

Abstract

GREENWOOD, CARMEN MARIE. Interactions between soil invertebrates and entomopathogenic nematodes in no-till and conventional-till corn in North Carolina. (Dr. Mary Barbercheck)

The conservation of naturally-occurring biological control agents, such as entomopathogenic nematodes (EPN), of soil-dwelling pests in agriculture may decrease the need for chemical pesticides, result in economic savings, promote a safer environment for both farm workers and native wildlife, and protect groundwater and surface water run-off. Thorough evaluation of abiotic and biotic interactions between EPN and the soil community and environment are important to assess both impacts to EPN populations and potential impacts on soil fauna resulting from the introduction of EPN.

Two experiments were conducted to evaluate the response of soil fauna to the application of EPN to the soil in no-till and conventional-till corn. Each experiment used a different application method (Bait experiment = EPN delivered via infected insect cadaver, Inundation experiment = EPN delivered in aqueous solution). Both experiments were designed as a stripped split split plot over four blocks. Each experiment was repeated on 6 different dates. Variables included: 4 blocks x 2 tillage regimes x 2 sampling times x 5 treatments. The treatments included: three nematode species treatments *Heterorhabditis bacteriophora* (CEFS strain), *Steinernema riobrave* (commercially available but does not naturally occur in NC), and *Steinernema carpocapsae* (CEFS strain) and two

control treatments, water and soil for inundation, and water and a dead insect control for bait. Response of soil fauna was measured at the levels of abundance (large traditional taxonomic affiliations of soil invertebrates), diversity, and community composition based on the finest level of taxonomic identification of invertebrates collected.

Responses of soil fauna differed between the two application methods. Experimental factors, including sampling date and time, tillage regime, and blocks significantly affected abundance, diversity and community composition of soil invertebrates in both experiments. Significant changes in abundance of individual soil invertebrate taxa due to the effect of nematode treatment were found in both experiments. Both positive responses and negative responses, were detected in various taxonomic categories. And, large taxonomic groupings of invertebrates exhibited responses that differed significantly from the responses of individual taxa within those large groupings.

**INTERACTIONS BETWEEN SOIL INVERTEBRATES AND
ENTOMOPATHOGENIC NEMATODES IN NO-TILL AND CONVENTIONAL-
TILL CORN IN NORTH CAROLINA**

By

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Biography

Carmen Marie Greenwood was born in the Panama Canal Zone on March 31st, 1964. After numerous relocations throughout the United States as part of a military family, she graduated from high school in Roscommon, Michigan in 1982. She went on to complete her Bachelor of Science degree in Biology at Western Carolina University in 1989 and a Masters of Science in Environmental Studies at Longwood University in 1998. She began the doctoral program in Entomology at North Carolina State University in 1999 working with soil invertebrates and sustainable agriculture under the tutorship of Dr. Mary Barbercheck.

Upon completion of her PhD she plans to relocate to Sault Ste. Marie, Michigan to assume a faculty position at Lake Superior State University. She will be accompanied by her loving husband, Jim Hardin, two dogs Pepi and Daisy, and snake Speedy.

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Chapter 1 Response of soil invertebrate fauna to entomopathogenic nematodes in till and no-till corn

Soil community and soil quality

Soil is home to a complex assemblage of micro- and macroinvertebrates. These organisms interact with each other, the soil biotic community and the soil abiotic environment in ways that have significant impacts on both above-ground and below-ground processes (Brown and Gange 1991, Neave and Fox 1997, Laakso and Setälä 1999, Neher and Barbercheck 1999, Ostfield and Keesing 2000, Coll and Guershon 2002). Soil-dwelling organisms play key roles in soil function. They provide the foundation for such critical processes as soil structure development, nutrient cycling, decomposition, bioremediation, promotion of plant health and diversity, and biological control of soil-dwelling insect pests (Coleman and Crossley 1996). The term soil quality refers to a somewhat variable and subjective measure of soil attributes based upon the expectations of the person evaluating the soil (Moore and deRuiter 1991, Coleman and Crossley 1996). In an agricultural context soil quality generally involves the capacity of a soil to produce and sustain vegetation. This encompasses a host of abiotic and biotic characteristics that are inextricably linked and interdependent in ways that can be complicated to understand (Coleman and Crossley 1996). Abiotic characteristics tend to be more predictable than biotic characteristics and are generally easier to quantify, hence they are most often used as defining characteristics of soil

quality. Because abiotic and biotic processes are interdependent, however, biotic processes are equally relevant components to overall quality of a soil (House and Stinner 1983, Ettema and Wardle 2002, Coleman and Crossley 1996).

Biological control in soil and entomopathogenic nematodes

One biotic character of soil quality that is of particular interest in an agricultural setting is the ability of the soil to suppress soil-dwelling invertebrate pests. A thriving heterogeneous community of soil organisms typically includes a wide range of predators, parasites and pathogens that aid in the suppression of agricultural pests (Mueller et al. 1990, House and Stinner 1983, Coll and Guershon 2002, Symondson, et al. 2002, Hummel, et al 2002, Millar and Barbercheck 2002).

Entomopathogenic nematodes (EPN) are widely distributed throughout the world and have been isolated from many types of natural and managed habitats in a wide variety of soils (Kaya and Gaugler 1993). These nematodes function as a naturally-occurring biological control agent of arthropods, that live all or part of their lives in the soil. Entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae require an arthropod host to complete their life cycle. The only soil-dwelling, free-living form of these nematodes is the infective juvenile (IJ). They enter the host's body through natural openings, such as spiracles, mouth or anus. Within the host they release a nematode family-

specific symbiotic bacterium, *Xenorhabdus spp.* in Steinernematidae, and *Photorhabdus spp.* in Heterorhabditidae, which ultimately kills the host and preserves it for the duration of the nematode's life cycle. Life cycle completion may take 5-8 days for steinernematid species and 10-15 days for heterorhabditid species. Tens of thousands of new IJ may be released from one infected host (figure 1).

The obligately symbiotic bacteria, *Xenorhabdus spp.* and *Photorhabdus spp.*, are virulent against a broad range of arthropod hosts. The bacteria, once released by the nematode, kill the host insect (septicemia) and release a wide variety of compounds that act to preserve the cadaver in soil. The bacteria also provide a nutrient source for the nematodes, as they complete their life cycle and potentially act to repel antagonists. These bacteria have never been isolated free-living from soil. (Kaya and Kopenhofe1996).

Soil ecology of entomopathogenic nematodes

Currently, many soil-borne insect pests are managed by the application of soil insecticides. Under current federal re-evaluation many soil insecticides will no longer be available for use in many crops. To move toward the goal of reduced synthetic inputs in sustainable agriculture will require growers to manage soil organisms to promote nutrient cycling and to suppress pests. Therefore, biological and cultural pest management alternatives will be needed. Naturally occurring predatory microarthropods and entomopathogenic nematodes (EPN) can serve as an effective force in controlling agricultural soil-

dwelling pest species. It will be especially important to understand how production systems and practices affect beneficial and pest organisms. This information can be used to devise ways to exploit soil properties and beneficial soil organisms, such as predators and pathogens of soil-dwelling insect pests, and to enhance agricultural sustainability.

Entomopathogenic nematodes exhibit many of the characteristics of an ideal biological control agent for soil-dwelling pests, including exemption from registration with the Environmental Protection Agency, and because of their potentially minimal non-target effects (Bathon 1996). Therefore, understanding their biology and ecology is an integral component of evaluating how their efficacy as a pathogen of pest insects might be optimized (Millar and Barbercheck 2002).

In addition to their natural occurrence, several EPN are commercially available for use against soil pests. Efficacy of commercially applied EPN is variable and it is still unresolved by what process and at what rate EPN are “lost” in the soil after application. Recoveries of EPN directly after application can be less than 50% (Van der Werf et al., 1995, Smits 1996, Laakso and Setala 1999) and can reach undetectable levels after four weeks (Georgis 1992, McCoy et al. 2000). Even when EPN are applied inundatively, as prescribed commercially for suppression of soil-dwelling insects, their population densities may be relatively low compared to the densities of other soil organisms (Wasilewska 1981).

Positive response of soil fauna to application of EPN

Some authors have observed an increase of soil fauna in response to the application of EPN. Various reasons for a positive response could include aggregation to areas where EPN have been applied, attraction to an introduced resource (direct response), attraction to other biota that may have responded positively to the introduced resource (indirect response), or arrest at a site of resources due to random movement. Semiochemicals resulting from EPN application may play a role in invertebrate response either directly or indirectly (Shapiro and Glazer 1996, Brown and Gaugler 1997, Koppenhofer et al. 1997, Shapiro and Lewis 1999, Shapiro-Ilan et al. 2002, Shapiro-Ilan et al. 2003).

