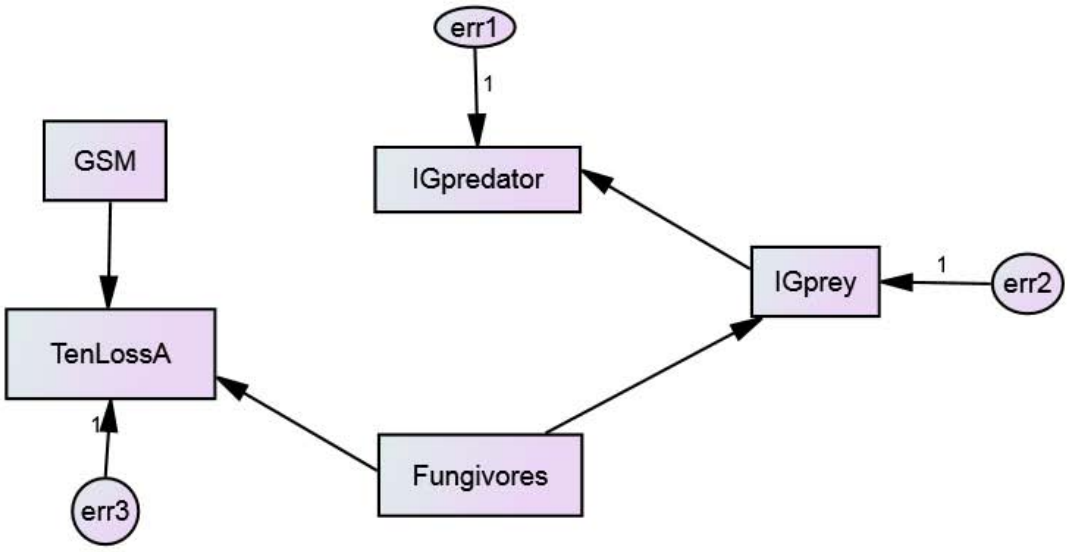

Figure 41. Structural equation model resulting from the investigation of how IGP interactions within the microarthropod community affects cotton strip tensile loss (TenLossA) in August 2015 that includes an interaction between gravimetric soil moisture (GSM) and TenLossA. Gravimetric soil moisture (GSM) and fungivores are highly correlated, therefore, this model was not run.

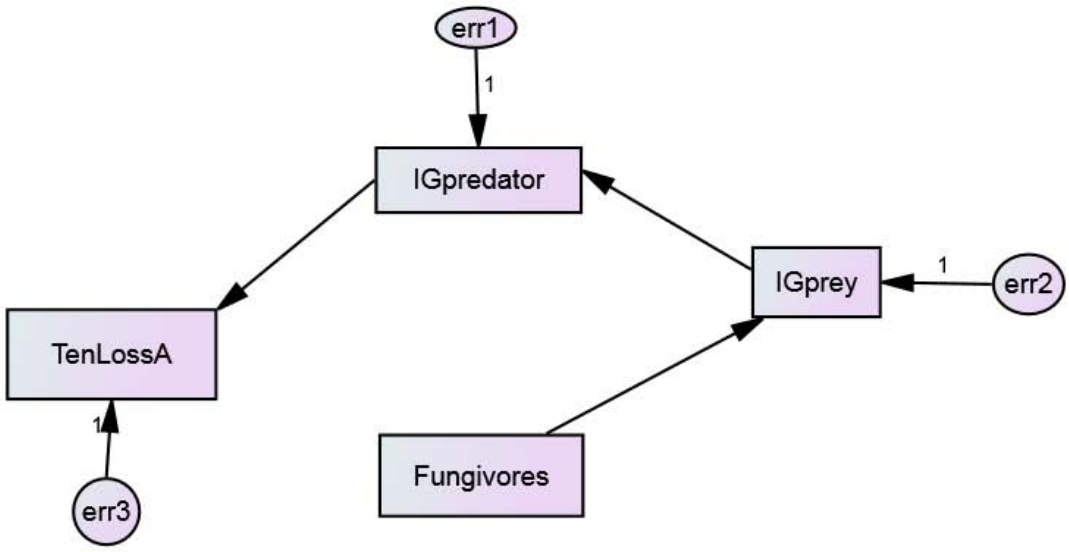

Figure 42. Structural equation model evaluated in the investigation of how IGP interactions within the microarthropod community affects cotton strip tensile loss (TenLossA) in August 2015 that includes an interaction between IG-predators and TenLossA. This model fit well, but the interaction between IG predators and tensile strength loss was not significant for any of the treatment groups (High unstand. estimate = -73.355, $P = 0.378$; Low unstand. estimate = 29.064, $P = 0.811$; No unstand. estimate = 71.437, $P = 0.116$. Goodness-of-fit statistics: $\chi^2 = 8.791$, df = 9, $P = 0.457$, CFI = 1.0, RMSEA = 0.00, AIC = 50.791.