The observed lack of persistence of applied EPN, even under optimal environmental conditions, indicates the necessity of evaluating potential biotic impacts on their populations. Many soil invertebrates have been described as microbivores or detritivores, and omnivory has been assumed to be rare in food webs (Pimm 1982, Mueller et al. 1990). However, a number of studies of soil invertebrates has revealed that omnivory is actually quite common, and many organisms usually described as fungivores include nematodes as a food resource (Gilmore 1970, Walter et al. 1986, Small 1987, Walter 1987ab, 1988, Walter et al. 1987, 1988 Walter and Ikonen 1989, Mueller et al. 1990). Generalist predators can effectively reduce prey populations (Greenstone 1989).

As many constituents of the soil community are known to maintain omnivorous feeding habits, predation of soil organisms by natural enemies is an obvious consideration. Literature regarding the impact of natural enemies on

EPN is sparse. Conversely, there are many studies on the interaction of plant-parasitic nematodes with soil biota. The study of enemies of nematodes with the goal of providing biological control of plant-parasitic nematodes has a long history (Cobb 1917, Thorne 1927). More than 200 pathogens, parasites and predators are known to attack plant-parasitic nematodes (Lehman and Reid 1993, Poinar and Jansson 1988, Sayre and Walter 1991, Small 1987, Stirling 1991, Van Gundy 1985). Natural enemies of nematodes occur among many microbial and invertebrate groups. Predatory invertebrates of nematodes include tardigrades, copepods, nematodes, mites, collembolans and other soil arthropods. There is no reason to assume that natural enemies of plant-parasitic and free-living nematodes do not also affect populations of EPN.

The widespread distribution of nematodes, mites collembolans and other microarthropods (e.g symphylans, diplurans, centipedes) in soil, their abundance and the high rates of predation observed for some species in the laboratory suggests that soil invertebrates may have a considerable impact on nematodes in the natural environment. The effect of a natural enemy on its prey depends on many factors, eg. voracity, specificity, survival at low prey densities, dispersal and distribution in relation to prey, and reproductive potential. Even specialist nematophagous invertebrates will attack a variety of nematode prey (Muraoko and Ishibashi, 1976, Small 1987, Walter et al 1987).

Under laboratory conditions, omnivorous and nematophagous predators can be voracious feeders. For example, one adult of the mesostigmatid mite, *Lasioseius scapulatus*, and its progeny consumed approximately 20,000

Aphelenchus avenae on agar plates in 10 days (Imbriani and Mankau, 1983). Some Collembolan species can also consume large numbers of nematodes (Gilmore, 1970). *Entomobryoides dissimilis* consumed more than 1000 nematodes in a 24 hour period. In field plots of rape up to 30% of *Heterodera cruciferae* cysts were damaged by collembolans, principally *Onychiurus armatus* (Murphy and Doncaster 1957). Predatory nematodes also typically exhibit high consumption rates with little indication of satiation (Bilgrami and Jairajpuri 1989ab, Hechler 1963, Nelmes and McCulloch 1975, Yeates 1969).

Interactions among EPN and other soil biota affect nematode survival and efficacy in simplified laboratory arenas and confirm that several soil organisms are capable of feeding, developing, and reproducing on nematodes (Walter et al. 1986, Walter 1987, Walter et al. 1989, Walter and Ikonen 1989, Rosenheim et al. 1995, Coll and Guershon 2002, Symondson, et al. 2002). Our ability to develop successful biological control programs may be enhanced by field studies that address the complexity of trophic interactions in agricultural systems (Cohen et al. 1993). Predation rates may differ between laboratory and field because of refugia in soil. Predators and pathogens of insects with both broad and narrow host ranges lead to complex trophic webs (Rosenheim et al. 1995, Coll and Guershon 2002, Symondson, et al. 2002).

Literature regarding the potential impact of microarthropod predators on entomopathogenic nematodes in the soil environment is scarce. Existing studies suggest that predation could affect the efficacy of entomopathogenic nematodes against soil dwelling insect pests. Gilmore and Potter (1993) observed that the

collembolans *Folsomia candida* and *Sinella caeca* consumed IJ of *S. glaseri*, *S. feltiae* and *S. carpocapsae* in plaster of paris/charcoal assay arenas. Both collembolan species readily consumed *S. carpocapsae*. *F. candida* also consumed *S. feltiae* but few *S. glaseri*. There was no evidence of nematode infection in either collembolan. Mortality of *G. mellonella* larvae was inversely related to the length of time that nematodes were exposed to predation by collembolans. As few as 5 *F. candida* significantly reduced nematode-induced mortality of *M. galleria* when exposed to 200 *S. carpocapsae*. However, in more realistic laboratory assays with Japanese beetles in turf, collembolans did not reduce insect mortality from nematodes. The authors suggested that subterranean nematodes may escape predation of collembola on the soil surface. We need to obtain better estimates of predation rates in soil, so that the impact of microarthropods on nematode populations can be predicted with greater certainty.

Nematode behavior may affect contact with predators. Infective juveniles of different nematode species employ different strategies in seeking out an insect host. Host-seeking behavior have been categorized as either “ambushing” or “cruising,” as the two extreme behaviors, or an intermediary of the two (Grewel et al. 1994, Campbell and Gaugler 1997). Ambushing behavior is characterized by IJ positioning vertically on the soil surface in a posture referred to as “nictation.” When a suitable host passes by and makes contact the IJ will attach to the host and proceed to enter the host. This behavior is observed frequently among the Steinernematidae (Kaya and Gaugler 1993, Grewel et al. 1995, Kopenhofer and

Kaya 1996). Alternatively, IJ that exhibit cruising behavior typically leave the soil surface, traveling through soil pores to search for a host underground. Cruising behavior is frequently associated with Heterorhabditid species, although host-searching behaviors typically lie in the continuum between both extreme versions of behavior (Lewis et al 1992, Kaya and Gaugler 1993, Lewis et al. 1993, Grewel et al. 1994, Grewel et al. 1995, Campbell and Gaugler 1997,).

Nematodes are generally assumed to be restricted to existing soil pores and other “soil activity hotspots” (Coleman and Crossley 1995) whereas microarthropods tend to be localized in the uppermost layers of the soil profile, in litter, and along roots. Nematodes with behaviors that keep them near the surface, e.g. *S. carpocapsae*, may be more likely to be preyed upon by microarthropods that tend to occur at the soil surface. Larger nematophages, such as, certain mesostigmatid mites and collembolans, may burrow through the soil (Inserra and Davis 1983, Sell 1988). Some microarthropods are small enough to have access to most of the pore spaces available to nematodes (<450 um length). Their chelicerae are only a few microns in diameter and can be extended to probe smaller pore spaces (Walter and Ikonen 1989). These predators may have access to EPN that move through the soil, e.g. *Heterorhabditis bacteriophora*.

The potential impact of predation on EPN in the soil is also confounded by both physical and biotic complexities of the soil environment. More heterogeneous systems, with less distinct trophic levels, have the capacity to buffer the effects of predation on “lower” trophic levels (Polis and Strong 1996,

Laakso and Setälä 1999). Nutrient-rich systems, such as the surface residue layer of reduced tillage agroecosystems, tend to exhibit more faunal heterogeneity and subsequently, less influence of top-down trophic cascades on the underlying microbe communities. Microbial communities under nutrient-rich conditions exert stronger bottom-up forces, which in turn, contribute to the maintenance of a more heterogeneous system (House and Stinner 1983, Polis and Strong 1996, Neave and Fox 1998, Laakso and Setälä 1999). A diverse food web, including predators, in the soil can also contribute to soil “resistance” to pest outbreaks (Finke and Denno 2002). In contrast, soil systems dominated by one or more specialized predator(s) have been shown to exhibit predation pressure on microbial feeding nematodes. Neither heterogeneous systems, which do not exert significant predation pressure on microbial-feeding nematodes, nor systems dominated by specialist predators affected microbial biomass (Laakso and Setälä 1999).

Most experimentation on the impacts of predation on EPN focus on the consumption of infective juveniles (IJ) by soil-dwelling invertebrates, because this is the form in which nematodes are typically applied commercially.

Recent interest has focused on the use of EPN-infected insect cadavers as a method for applying EPN to the soil. Preliminary trials have yielded superior efficacy in pest suppression in certain cases, when EPN are introduced using this technique (Shapiro-Ilan et al. 2003). Nematodes applied within their infected cadaver are in a much more concentrated state (potentially tens of thousands per cadaver) and they are immersed in large quantities of their symbiotic bacteria

and the metabolites produced by the bacteria (Kaya and Kopenhofner 1996, Shapiro-Ilan et al. 2003). Therefore, to increase efficacy of EPN as a biological control agent, it will be important to know how biotic factors impact both the presence of IJ in the soil, as well as the presence of the nematode-bacteria-cadaver complex (Jansson et al. 1993, Parkman et al. 1993, Shapiro and Glazer 1996, Brown and Gaugler 1997, Kopenhofner et al. 1997, Shapiro and Lewis 1999, Brown et al 2002, Shapiro-ilan et al. 2002, Shapiro-ilan et al. 2003).

Negative or no response of soil fauna to application of entomopathogenic nematodes

A lack of significant response from soil fauna to the application of EPN may be an important consideration in evaluating non-target effects of EPN as a biological control agent (Bathon 1996, Millar and Barbercheck 2002). Negative response of soil fauna to the presence of EPN may indicate characteristics of EPN that exhibit a “repellent” quality (Kaya and Kopenhofner 1996).

Introducing EPN to soil via an infected insect cadaver simulates the way in which EPN enter the soil following a natural insect infection. Entomopathogenic nematodes in this state, however, exist as a complex of the nematodes, their associated symbiotic bacteria, and the compounds produced by the bacteria within their host cadaver (Kaya and Kopenhofner 1996, Kopenhofner et al. 1997, Lewis and Shapiro-Ilan 2002). Therefore, the response of soil fauna to the introduction of the EPN-bacteria-chemical complex cannot be attributed solely to the presence of EPN (Kaya and Kopenhofner 1996), as would be the case when

IJ are applied inundatively. Kaya and Kopenhagenfer (1996) found that compounds produced by *Xenorhabdus spp.* appeared to be effective in inhibiting the growth of *Photorhabdus spp.*, thereby potentially conferring superior competitive ability over *Photorhabdus spp.* (Kaya and Kopenhagenfer 1996). Other compounds associated with *Photorhabdus spp.* appeared to be effective in inhibiting certain antagonists, including some fungi and arthropods (eg. ants) (Kaya and Kopenhagenfer 1996, Baur, et al. 1997, Zhou, X. et al. 2002, Shapiro-Ilan et al. 2003).

Lewis et al. (2001) examined the effect of the EPN, *Steinernema feltiae*, in conjunction with its symbiotic bacteria-exudate complex on a plant-parasitic nematode (*Meloidogyne incognita*). Their data showed that *S. feltiae* applications decrease *M. incognita* galling, egg production per plant, and egg hatch but not individual female egg production (Lewis et al. 2001).

The response of predators to insect larvae infected with EPN in the laboratory suggests that semiochemicals produced by the symbiotic bacteria associated with EPN may play a critical role in the impact of predation on EPN that exist within a host (Kopenhagenfer and Kaya 1996).

Assessment of soil community interactions

An increased focus on soil ecology within agroecosystems has been followed by attempts to assess and understand biotic interactions within the soil community. Whereas most researchers agree on the importance of this objective there is much controversy over how it might be achieved (Mueller et al. 1990,

Edwards 1991, de Goede and Brussard 2002, Scheu 2002), Soil organisms, which are both extremely abundant and diverse, are difficult to observe in their opaque medium. They vary in size over many magnitudes, they span over every known ecological niche, with single organisms often filling more than one niche, and they are extremely patchy in their distribution and sometimes mobile and transient (Mueller et al. 1990, Edwards 1991, Hooper et al. 2000, de Goede and Brussard 2002, Scheu 2002). The use of traditional survey methods to assess the soil community and their interactions is complicated by their diversity and patchy (spatial and temporal) distribution. Typically assessments evaluate soil community interactions at the level of diversity and abundance and often group soil organisms into large taxonomic categories

Abundance and diversity

Soil invertebrates have been traditionally categorized into large taxonomic groups, due to the difficulty in identifying them to lower taxonomic levels. Generalized assumptions are then made about their trophic behavior, as well as their ecological orientation. For example, soil mites are often grouped at the suborder level into the Prostigmata, Mesostigmata, Astigmata (currently contained in the Oribatida), and Oribatida (Cryptostigmata). The Oribatida are generalized as fungal-feeders and the Mesostigmata (except for the uropodids) as predators. These two groups have also often been affiliated with environments produced by no-till or conservation tillage practices (Crossley et al. 1992, Krantz 1978, Lagerlof and Andren 1988). Prostigmatid mites are often

more numerous and diverse in conventional tillage systems and contain representatives of most trophic niches (Van de bund 1970).

More recent studies, however, have attempted to group soil invertebrates into trophic or functional groupings as a way of more accurately assessing ecological interactions in the soil (Walter et al. 1986, Walter and Kaplan 1990, Mueller et al. 1990, Scheu 2002). Whereas this technique may be more effective in defining certain soil community interactions, it is also more difficult and time-consuming as it involves identification of invertebrates to lower taxonomic levels. Different functional groups have been found to occur even within single genera (Mueller et al. 1990, Scheu 2002, Greenwood, unpublished data).

Community composition

To accurately assess interactions at the level of community composition requires a cumbersome amount of time and highly specialized identification skills (Mueller et al. 1990, Scheu 2000). New technologies involving various molecular methodologies, including the use of stable isotopes and fluorescence in situ hybridization are also being considered for the purpose of assessing interactions in the soil community (Scheu 2002). The scarcity of basic biological information on many soil invertebrates also adds to the difficulty in ecological assessments (Mueller et al. 1990, Walter and Kaplan 1990, de Goede and Brussard 2002).

Interactions between soil communities and the abiotic environment

Cultural variables can alter the occurrence of predators and disease in insect populations. One of the cultural practices with the greatest impact in agriculture is tillage. Soils managed by conventional- or reduced-tillage practices have distinct biological and functional properties (Doran 1980, Hendrix et al. 1986). Physical (abiotic) characteristics of soil environments most conducive to producing these types of very diverse communities are often more frequently found in no-till or conservation tillage environments. Temperature and moisture regulating properties that result from a substantial residue layer or from the protection of a cover crop or weed growth can be particularly important for fungal and nematode entomopathogens and arthropods (House and Stinner 1983, Brust 1985, House and Alzugaray 1989, Stinner and House 1990, Barbercheck and Millar 2000, Coll and Guershon 2002, Symondson et al. 2002).

Diversity and abundance of arthropod predators are greater under no-tillage in comparison to conventional tillage and natural control of pest insects in soil may be enhanced in conservation tillage systems (Brust 1985, House and Alzugaray 1989, Stinner and House 1990, Barbercheck unpub., Carmona et al. 1995, Pfiffner and Niggli 1996, Carmona and Landis 1999, Shapiro et al. 1999, Menalled et al. 2000, Hummel et al. 2002, Millar and Barbercheck 2002).

Reduced tillage leaves most of the previous crop's residue on the soil surface, and results in changes in physical and chemical properties of the soil (Blevins et al. 1983). Surface residues retain moisture and dampen temperature fluctuations

which may favor the development of disease in insect populations (Barbercheck 1992, Burges and Hussey 1971, Sloderbeck and Yeargan 1983). These conditions may be conducive to nematode survival and recycling (Brust 1991), but also to generalist predators, which could reduce nematode numbers. In preliminary studies (Barbercheck, unpubl.), there was a trend for the frequency of detection of EPN and number of bait insects killed per sample by EPN that appeared to differ in conventionally tilled soil than in no-till soil. This trend was species-specific, with *Steinernema riobrave* and *Heterorhabditis bacteriophora* favoring conventionally-tilled soil and *Steinernema carpocapsae* (CEFS strain) favoring no-till soil (Millar and Barbercheck 2002).

This research

This research is part of a larger program to evaluate the effects of biotic factors on the biology, fate and efficacy of entomopathogenic nematodes and other beneficial soil organisms. In the research presented here, we focus on the response of soil arthropod fauna to entomopathogenic nematodes. Although these nematodes are available commercially, relatively little is known about the interactions between these nematodes and the rest of the soil community, once they are introduced. Two experiments were conducted to evaluate on the response of soil fauna when entomopathogenic nematodes were introduced to the soil using two different delivery methods. The specific objectives of this research are to answer the questions:

What are the responses of soil invertebrate fauna to the inundative application (commercial isolate) or augmentation (native isolates) of IJ of EPN to the soil?

What is the response of soil invertebrate fauna to the presence of an insect cadaver infected with native or introduced EPN to the soil?

How do tillage practices affect the response of soil invertebrate fauna to application of native and introduced EPN?