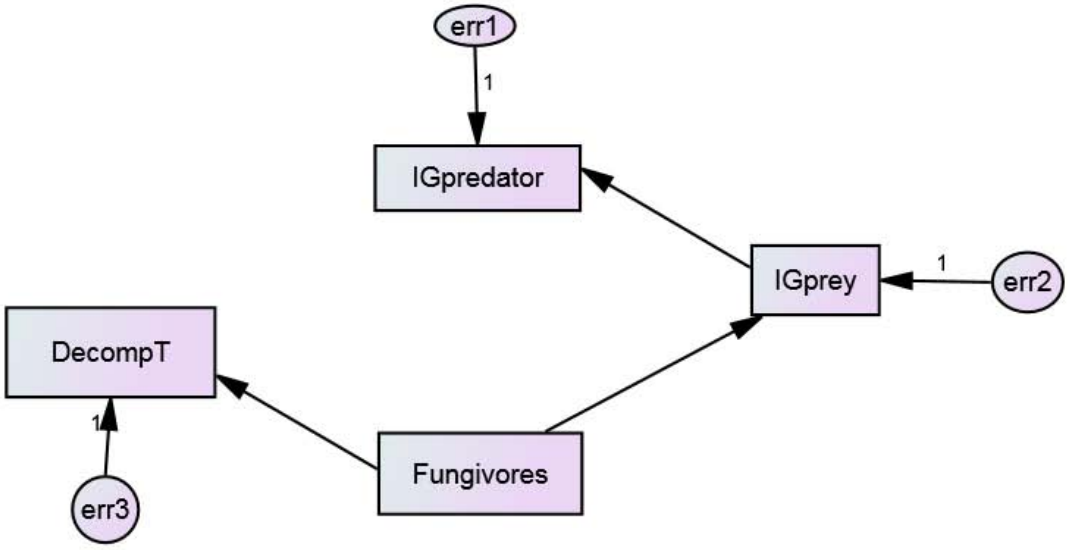

Figure 43. Structural equation model evaluated in the investigation of how IGP interactions within the microarthropod community affects cotton strip "rotting rate" (DecompT) in August 2015. This was an ill-fitting model. Goodness-of-fit statistics: $\chi^2 = 10.562$, df = 9, $P = 0.307$, CFI = 0.913, RMSEA = 0.044, AIC = 52.562.