References

- Akhurst, R.J.** 1992. An epizootic of *Heterorhabditis* spp. (Heterorhabditidae:Nematoda) in sugar cane Scarabaeidae (Coleoptera). *Fundam. Appl. Nematol.* 15: 71-73.
- Andrén, O. and J. Lagerlöf.** 1983. Soil fauna (microarthropods, enchytraeids, nematodes) in Swedish agricultural cropping systems. *Acta Agricultural Scandinavia* 33: 33-52.
- Balogh, J.** 1972. The oribatid genera of the world. *Akademiai Kiado.* Budapest. 331 pp.
- Barbercheck, M.E. and H.K. Kaya.** 1991a. Effect of host condition and soil texture on host finding by the entomogenous nematodes *Heterorhabditis bacteriophora* (Rhabditida: Heterorhabditidae) and *Steinernema carpocapsae* (Rhabditida: Steinernematidae). *Environ. Entomol.* 20: 582-589.
- Barbercheck, M.E. and H.K. Kaya.** 1991b. Competitive interactions between entomopathogenic nematodes and *Bearveria bassiana* (Deuteromycotina: Hyphomycetes) in soilborne larvae of *Spodoptera exigua* (Lepidoptera: Noctuidae). *Environ. Entomol.* 20: 707-712.
- Barbercheck, M.E. and L.C. Millar.** 2000. Environmental impacts of entomopathogenic nematodes used for biological control in soil. Chapter 17 in: *Nontarget Effects of Biological Control*. P. Follett and J. Duan, eds. Kluwer Academic Publishers.
- Barbercheck, M.E.** 1992. Effect of soil physical factors on biological control agents of soil insect pests. *Fl. Entomol.* 75: 539-548.
- Beare, M.H., P.Hendrix, and D. Coleman.** 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. *Ecol. Monogr.* 62: 569-591.
- Beavers, J.B., C. McCoy and D. Kaplan.** 1983. Natural enemies of subterranean *Diaprepes abbreviatus* (Coleoptera: Curculionidae) larvae in Florida. *Environ. Entomol.* 12: 840-843.
- Belnap, J. and S. L. Phillips.** 2001. Soil biota in an ungrazed grassland: Response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications*, 11 (5): 1261-1275.
- Bilgrami, A.L., Jairajpuri, M.S.** 1989a. Predatory abilities of *Mononchoides longicaudatus* and *M. fortidens* (Nematoda: Diplogasterida) and factors influencing predation. *Nematologica* 35, 475-488.
- Bilgrami, A.L., Jairajpuri, M.S.** 1989b. Resistance of prey to predation and strike rate of the predators *Mononchoides longicaudatus* and *M. fortidans* (Nematoda: Diplogasterida). *Revue de Nematologie* 12, 45-49.
- Blevins, R.L., D. Cook, S. Phillips, R. Phillips and W. Frye.** 1983. Influence of conservation tillage on soil properties. *J. Soil and Water Conserv.* 38: 301-304.
- Bommarco, Riccardo.** 1998. Reproduction and energy reserves of a predatory Carabid beetle relative to agroecosystem complexity. *Ecol. Appl.* 8(3): 846-853.

- Boulton, A.M., B.A. Jaffee, and K.M. Scow.** 2003. Effects of a common harvester ant (*Messor andrei*) on richness and abundance of soil biota. *Applied Soil Ecology* 23: 257-265.
- Brown, V.K. and Gange, A.C.** 1991. Effects of root herbivory on vegetation dynamics. pp. 453-467 in: Atkinson, D. (ed.) *Plant Root Growth: An Ecological Perspective*. Special Publication Number 10 of the British Ecological Society. Blackwell Scientific Publications, Oxford, UK.
- Brown, I.M., Gaugler, R.** 1997. Temperature and humidity influence emergence and survival of entomopathogenic nematodes. *Nematologica* 43, 363-375.
- Brown, I.M., Lovett, B.J, Grewal, P.S., Gaugler, R.** 2002. Latent infection: a low temperature survival strategy in steinernematid nematodes. *Journal of Thermal Biology* 27, 531-539.
- Brust, G.E.** 1985. Tillage and soil insecticide effects on predator-black cutworm interactions in corn agroecosystems. *J. Econ. Entomol.* 78: 1389-1392.
- Brust, G.E.** 1991. Augmentation of an endemic entomogenous nematode by agroecosystem manipulation for the control of a soil pest. *Agric. Ecosyst. Environ.* 36: 175-184
- Campbell, J. and R. Gaugler.** 1997. Interspecific variation in entomopathogenic nematode foraging strategy: dichotomy or variation along a continuum? *Fundamental and Applied Nematology* 20: 393-398.
- Carcamo, H.A., J.K. Niemala, and J.R. Spence.** 1995. Farming and ground beetles: effects of agronomic practice on populations and community structure. *Can. Entomol.* 127:123-140.
- Carmona, D. M., and Landis, D. A.** 1999. Influence of refuge habitats and cover crops on seasonal activity-density of ground beetles (Coleoptera: Carabidae) in field crops. *Biological Control* 28: 1145-1153.
- Christiansen, K.A. and B.F. Bellinger.** 1979. *The Collembola of North America North of the Rio Grande*. Grinnell College, IA.
- Cobb, N.A.** 1917. The mononchs (*Mononchus* Bastian, 1866) a genus of free-living predatory nematodes. *Soil Science* 3: 431-486.
- Coll, M. and M. Guershon.** 2002. Omnivory in terrestrial arthropods: Mixing plant and prey diets. *Annu. Rev. Entomol.* 2002. 47: 267-297.
- Coleman, D.C. and D.A. Crossley Jr.** 1996. *Fundamentals of Soil Ecology*. Academic Press. 205pp.
- Crossely, D.A., Jr., Coleman D. and E. Odum.** 1992. Biodiversity of microarthropods in agricultural soils: relations to processes. *Agric. Ecosys. Environ.* 40: 37-46.
- De Goede, R.G.M. and L. Brussard.** 2002. Soil zoology: An indispensable component of integrated ecosystem studies. *European J. Soil Biology* 38 (2002): 1-6.
- Dindal, D.L.** 1990. *Soil Biology Guide*. New York: John Wiley and Sons.
- Edwards, C.A.** 1991. The assessment of populations of soil-inhabiting invertebrates. *Agriculture, Ecosystems and Environment* 34: 145-176.
- Ettema, C.H. and D. A. Wardle.** 2002. Spatial soil ecology. *TRENDS in Ecology and Evolution* Vol. 17. No. 4 April 2002: 177-183.

- Ferriss, R.S.** 1984. Effects of microwave oven treatment on microorganisms in soil. *Phytopathology* 74: 121-126.
- Georgis, R.** 1992. Present and future prospects for entomopathogenic nematode products. *Biocontrol. Sci. Tech.* 2: 83-99.
- Gilmore, S.K. and D.A. Potter.** 1993. Potential role of Collembola as biotic mortality agents for entomopathogenic nematodes. *Pedobiologia* 37: 30-38.
- Glazer, I., E. Kozodoi, L. Salame, and D. Nestel.** 1995. Spatial and temporal occurrence of natural populations of *Heterorhabditis* spp. (Nematoda: Rhabditida) in a semiarid region. *Biol. Control* 6: 130-136.
- Grewel, P., E. Lewis, J. Campbell, and R. Gaugler.** 1994. Searching behavior as a predictor of foraging strategy for entomopathogenic nematodes. *Parasitology* 108: 207-215.
- Grewel, P., R. Gaugler, and R. Georgis.** 1995. Predictors of foraging strategy in entomopathogenic nematodes. In: *Ecology and Transmission Strategies of Entomopathogenic Nematodes*. C.T. Griffin, R.L. Gwynn and J.P. Masson, eds. European Commission Luxembourg. pp 95-104.
- Hechler, H.C.** 1963. Description, developmental biology and feeding habits of *Seinura tenuicaudata* (DeMan) J.B. Goodey, (1960). (Nematoda: Aphelenchoididae) a nematode predator. *Proceedings of the Helminthologica Society of Washington* 30: 182-195.
- Hendrix, P.F., R. Parmalee, R. Crossley, D. Coleman, E. Odum and P. Groffman.** 1986. Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience* 36: 374-380.
- Hooper, D., D.E. Bignell, V.K. Brown, L. Brussard, J.M. Dangerfield, D.H. Wall, D.A. Wardle, D.C. Coleman, K.E. Giller, P. Lavelle, W.H. Van der Putten, P.C. DeRuiter, J. Rusek, W.L. Silver, J.M. Tiedje, and V. Wolters.** 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: Patterns, Mechanisms, and Feedbacks. *BioScience* Vol. 50 No. 12: 1049-1061.
- House, G.J. and M.D.R. Alzugaray.** 1989. Influence of cover cropping and no-tillage practices on community composition of soil arthropods in a North Carolina agroecosystem. *Environ. Entomol.* 18: 302-307.
- House, G.J. and B.R. Stinner.** 1983. Arthropods in no-tillage soybean agroeco-systems: Community composition and ecosystem interactions. *Environmental management* 7(1): 23-28.
- Huhta, V., P. Sulkava and K. Viberg.** 1998. Interactions between enchytraeid (*Cognettia sphagnetorum*), microarthropod and nematode populations in forest soil at different moistures. *Applied Soil Ecology*: 53-58.
- Hummel, R.L.** 2000. Tillage, insecticide inputs, crop rotation and intercropping: Factors that affect insect pests and natural enemies in vegetable systems in western North Carolina. PhD dissertation. North Carolina State Univ.
- Hummel, R.L., J. F. Walgenbach, M.E. Barbercheck, G.G. Kennedy, G.D. Hoyt, and C. Arellano.** 2002. Effects of production practices on soil-borne entomopathogens in western North Carolina vegetable systems. *Environ. Entomol.* 31 (1): 84-91.