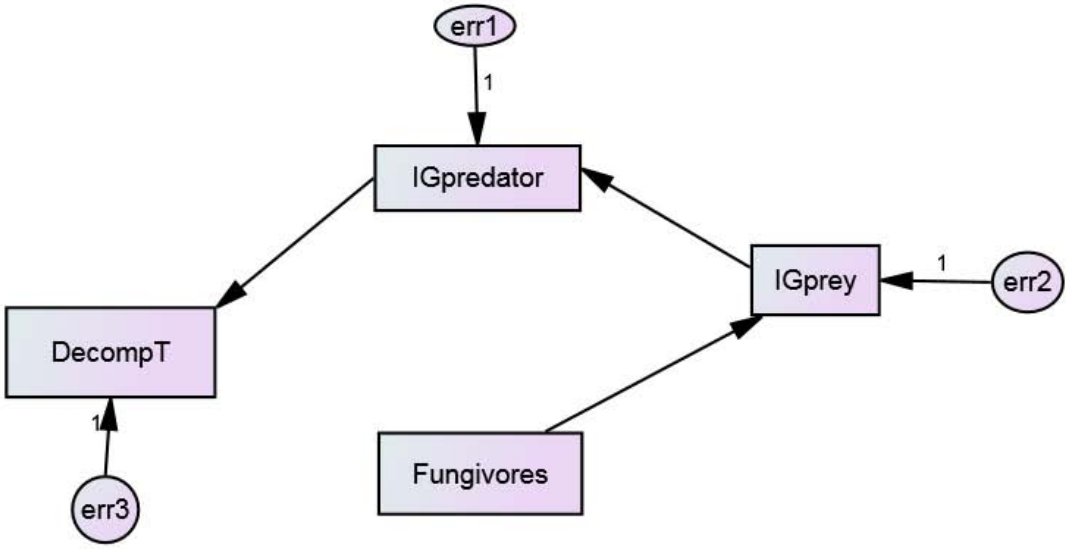

Figure 44. Structural equation model evaluated in the investigation of how IGP interactions within the microarthropod community affects cotton strip "rotting rate" (DecompT) in August 2015, that includes an interaction between IG-predators and DecompT. This was an ill-fitting model. Goodness-of-fit statistics: $\chi^2 = 10.338$, df = 9, $P = 0.324$, CFI = 0.925, RMSEA = 0.041, AIC = 52.338.

TESTS FOR CHAPTER FOUR DECOMPOSITION MODEL

Of note is that there was a slightly negative effect of fungivores on tensile strength loss in communities receiving enhancement, and an almost equivalent positive effect on tensile strength loss in plots receiving enhancement. There was no invariance or other significant differences in interaction strength of any pathways (Table XXI and Table XXII).

In contrast to the enhancement-no enhancement analysis, there is evidence of a difference in the interaction strengths between the three treatment groups in both IGP and tensile strength loss, though this is not observed across the entire model (Table XXIII). The effect of IG-prey on IG-predators in High-level enhancement plots appears to be much higher in than in Low-level enhancement plots (Table XXIV). There is also some evidence of a possible difference this effect size between High and No enhancement plots, but it is a much smaller difference (Table XXIV).

The response of fungivores in communities receiving Low-level enhancement affected tensile strength loss the most negatively. Figure 23 shows fungivores have a marginally significant effect that is not seen in either High or No enhancement communities. Though a test of path invariance does not show the interaction between fungivores and loss of tensile strength to be variant between treatments (Table XXV), a Student's t-test of the regression slopes revealed that fungivore reduction in tensile strength loss is very difference from Low versus No enhancement plots (Table XXVIC). In No enhancement, or control plots, fungivores cause an increase in tensile strength loss of around 31 N, while in Low enhancement plots, loss is reduced by approximately 96 N. In High treatment plots, tensile strength loss is reduced by about 10 N (unstandardized coefficients; Figure 23 and Table XXVI). Fungivores are encouraging microbial activity, through compensatory growth, compensatory activity, or both in communities receiving No enhancement and reducing microbial activity in plots receiving enhancement, especially Low-level enhancement.

TABLE XXI

RESULTS OF MULTIGROUP INVARIANCE TESTS FOR PATH ESTIMATES COMPARING IGP COMMUNITY STRUCTURE INFLUENCE ON CSTL IN COMMUNITIES THAT RECEIVED DETRITAL ENHANCEMENT TO COMMUNITIES RECEIVING NO ENHANCEMENT IN AUGUST 2015[a]

A. August 2015	df	χ^2	*P*	CFI	df	$\Delta\chi^2$	P_{diff}	ΔCFI
Unconstrained	6	5.961	0.428	1.0	3	3.37	0.338	0.03
Constrained	9	9.331	0.407	0.97				

SEM path[b]		df	χ^2	*P*
IGprey	← Fungivores	7	7.789	0.352
IGpredator	← IGprey	7	5.986	0.541
Tensile strength loss	← Fungivores	7	7.278	0.381

[a] χ^2 = Chi-squared; RMSEA = root-mean-squared error of approximation; and CFI = comparative fit index are included. $\Delta\chi^2$ and ΔCFI are the differences in χ^2 and CFI, respectively, for the unconstrained and fully constrained models.

[b] SEM paths describe causal relationships, with variables in the first column being affected by the variable in the second column.

[c] Asterisks (*) denote model or path invariance between groups.

TABLE XXII

RESULTS FOR TEST OF DIFFERENCE IN REGRESSION ESTIMATES BETWEEN ENHANCEMENT AND NO ENHANCEMENT SAMPLES IN AUGUST 2015[a]

SEM Path[b]		Treatment (n)	Estimate	S.E.	*t*	*P*
IGprey	**← Fungivores**	Enhancement (47)	0.17	0.086	1.388	0.168
		No Enhancement (46)	0.418	0.16		
IGpredator	**← IGprey**	Enhancement (47)	0.193	0.134	0.159	0.874
		No Enhancement (46)	0.219	0.096		
Tensile strength loss	**← Fungivores**	Enhancement (47)	-35.964	40.036	1.249	0.215
		No Enhancement (46)	30.978	36.406		

[a] Unstandardized path coefficients (Estimate), standard error of regression (S.E.), the calculated *t* statistic (*t*), and the two-tailed probability value (*P*) are included.

[b] SEM paths describe a causal relationship, with variables in the first column being affected by the variable in the second column.

TABLE XXIII

RESULTS OF MULTIGROUP INVARIANCE TESTS FOR PATH ESTIMATES COMPARING INFLUENCE OF IGP COMMUNITY STRUCTURE ON CSTL FOR ALL TREATMENT GROUPS IN AUGUST 2015[a]

August 2015	df	χ^2	*P*	CFI	df	$\Delta\chi^2$	P_{diff}	ΔCFI
Unconstrained	9	8.129	0.521	1.00	6	9.769	0.135	0.184
Constrained	15	17.898	0.268	0.816				

SEM path[b]		df	χ^2	*P*
Tensile strength loss	← Fungivores	11	11.91	0.37
IGprey	← Fungivores	11	10.46	0.49
IGpredator	← IGprey	11	11.79	0.38

[a] χ^2 = Chi-squared; RMSEA = root-mean-squared error of approximation; and CFI = comparative fit index are included. $\Delta\chi^2$ and ΔCFI are the differences in χ^2 and CFI, respectively, for the unconstrained and fully constrained models.

[b] SEM paths describe causal relationships, with variables in the first column being affected by the variable in the second column.

[c] Asterisks (*) denote model or path invariance between groups.

TABLE XXIV

RESULTS FOR TEST OF DIFFERENCE IN REGRESSION SLOPES BETWEEN ALL TREATMENT GROUPS IN AUGUST 2015[a]

SEM Path[b]		Treatment (n)	Estimate	S.E.	*t*	*P*
A.						
Tensile strength loss	← **Fungivores**	High (23)	-10.507	44.957	1.262	0.213
		Low (24)	-96.621	52.939		
IGprey	← **Fungivores**	High (23)	0.151	0.066	0.251	0.803
		Low (24)	0.198	0.176		
IGpredator	← **IGprey**	High (23)	0.651	0.298	1.928	0.060
		Low (24)	0.061	0.111		
B.						
Tensile strength loss	← **Fungivores**	High (23)	-10.507	44.957	0.695	0.489
		No (46)	30.978	36.406		
IGprey	← **Fungivores**	High (23)	0.151	0.066	1.165	0.248
		No (46)	0.418	0.160		
IGpredator	← **IGprey**	High (23)	0.651	0.298	1.764	0.082
		No (46)	0.219	0.096		
C.						
Tensile strength loss	← **Fungivores**	Low (24)	-96.621	52.939	2.047	0.045
		No (46)	30.978	36.406		
IGprey	← **Fungivores**	Low (24)	0.198	0.176	0.872	0.386
		No (46)	0.418	0.160		
IGpredator	← **IGprey**	Low (24)	0.061	0.111	1.031	0.306
		No (46)	0.219	0.096		

[a] Unstandardized path coefficients (Estimate), standard error of regression (S.E.), the calculated *t* statistic (*t*), and the two-tailed probability value (*P*) are included.

[b] SEM paths describe a causal relationship, with variables in the first column being affected by the variable in the second column.

TABLE XXV

LISTING OF TAXA PLACED INTO INTRAGUILD-PREDATION COMMUNITY CATEGORIES WITH THEIR LARGER TAXONOMIC DESIGNATION

FUNGIVORES		**IG-PREY**		**IG-PREDATOR**	
Family		**Family**		**Family**	
Entomobryidae	Collembola	Ascidae	Mesostigmata	Laelapidae	Mesostigmata
Isotomidae	Collembola	Rhodacaridae	Mesostigmata	Parasitidae	Mesostigmata
Hypogastruridae	Collembola	juvenile	Mesostigmata	Parholaspididae	Mesostigmata
Neelidae	Collembola	Bdellidae	Prostigmata	Veigaiidae	Mesostigmata
Onychiuridae	Collembola	Cunaxidae	Prostigmata	Rhagidiidae	Prostigmata
Sminthuridae	Collembola	Eupodidae	Prostigmata	Trombidiidae	Prostigmata
Tomoceridae	Collembola	Microtrombidiidae	Prostigmata		
Aphelacaridae	Oribatida	Pomerantziidae	Prostigmata		
Carabodidae	Oribatida				
Ceratozetidae	Oribatida				
Galumnidae	Oribatida				
Lincermaeidae	Oribatida				
Oribatellidae	Oribatida				
Oripodidae	Oribatida				
Phthiracaridae	Oribatida				
Scheloribatidae	Oribatida				
Tectocepheidae	Oribatida				
Unduloribatidae	Oribatida				
juvenile	Oribatida				
Microdispidae	Prostigmata				
juvenile	Prostigmata				
Pygmephoridae	Prostigmata				
Scutacaridae	Prostigmata				
Tarsonemidae	Prostigmata				
Tydeidae	Prostigmata				