- Jansson, R.K., Locrone, S.H., Gaugler, R.** 1993. Field efficacy and persistence of entomopathogenic nematodes (*Rhabditida: Steinernematidae, Heterorhabditidae*) as biological control agents of the sweetpotato weevil (*Coleoptera: Apionidae*) in southern Florida. *J. Econ. Entomol.* 86:1055-1063.
- Kaya, H.K. and R. Gaugler.** 1993. Entomopathogenic nematodes. *Ann Rev. Entomol.* 38: 181-206.
- Kaya, H. and S. Stock.** 1997. Techniques in insect nematology in: *Manual of Techniques in Insect Pathology*. L.A. Lacey, ed. Academic Press. London. Pp. 281-324.
- Kajak, A. and H. Jakubczyk.** 1977. Experimental studies on predation in the soil-litter interface. *Ecol. Bull.* (Stockholm) 25: 493-496.
- Koppenhöfer A.M, and H. Kaya.** 1996. Coexistence of entomopathogenic nematode species (*Steinernematidae* and *Heterorhabditidae*) with different foraging behavior. *Fundamentals of Applied Nematology* 19: 175-183.
- Koppenhöfer A.M., Baur, M.E., Stock S.P., Choo H.Y., Chinnasri B., Kaya, H.K.** 1997. Survival of entomopathogenic nematodes within host cadavers in dry soil. *Applied Soil Ecology* 6, 231-240
- Krantz, G.W.,** 1978. *A Manual of Acarology*. (second edition), Oregon State University Press. Corvallis, Oregon. 509 pp.
- Laakso, J. and H. Setälä.** 1999. Population and ecosystem level effects of Predation on microbial-feeding nematodes. *Oecologia* 120: 279-286.
- Lagerlof, J. and O. Andren.** 1988. Abundance and activity of soil mites (Acari) in four cropping systems. *Pedobiologia* 32: 129-145.
- Lewis, E., R. Gaugler and R. Harrison.** 1992. Entomopathogenic nematode host finding: response to host contact cues by cruise and ambush foragers. *Parasitology* 105: 309-319.
- Lewis, E., R. Gaugler and R. Harrison.** 1993. Response of cruiser and ambusher entomopathogenic nematodes (*Steinernematidae*) to host volatile cues. *Canadian Journal of Zoology* 71: 765-769.
- Lewis, E.E., P.S. Grewal, and S. Sardanelli.** 2001. Interactions between the *Steinernema feltiae-Xenorhabdus bovienii* insect pathogen complex and the root knot nematode *Meloidogyne incognita*. *Biological control.* 21 (1). May 2001: 55-62.
- McCoy, C.W., Shapiro, D.I., Duncan, L.W.** 2000. Application and evaluation of entomopathogens for citrus pest control. In: Lacey, L., Kaya, H.K. (Eds.), *Field Manual of Techniques in Insect Pathology*, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 577-596.
- Menalled, F., D. Landis, J. Lee, S. White, and K. Renner.** 2000. Ecology and management of weed seed predators in Michigan agroecosystems. *MSU Extension bulletin E-2716*
- Mikola, Juha and H. Setälä.** 1998. No evidence of trophic cascades in an Experimental microbial-based soil food web. *Ecology* 79(1): 153-164.
- Millar, L.C. and M.E. Barbercheck.** 2002. Effects of tillage practices on Entomopathogenic nematodes in a corn agroecosystem. *Biological Control* 25: 11-20.

- Mueller, B.R., M.H. Beare and D.A. Crossley, Jr.** 1990. Soil mites in detrital food webs of conventional and no-tillage agroecosystems. *Pedobiologia* 34: 389-401.
- Murphy, P.W., Doncaster C.C.** 1957. A culture method for soil meiofauna and its application to the study of nematode predators. *Nematologica* 2, 202-214.
- Neave, P. and C.A. Fox.** 1998. Response of soil invertebrates to reduced tillage systems established on a clay loam soil. *Applied Soil Ecology* 9: 423-428.
- Neher, D. and M. Barbercheck.** 1990. Diversity and function of soil mesofauna. Chapter 3 of: *Biodiversity in Agroecosystems*. W.W. Collins and C.O. Qualset, eds. CRC Press.
- Nelmes, A.J., McCulloch, J.S.** 1975. Numbers of mononchid nematodes in soils sown to cereals and grasses. *Annals of Applied Biology* 79, 231-242.
- Ostfield, R.S and F. Keesing.** 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *TREE* Vol. 15 No. 6. June 2000: 232-238.
- Parkman, J.P., Hudson, W.G., Frank, J.H., Nguyen, K.B., Smart, G.C.** 1993. Establishment and persistence of *Steinernema scapterisci* (Rhabditida:Steinernematidae) in field populations of *Scapteriscus spp.* mole crickets (Orthoptera: Gryllotalpidae). *J. Entomol. Sci.* 28:182- 190.
- Pfiffner, L. and U. Niggli.** 1996. Effects of bio-dynamic, organic and conventional farming on ground beetles (Colembola: Carabidae) and other epigeaic arthropods in winter wheat. *Biol. Agric. Hort.* 12: 353-364.
- Pimm, S.L.** 1982. *Food webs*. Chapman and Hall, NY. 219 pp.
- Raulston, J.R. et al.** 1992. Prepupal and pupal parasitism of *Helicoverpa zea* and *Spodoptera frugiperda* (Lepidoptera: Noctuidae) by *Steinernema* sp. in cornfields in the lower Rio Grande valley. *J. Econ. Entomol.* 85: 1666-1670.
- Rosenheim, J.A., H.K. Kaya, L.E. Ehler, J.J. Marois and B.A. Jaffee.** 1995. Intraguild predation among biological-control agents: Theory and evidence. *Biological Control* 5: 303-335.
- Scheu, Stefan.** 2002. The soil food web: Structure and perspectives. *European J. of Soil Biology* 38: 11-20.
- Shapiro-Ilan, D.I., Gaugler, R.** 2002. Production technology for entomopathogenic nematodes and their bacterial symbionts. *J. Ind. Microbiol. Biot.* 28: 137-146.
- Shapiro, D. I., Glazer, I.** 1996. Comparison of entomopathogenic nematode dispersal from infected hosts versus aqueous suspension. *Environ. Entomol.* 25: 1455-1461.
- Shapiro D.I., Lewis E.E.** 1999. Comparison of entomopathogenic nematode infectivity from infected hosts versus aqueous suspension. *Environ. Entomol.* 28: 907-911.
- Shapiro-ilan, D., E.E. Lewis, S.W. Youngsoo, and L. Tedders.** 2003. Superior efficacy observed in entomopathogenic nematodes applied in infected host cadavers compared with application in aqueous suspension. *J. of Invertebrate Pathology* 83 (3) July 2003: 270-272.

- Shapiro, D.I., Obrycki, J.J., Lewis, L.C. and Jackson, J.J.** 1999. Effects of crop residue on the persistence of *Steinernema carpocapsae*. *J. Nematol.* 31: 517-519.
- Sloderbeck, P.E. and K.V. Yeargen.** 1983. Green cloverworm populations in conventional and double-cropped no-till soybeans. *J. Econ. Entomol.* 76: 785-791.
- Smits, P.** 1996. Post-application persistence of entomopathogenic nematodes. *Biocontrol Science and Technology* 6: 379-387.
- Steen, E.** 1983. Soil animals in relation to agricultural practices and soil productivity. *Swedish J. Agricultural Res.* 13: 157-165.
- Stinner, B.R. and G.J. House.** 1990. Arthropods and other invertebrates in conservation-tillage agriculture. *Ann. Rev. Entomol.* 35: 299-318.
- Symondson, W.O.C., K.D. Sunderland and M.H. Greenstone.** 2002. Can Generalist predators be effective biocontrol agents? *Annu. Rev. Entomol.* 2002, 47: 561-594.
- Thorne, G.** 1927. The life history, habits and economic importance of some mononchs. *J. Agric. Res.* 34:265-286.
- Van de Bund, C.F.** 1970. Influence of crop and tillage on mites and springtails in arable soil. *Neth. J. Agric. Sci.* 18: 308-314.
- Van der Werf, W.** 1995. Concepts and prospects for modelling the efficacy and ecology of entomopathogenic nematodes. Pp. 42-51 in Ecology and transmission strategies of entomopathogenic nematodes, **C.T. Griffen, R.L. Gwynn and J.P. Masson** (eds.) European commission , Luxembourg.
- Walter, D.E, R.A. Hudgens, and D.W. Freckman.** 1986. Consumption of nematodes by fungivorous mites, *Tyrophagus* spp. (Acarina: Astigmata: Acaridae). *Oecologia* (Berlin) 1970: 357-361.
- Walter, D.E.** 1987. Trophic behavior of "mycophagous" microarthropods. *Ecology* 68(1): 226-229.
- Walter, D.E. and E.K. Ikonen.** 1989. Species, guilds, and functional groups: taxonomy and behavior in nematophagous arthropods. *J. Nematol.* 21: 315-327.
- Walter, D.E., J.C. Moore, and S.J. Loring.** 1989. *Symphylela* sp. (Symphyla: Scolopendrellidae) predators of arthropods and nematodes in grassland Soils. *Pedobiologia* 33: 113-116.
- Walter, D.E. and D.T. Kaplan.** 1990. Feeding observations on two astigmatic mites, *Schwiebea rocketti* (acaridae) and *Histiostoma bakeri* (Histiostomatidae) associated with *Citrus* feeder roots. *Pedobiologia* 34: 281-286.
- Yeates, G.W.** 1984. Variation in soil nematode diversity under pasture with soil and year. *Soil Biol. Biochem.* 16: 95-102.

Chapter 2 Response of soil fauna to inundative application of entomopathogenic nematodes

Abstract

Entomopathogenic nematodes (EPN) in the families Steinernematidae and Heterorhabditidae occur naturally in the soil, are world-wide in distribution and have been produced commercially for use in soil-dwelling pest suppression. Current re-evaluation of traditional synthetic soil-dwelling pest suppression agents has increased interest in soil ecology and the use of biological pest suppression. The use of EPN for soil-dwelling pest suppression requires evaluation that extends beyond simple efficacy. The introduction of EPN to a soil community can elicit a variety of responses, positive or negative, from the existing soil fauna. Interactions between EPN and the existing soil community require thorough evaluation, both in terms of effects on EPN persistence, and on potential impacts to the soil community.

Response of soil fauna to the application of EPN to both no-till and conventional-till corn was evaluated at the levels of abundance, diversity and community composition. Entomopathogenic nematodes were applied to the soil in aqueous solution as is commonly prescribed commercially for biological control applications. Infective juveniles of three different strains of EPN were suspended in water at the rate of 2.5 billion per hectare. The experiment was designed as a stripped split split plot over four blocks. Nematodes were applied on 3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01. Variables included: 4

blocks x 2 tillage regimes x 2 sampling times (4hours and 24 hours after application time) x 5 treatments. The treatments included: three nematode species treatments *Heterorhabditis bacteriophora* CEFS strain, *Steinernema riobrave* (commercially available but does not naturally occur in NC), and *Steinernema carpocapsae* CEFS strain and two control treatments, soil only, and an application of water without EPN. Response of soil fauna was measured at the levels of abundance (large traditional taxonomic affiliations of soil invertebrates), diversity, and community composition.

Experimental factors including sampling date and time, tillage regime, and blocks, as well as their interactions, significantly affected abundance, diversity and community composition of soil invertebrates at all levels. Significant changes in abundance due to the effect of treatment were also found in both large taxonomic groupings and in finer taxonomic categories. Certain taxa decreased in abundance in the presence of EPN while others increased. Differences in abundance of taxa due to nematode treatments were also found to differ within different tillage regimes and at different sampling times and sampling dates. Large taxonomic groupings of invertebrates exhibited responses that differed significantly from the responses of individual taxa within those large groupings.

Introduction

Soil organisms provide the foundation for such critical processes as soil structure development, nutrient cycling, decomposition, and biological control. To move toward the goal of sustainable agriculture, growers will need to manage

soil organisms to promote nutrient cycling and suppress pests. Currently, many soil-borne insect pests are managed by the application of soil insecticides. Under current federal re-evaluation many soil insecticides will no longer be available for use in many crops. Therefore, biological and cultural pest management alternatives will be needed. Naturally occurring predatory microarthropods and entomopathogenic nematodes can serve as an effective force in regulating soil-dwelling arthropod pest species (House and Stinner 1983, Rosenheim et al. 1995, Barbercheck and Millar 2000). To reduce the use of synthetic inputs it will be especially important to understand how agricultural production systems and practices affect beneficial and pest organisms. This information can be used to devise ways to exploit beneficial soil organisms and properties, suppress pests, and enhance soil quality and agricultural sustainability.

A biotic characteristic of soil quality that is of particular interest in an agriculture is the ability of the soil to suppress or regulate the populations of soil-dwelling invertebrate pests of agriculture. A thriving heterogeneous community of soil organisms typically includes a wide range of predators, parasites and pathogens that aid in the suppression or regulation of agricultural pests (House and Stinner 1983, Mueller et al. 1990, Coll and Guershon 2002, Symondson, et al. 2002, Hummel et al 2002, Millar and Barbercheck 2002).

Abiotic characteristics of soil environments most conducive to producing these types of very diverse communities are frequently found in no-till or conservation tillage management systems (Barbercheck 1992, Brown and

Gaugler 1997). Temperature and moisture regulating properties that result from a substantial residue layer or from the protection of a cover crop or weed growth are particularly important for fungal and nematode entomopathogens, and predatory microarthropods (House and Stinner 1983, Brust 1985 and 1991, House and Alzugaray 1989, Stinner and House 1990, Carcamo et al. 1995, Carmona and Landis 1999 Barbercheck and Millar 2002, Coll and Guershon 2002, Symondson et al. 2002).

Entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae are widely distributed throughout the world and have been isolated from many types of natural and managed habitats in a wide variety of soil types (Kaya and Gaugler 1993). These nematodes function as a naturally-occurring biological control agent of insects that live or spend part of their lives in the soil.

Several entomopathogenic nematode species are commercially available for use against soil arthropod pests and are applied as an aqueous solution of infective juveniles to the soil. Efficacy of commercially applied nematodes is variable and it is still unresolved by what process and at what rate entomopathogenic nematodes are “lost” in the soil after application. Recoveries directly after application can be less than 50%. This rapid decline in numbers of EPN may be due to biotic factors, including predation (Jansson et al. 1993, Van der Werf et al. 1995, Smits 1996, Laakso and Setälä 1999).

The occurrence of organisms in the soil can be altered by many cultural variables. One of the practices with the greatest impact in agriculture is tillage

(Shapiro et al. 1999). Plant residue is distributed throughout the plowed layer in fields managed with conventional tillage. Reduced tillage leaves most of the previous crop's residue on the soil surface, and results in changes in physical and chemical properties of the soil (Blevins et al. 1983). Conditions resulting from surface residues that retain moisture and dampen temperature fluctuations may favor the development of disease in insect populations (Sloderbeck and Yeagan 1983 Hummel et al. 2002, Millar and Barbercheck 2002).

Understanding the biology and fate of the nematodes in the soil environment is critical to improving their predictability as a biological control agent (Laakso and Setala 1999, Mueller et al. 1990). With a better understanding of the ecology of these nematodes and the impact of agricultural practices, e.g., tillage, we may be able to enhance the efficacy of endemic entomopathogenic nematodes or better predict the efficacy of applied nematodes for soil pest management, and their potential for non-target effects (Bathon 1996).

Here we report the response of soil fauna introduced to the soil as infective juveniles in solution at the rate prescribed for commercial application.

We also examine how different tillage practices affect soil biota in reference to the conservation of beneficial entomopathogenic nematodes and the abundance and diversity of soil microarthropods.

Materials and methods

Field site

This research was conducted at the Center for Environmental Farming Systems (CEFS), near Goldsboro, North Carolina in the no-till and conventional-till corn plots that are part of a larger randomized complete block design experiment (Millar and Barberchek 2002) referred to as the Tillage Unit (Appendix B). Conventional-till plots are chisel plowed and disked in the fall and disked in the spring.

Portions of the field used for this study were treated with fertilizer and herbicides, but were not treated with soil insecticides. Soil type at the site is predominantly Wickham fine sandy loam. Rainfall and air temperatures are monitored at the CEFS.

Production of entomopathogenic nematodes

Three isolates of entomopathogenic nematodes were used in this research: *Heterorhabditidae bacteriophora*, and *Steinernema carpocapsae* (isolated from the research site), and *Steinernema riobrave*, originally from Texas, which we included to discern differences in effects of using native versus introduced biological control agents. All nematodes were reared in the lab using larvae of the Greater Wax Moth (*Galleria mellonella*) as the host species. Nematodes in water were maintained in tissue culture flasks cultured at 10° C for no longer than two weeks before use (Murphy and Doncaster 1957, Kaya and Stock 1997).

Microplot inundations (1999, 2000 and 2001)

Experiments were initiated on August 3, 1999, May 23, June 21 and August 1 of 2000, and, June 4 and July 2 of 2001. Treatments were applied to microplots consisting of the circular area (4.94 cm^2) contained within a 2.5cm diameter, 5cm length, cylindrical soil core when it was placed on the surface of the soil. Consistent with the commercial rate of application, 124 nematodes were suspended (and applied) in 15ml of water to each microplot. This rate is equivalent to the commonly recommended commercial rate of 2.5 billion per hectare. During each application microplots were delineated by placing a metal cylinder on the soil surface and pushing it in slightly so it would contain the nematode solution while it soaked into the ground. The cylinder was removed after all of the liquid soaked into the soil. This microplot was then designated with a flag and the imprint of the soil corer remained to mark the location of the treatment. Six repetitions of each nematode application were made for each of 5 treatments. The treatments included three nematode species (*Heterorhabditis bacteriophora* (CEFS strain), *Steinernema riobrave* (commercially available but does not naturally occur in NC), and *Steinernema carpocapsae* (CEFS strain) and two control treatments. The controls consisted of a sample of undisturbed soil removed with the metal cylinder from a location within the plots but not previously disturbed), and, a sample of soil treated with just 15ml of water (water only control) to help separate the effects of soil moisture on the response of soil invertebrates from the response of invertebrates to the presence of IJ.

The design of this experiment was a stripped split split plot over four blocks. Four 0.25 hectare corn fields served as blocks. Each of the corn fields was divided into a no-till (NT) and conventional-till (CT) field in each block.