TABLE XXVI

TAXA COLLECTED DURING THIS EXPERIMENT

MITES (order Acari)		**Order COLLEMBOLA**		**OTHER INVERTEBRATES**	
Family		**Family**		**Taxon**	
Acaridae	Astigmata	Entomobryidae	Collembola	Aranae	spiders
Histiostomatidae	Astigmata	Hypogastruridae	Collembola	Aphidae	aphids
Alycidae	Endeostigmata	Isotomidae	Collembola	Blaniulidae	millipede
Ascidae	Mesostigmata	Neelidae	Collembola	Chilopoda	centipede
Blattisociidae	Mesostigmata	Onychiuridae	Collembola	*Cylindroiulus* sp.	millipede
Eviphididae	Mesostigmata	Sminthuridae	Collembola	Coleoptera	juvenile
juvenile	Mesostigmata	Tomoceridae	Collembola	Conotylidae	millipede
Laelapidae	Mesostigmata			Diplura	
Macrochelidae	Mesostigmata			Diptera	adult
Ologamasidae	Mesostigmata			Diptera	juvenile
Pachylaelapidae	Mesostigmata			Formicidae	ants
Parasitidae	Mesostigmata			Hemiptera	juvenile
Parholaspididae	Mesostigmata			Isopoda	
Phytoseiidae	Mesostigmata			Lepidoptera	juvenile
Podocinidae	Mesostigmata			*Ophyiulus pilosus*	juvenile
Rhodacaridae	Mesostigmata			Opiliones	juvenile
Uropodina	Mesostigmata			Orthoptera	
Veigaiidae	Mesostigmata			Pauropoda	
Amerobelbidae	Oribatida			*Polydesmus* sp.	juvenile
Ameroseiiae	Oribatida			Protura	
Aphelacaridae	Oribatida			Pseudoscorpiones	
Astegistidae	Oribatida			Psocoptera	
Autognetidae	Oribatida			Ptiliidae	adult
Brachychthoniidae	Oribatida			Staphylinidae	adult
Carabodidae	Oribatida			Symphyla	
Ceratozetidae	Oribatida			Thripidae	thrips
Crotoniidae	Oribatida			Tiphiidae	wasps
Damaeidae	Oribatida			worms	
Epilohmanniidae	Oribatida				
Eremaeidae	Oribatida				
Eremobelbidae	Oribatida				
Euphthiracaridae	Oribatida				
Galumnidae	Oribatida				
Haplozetidae	Oribatida				
Lamellareidae	Oribatida				
Liacaridae	Oribatida				
Lincermaeidae	Oribatida				
Micreremidae	Oribatida				
Mochlozetidae	Oribatida				
Nothridae	Oribatida				
Oribatellidae	Oribatida				
Oribatulidae	Oribatida				

TABLE XXVI (continued)

TAXA COLLECTED DURING THIS EXPERIMENT

MITES (order Acari)	
Family	
Oripodidae	Oribatida
Otocepheidae	Oribatida
Parakalummidae	Oribatida
Pedrocortesellidae	Oribatida
Peloppiidae	Oribatida
Phthiracaridae	Oribatida
Scheloribatidae	Oribatida
Tectocepheidae	Oribatida
Thyrisomidae	Oribatida
Unduloribatidae	Oribatida
juvenile	Oribatida
Anystidae	Prostigmata
Bdellidae	Prostigmata
Cunaxidae	Prostigmata
Eupodidae	Prostigmata
Microdispidae	Prostigmata
Microtrombidiidae	Prostigmata
juvenile	Prostigmata
Pomerantziidae	Prostigmata
Pygmephoridae	Prostigmata
Rhagidiidae	Prostigmata
Scutacaridae	Prostigmata
Tarsonemidae	Prostigmata
Trombidiidae	Prostigmata
Tydeidae	Prostigmata

VITA

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Department of Art and Design, Robert Morris University, Chicago, Illinois: Instructor, *2-D Design, Typography*, January 2001-March 2004

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Center for Life Sciences Education, The Ohio State University, Columbus, OH: Teaching Assistant, Introductory Biology Laboratory, March-September 2008.