Sites of treatment application were selected in areas of uniform soil and placed at 1-meter intervals within three randomly chosen corn rows, with one corn row between each treatment row. Ten microplots were set up in each tillage treatment so that half could be sampled four and 24 hrs after application, respectively. The soil sample consisted of one soil core containing the entire contents of the microplot (150 ml soil) in which nematodes or control treatments were applied. Each soil core was placed in a zip-lock bag, labeled and protected from heat and light for transit to the laboratory for extraction of microarthropods.

This design yielded a total of 480 observations per experiment (2 tillage treatments x 4 blocks x 5 treatments x 2 time increments x 6 repetitions = 480 samples). This experiment was repeated on 1 date in 1999, 2 dates in 2000 and 2 dates in 2001 (during the summer growing season) for a total of 6 replicate dates.

Extraction of microarthropods from soil

Single soil cores were placed in modified Tullgren funnels (Coleman and Crossley 1996) for five days during which soil microarthropods were collected in 70% alcohol in vials attached to the bottom of the funnels. Microarthropods were enumerated and prepared for identification. Complete specimens from alcohol were mounted on microscope slides in Berlese's fluid (8g gum acacia, 8 ml distilled water, 5 ml glycerol, 70 g chloral hydrate, 3 ml glacial acetic acid).

Taxonomy followed keys in Dindal (1990), Christiansen and Bellinger (1979), Balogh (1972) and materials from the Summer Program in Acarology at the Ohio State University.

Statistical analysis

The overall design of the tillage study at the CEFS is a randomized complete block design with four replicates of each treatment. This experiment was laid out as a split split plot in four blocks, with whole plot factor tillage (NT and CT), subplot factor treatment (3 EPN and two controls), and sub-sub-plot factor time (4 and 24 hour).

Data were transformed (arcsine for proportions, square root or log for counts) and subjected to contrasted ANOVA. All data were analyzed using the general linear model procedure (PROC GLM, SAS Institute 1996), and means were separated with the least significant difference procedure (LSD SAS Institute 1996) (Appendices C and D). To address the three objectives, we compared abundance, diversity measures and community composition of soil micro-invertebrates. Untransformed data are presented in all tables and figures.

Abundance

Abundance data consisted of an evaluation of invertebrates collected and grouped at a higher taxonomic level. Invertebrates were grouped into six categories. All soil mites (Arachnida: Acari) were grouped separately into four suborders, Mesostigmata, Oribatida, Prostigmata and Astimata (currently contained within the Oribatida). The other two categories contained the remaining types of invertebrates. A few non-arthropods (predatory nematodes,

segmented worms, such as annelids and enchytraeids, and myriapods) were also collected. These, along with non-mite arthropods were divided into the Collembola (most abundant invertebrates after soil mites), and, “other invertebrates” which included the other soil arthropods and non-arthropod invertebrates. The sum of all individuals contained in these 6 categories constituted a seventh category entitled “total invertebrates” (Table-2-1). These large groupings based on taxonomic affiliation have been traditionally used as a means of sorting and grouping soil organisms to evaluate soil community interactions (Krantz 1978, Lagerlof and Andren 1988, Mueller et al. 1990, Walter and Kaplan 1990, Crossley et al. 1992, de Goede and Brussard 2002). All seven categories were subjected to statistical analysis using ANOVA and the General Linear Model procedure (PROC GLM, SAS Institute 1996), and means were separated with the least significant difference (LSD SAS Institute 1996).

Major factors in the model evaluated included date of experiment, block, time, 4 hours or 24 hours after EPN application, tillage type (no-till=NT and conventional-till=CT corn fields), and treatment (Soil control, Water only control, Sc = *Steinernema carpocapsae* CEFS strain, Rb = *Steinernema riobrave* (commercial strain), and Hb = *Heterorhabditis bacteriophora* CEFS strain). Planned contrasts within treatments were made to further evaluate how individual taxa responded to specific treatments. Controls were contrasted against each other and against nematode treatments, and nematode treatments were contrasted against each other. Interactions involving major factors (eg.

Date*time) or major factors and treatment (eg.Till*trt) were also evaluated (p<0.05).

All analyses of major factors, interactions and contrasts, and corresponding error terms are exhibited in the generic GLM model (Appendix S).

Diversity

Diversity was evaluated as richness (S), or number of taxa, and evenness (relative abundance of individuals among the taxa detected), and also by incorporating measures of richness and evenness using five different diversity indices (Ludwig and Reynolds 1988): Simpson's index (Simpson 1949), Shannon's index (Shannon and Weaver 1949), Hill's diversity numbers (1 and 2) (Hill 1973) and evenness. The following formulas were used:

$$\text{Simpson's index } D = \sum_{i=1}^S n_i(n_i-1)/n(n-1)$$

$$\text{Shannon's index } H' = -\sum_{i=1}^S [(n_i/n)\ln(n_i/n)]$$

$$\text{Evenness} = \ln(N2)/\ln S$$

$$\text{Hill's 1} = N1 = e^{H'}$$

$$\text{Hill's 2} = N2 = 1/D$$

$$\text{Number of taxa} = S$$

$$\text{Number of taxa in each sample} = n$$

Community composition

Diversity and abundance evaluations at the finest level of taxonomic classification focused in on specific interactions involving specific taxa within

treatments and other experimental factors. Evaluations were made of major physical experimental factors, as well as experimental treatment factors. Major factors evaluated included: Date (sampling date), block (experimental treatments were repeated in each of four different blocks), time (length of time after nematode application that soil was sampled, 4 hours or 24 hours), tillage type (experimental treatments were applied in both no-till=NT and conventional-till=CT corn fields), and treatment (5 treatments were applied: Soil (control), Water (same amount of water applied without nematodes in solution served as a water control), Sc =*Steinernema carpocapsae* CEFS strain, Rb=*Steinernema riobrave* (commercial strain), and Hb=*Heterorhabditis bacteriophora* CEFS strain). Contrasts within treatments were made to further evaluate how individual taxa responded to specific treatments. Controls were contrasted against each other and against nematode treatments, and nematode treatments were contrasted against each other. Interactions involving major factors (eg. Sampling date by sampling time = Date*time) or major factors and treatment (eg. Tillage type by treatment = Till*trt) were also evaluated ($p < 0.05$).

All analyses of major factors, interactions and contrasts, and corresponding error terms are exhibited in the generic GLM model (Appendices C, D and S).

Invertebrates collected in this experiment were identified to 131 different taxa. Due to the patchy distribution and scarcity of many of these taxa (some represented by only one or a few individuals) they were grouped into 49 representative categories (each category containing at least 100 individuals) for

statistical analyses, using ANOVA and the General Linear Model procedure (PROC GLM, SAS Institute 1996), and means were separated with the least significant difference (LSD SAS Institute 1996) (Appendices C, D and S). The 49 representative groups were maintained at the lowest taxonomic level that would meet the criterion of a minimum of 100 individuals. Therefore, most groups are maintained as genera or families. In the Mesostigmata, the “other Mesostigmata” category contains unidentified adult male mesostigmatid mites, and individuals of rare (less than a total of one hundred individuals over all replicate dates) and obscure taxa. In the Oribatida, Astigmata and Prostigmata the “other oribatids,” “other astigmatids,” and “other prostigmatids” consist primarily of rare taxa (genera or families represented by just a few individuals),

This combination of data provided information on the response of indigenous soil fauna to the application of native and introduced nematodes.

Results

A total of 44,996 individual invertebrates summed over 6 sampling dates, 2 sampling times, 2 tillage regimes and 5 treatments during 1999, 2000 and 2001. These individuals were identified in to 131 taxa.

Abundance

Sampling date significantly affected abundance of all seven large groups at the 95% confidence level. Block effects of $Pr < F = < 0.0001$ were evident for all four groups of soil mites (Mesostigmata, Oribatida, Prostigmata and Astigmata) and in the other invertebrates. Block I contained the largest total

abundance of invertebrates. The Astigmata were most abundant in block I, Mesostigmata and Oribatida were most abundant in block III and the Prostigmata were most abundant in block II. Block effects were not significant for Collembola and total invertebrates (Figure 2-1).

Significant effects due to tillage occurred in the categories Total invertebrates, oribatid mites, astigmatid mites, Collembola and other invertebrates. All major groups, except for the Prostigmata had higher abundance in no-till (Table 2-2, Table 2-3, Table 2-4, Table 2-5) than in conventional-till corn. The factor of time after nematode application was significant at $p < 0.05$ for all major groups except Prostigmatid mites. All major groups were higher in abundance at 4 hours than at 24 hours (Table 2-2, Table 2-3, Table 2-4, Table 2-5).

Interactions among some of the major factors also proved to have significant effects on abundance of certain large groupings of invertebrates. The interaction of time*date was universally significant among all groups at the $p < 0.0001$ level. Tillage*date was also highly significant for all groups. Tillage*time was significant in the mesostigmatid mites and the Collembola. Tillage*nematode treatment was only significant in the oribatid mites (Table 2-2, Table 2-3, Table 2-4, Table 2-5).