PUBLICATIONS: Farfan, M. A. and Klompen, H. 2012. Phoretic mite associates of millipedes (Diplopoda, Julidae) in the northern Atlantic region (North America, Europe). The International Journal of Myriapodology. 7, 69-91.

AWARDS, HONORS, FELLOWSHIPS:

LEAP IGERT-NSF Fellowship ($30,000/yr plus tuition), University of Illinois at Chicago, August 2010-August 2012

Visiting Researcher Scholarship ($1200), The Field Museum of Natural History February 2009.

Graduate Enrichment Fellowship ($25,000/yr plus tuition), The Ohio State University, Columbus, OH, 2008-2009

Ralph Davidson Scholarship ($1000), Department of Entomology, The Ohio State University, Columbus, OH, August-December 2007 and January-March 2008.

PROFESSIONAL MEMBERSHIP:

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Ecological Society of America
Entomological Society of America
Soil Ecology Society

INVITED SYMPOSIUM TALKS:

Farfan, M. A., Henderson, A., Ross, K. A., and Wise, D. H. Variation in the structure of mite communities in forest soils across a metropolitan landscape. International Congress of Entomology, Orlando, FL. 29 September 2016. Additionally, I co-organized the symosium, Advances in Acarology, with Jose Carlos Verle Rodrigues for the 2016 ICE.

INVITED LECTURES:

Farfan, M. A. Estimating soil mite diversity in the Chicago region. DePaul University, Chicago, IL 23 April 2013

Farfan, M. A., Belaire, J. A., Milz, D., Sweeney, E., Davis, A. Y., and Minor, E. S. Urban green infrastructure and the availability of ecosystem services across Chicago, Illinois, U.S.A. Planning for Biodiversity, College of Urban Planning and Public Affairs, Univ. of Illinois-Chicago. 13 March 2012.

INVITED LECTURES:

Farfan, M. A. Millipedes and Centipedes: the diversity under your feet. Marietta Natural History Society, Marietta, OH. 8 April 2010.

Farfan, M. A. Study of the origins and relatedness of the family Julidae in the U.S. British Myriapod and Isopod Group Annual Field Meeting. Cornwall, UK. 15 April 2009.

MEETING PRESENTATIONS:

Farfan, M. A., Ross, K. A., and Wise, D. H. A place for mites and man? structural forms of soil mite communities in woodland ecological restorations in the Chicago region. Soil Ecology Society Biennial Meeting, Camden, NJ. 13 June 2013.

Farfan, M. A., Davis, A. Y., Belaire, J. A., Milz, D., Sweeney, E. R., Loss, S. R. , and Minor, E. S. Urban green infrastructure and the availability of ecosystem services across Chicago, Illinois, U.S.A. Chicago Wilderness Congress, Chicago, IL. 15 November 2012.

Farfan, M. A., Ross, K. A., and Wise, D. H. Structure of soil mite communities in woodlands undergoing ecological restoration in the Chicago region. Chicago Wilderness Congress, Chicago, IL. 15 November 2012.

Farfan, M. A., Ross, K. A., and Wise, D. H. Structure of soil mite communities in woodlands undergoing ecological restoration in the Chicago region. Acarological Society of America Annual Meeting, Knoxville, TN. 11 November 2012.

Milz, D., Farfan, M. A., Marshall-Gillespie, K., and Wise, D. H. . Measuring sustainability of socio-ecological systems using Fisher's information: challenges and future directions. The Association of Collegiate Schools of Planning Annual Conference, Cincinnati, OH. 3 November 2012.

Farfan, M. A. Restoration by fire: the history of fire in Chicago. American Society of Environmental History Annual Meeting, Madison, WI. 31 March 2012.

Farfan, M. A. and Klompen, H. Study of relatedness of populations of introduced species of millipedes (Class Diplopoda) in the family Julidae. Entomological Society of America Annual Meeting. Indianapolis, IN. 14 December 2009.

Horn, D. J., Farfan, M. A. and Purrington, F. F. Ecological impacts of oil pipeline installation through previously intact forest in Hocking County, Ohio. The 6th Ohio Natural History Conference. Columbus, OH. 28 Feb. 2009.

Farfan, M. A. Ecological impact of oil pipeline installation on millipedes (Diplopoda) in a mixed deciduous forest in southern Ohio. The OSU Denman Undergraduate Research Forum, Columbus, OH. 14 May 2008.

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