Abundance effects due to treatment

Significant effects due to treatment were evident in the categories of Total invertebrates , prostigmatid mites, astigmatid mites and Collembola (Table 2-2, Table 2-3, Table 2-4, Table 2-5) Contrasts between treatments indicated

significant effects either between controls which, in turn, were different from each other, between controls and nematode treatments, or, between nematode treatments. The prostigmatid mites were more abundant in the water control than in the soil control, but less abundant in all three nematode treatments than in either control. The astigmatid mites were more abundant in the three nematode treatments, relative to controls, and more abundant in the water control than in the soil control. Both Collembola and total invertebrates were more abundant in the water control, and less abundant in the soil control, with nematode treatments being intermediate in abundance (Table 2-2, Table 2-3, Table 2-4, Table 2-5).

Interactions between experimental factors involving treatment

Significant effects of soil*water occurred in abundance of total invertebrates, oribatid mites, and Collembola. The abundance of all 3 groups was higher in the water control than in the soil control at both 4 and 24 hours, with the exception of total invertebrates and Collembola, which were more abundant in the soil control at 4 hours. The contrast of soil*nematode treatments was significant in total invertebrates, mesostigmatid mites, prostigmatid mites, astigmatid mites, and Collembola. Of these five groups, the Prostigmata were the only group to show consistently lower abundance in the nematode treatments than in the soil control. The Collembola and mesostigmatid mites had higher abundance in the nematode treatments than in the soil control. Collembola exhibited a particularly strong positive response to nematode treatments in the

conventionally-tilled soil. The astigmatid mites also exhibited higher abundance but were very sporadic in their distribution (Table 2-2, Table 2-3).

The interaction of the water only control*nematode treatment was significant in Total invertebrates and Prostigmatid mites. Prostigmatid mites were consistently less abundant in the nematode treatments than in the water control. Abundance of total invertebrates, however, were less consistent. In conventionally-tilled soil total invertebrates were less abundant in Sc and Rb, and more abundant in Hb, than in the water control, at 4 hours. At 24 hours total invertebrates were less abundant in Hb treatment and more abundant in Rb and Sc, than in the water control. In no-till soil total invertebrates were less abundant in Rb than in the water control at both 4 and 24 hours and less abundant in Sc than in the water control at 24 hours (Table 2-2, Table 2-3).

A contrast of Hb*Sc, Rb was significant for total invertebrates. In conventionally-tilled soil total invertebrates were less abundant in Sc and Rb, and more abundant in Hb at 4 hours, whereas, at 24 hours, they were more abundant in both Sc and Rb than in Hb. In no-till soil total invertebrates were higher in Hb, than Sc and Rb at both 4 and 24 hours (Table 2-2, Table 2-3).

Diversity

All calculated diversity measures revealed differences ($P < 0.01$) due to date (Table 2-11). The interactions of till*date and block*date were also universally significant ($P < 0.01$) for all of the measures of diversity. Significant effects on richness (number of taxa) due to tillage, time, and treatment ($df = 4, 30$ $F = 2.92$, $P = 0.0426$) were evident, as well as an effect due to the interaction of

treatment by sampling date = (df =4,30, F=1.69, P=0.0348). Significant Effects of tillage type, blocks and date of sampling were evident in many of the measures of diversity (Table 2-11).

Community composition

Of the 49 taxonomic groups evaluated in this experiment, 21 exhibited significant effects due to sampling time, 17 taxa exhibited significant effects due to tillage type, 38 taxa exhibited significant effects due to blocks and 39 taxa exhibited significant effects due to sampling date (Appendices F and G). Four taxa showed significant effects due to treatment. These four taxa include one mesostigmatid mite, *Hypoaspis spp.*, immature oribatid mites, Sminthuridae, and adult Coleoptera (Table 2-6).

Community composition effects due to treatment

Taxa significantly affected by treatment (Table 2-6), were subjected to planned contrasts of means between controls and treatments to further evaluate significant effects due to treatment. The mesostigmatid mite, *Hypoaspis spp.* showed a significant response to a contrast of soil vs. water (df=1, 24, F=7.98, p=0.0094), and to the contrast of soil vs. nematode treatments (df=1,24, F=9.44, p=0.0052). Abundance of *Hypoaspis spp.* was much higher in all three nematode treatments, and in water control, than in the soil control at 4 hours in conventional-till. Abundance in the nematode treatments in conventional-till, however, dropped to levels much lower than the soil control at 24 hours (Appendix F). In no-till soil *Hypoaspis spp.* was more abundant in both nematode and water treatments than in soil control at both 4 and 24 hours, but to

a lesser degree at 24 hours (Appendix F). Immature oribatid mites were significantly affected by the contrast of water vs. nematode treatments ($df=1,24$, $F=5.23$, $P=.0313$), and by Rb vs. Hb,Sc ($df=1,24$, $F=8.44$, $P=.0078$). Numbers of immature oribatid mites were much higher in the water, Sc and Rb treatments than in the soil control, at both 4 and 24 hours in conventional-till. In the no-till soil immature oribatids were higher in the soil control than in the water and nematode treatments at 4 hours, and, at 24 hours, the water treatment and Hb treatment were higher than the soil control (Appendix F).

Adult Coleoptera responded significantly to soil vs. water ($df=1,24$, $F=13.06$, $p=.0014$) and to water vs. nematode treatments ($df=1,24$, $F=6.19$, $P=.0202$). In both conventional-till and no-till soil adult Coleoptera were more abundant in the Sc and water treatments, at both 4 and 24 hours, than in any of the other treatments (Appendix F).

Interactions

Interactions involving the significant experimental factors were also generally significant among a majority of the taxa evaluated. Of the 49 taxa evaluated, 40 responded significantly to time*date, 38 responded significantly to till*date, and 9 taxa significantly responded to till*time (Appendices A, F and G,).

Some taxa also exhibited a significant response to interactions involving treatment. Four taxa (*Tectocepheus spp.*, other oribatid mites (a category which included all of the rare oribatid mites), other prostigmatid mites (a category which included all of the rare prostigmatid mites) and Collembola) responded significantly to the interaction of tillage type by treatment (till*trt) (Table 2-8,

Appendices F, H and I). *Tectocephus spp.* were more abundant in the water and nematode treatments in both no-till and conventional-till with the exception of the Rb treatment in no-till where it was lower in abundance. In the conventional-till soil, abundance of *Tectocephus spp.* fluctuated in the Sc treatment (Appendices F, H and I). Other oribatids were more numerous in the water, Sc, Rb and Hb treatments respectively, than in the soil control in conventionally-tilled soil. In no-till soil other oribatids were particularly abundant in the Hb treatment, followed by the soil control and then water, Sc and Rb treatments respectively (Appendix I). Other prostigmatid mites exhibited a very strong negative response to all treatments other than the soil control in no-till soil and very little response to any of the treatments in conventionally-tilled soil (Appendix I). Collembola, likewise, exhibited a strong negative response to all treatments other than the soil control in no-till soil. In conventionally-tilled soil Collembola were much more abundant in water and nematode treatments than in the soil control (Appendix I).

Four taxa (*Nothrus spp.*, *Scheloribates spp.*, Entomobryidae, and immature Diptera) responded to the interaction of sampling time by treatment (time*trt) (Table 2-9, Appendices F, H and J). *Nothrus spp.* were more abundant in the Hb and Rb treatments respectively, followed by Sc, soil and water. At 24 hours after application *Nothrus spp.* were more abundant in all water and nematode treatments than in the soil control (Appendix J). *Scheloribates spp.*, Entomobryidae and immature Diptera all exhibited a fairly consistent negative response to water and nematode treatments at 4 hours and a consistent positive response to the same treatments at 24 hours (Appendix J).

Eight taxa also exhibited significant response to the interaction of treatment by sampling date trt*date (Table 2-10).

Discussion

In laboratory experiments, infective juveniles (IJ) of EPN applied for biological control persist in the soil at very low densities (Kaya and Gaugler 1993). It has been hypothesized that their scarcity, small size and cryptic morphology aid in minimizing their attractiveness to potential predators (Glazer 1996) Environmentally-resistant infective juveniles are protected by the retained 2nd stage cuticle, therefore this stage is less likely to excrete compounds that might potentially attract predators (Glazer 1996). Infective juveniles applied inundatively at the commercial rate of 2.5 billion per hectare are still relatively scarce, compared to the abundance of other soil invertebrates, and research suggests that abiotic factors, such as dessication, exposure to UV, and temperature extremes may have significant impacts on their populations (Smits 1996, Hummel et al 2002).

Rapid declines in nematode numbers immediately following application of infective juveniles in solution are likely due to a combination of environmental factors as well as biotic mortality factors (Smits 1996, Laakso and Setala 1999, Hooper et al. 2000, Coll and Guershon 2002, deGoede and Brussard 2002). Interactions within the soil community, however, tend to be confounded by the complication of indirect effects (Polis 1994, Rosenheim et.al 1995). Therefore, inferences might be made regarding the nature of soil fauna responses, but without further detailed investigation these deductions are inconclusive (Polis

1994, Wootton 1994, Elkschmitt and Griffiths 1998, Andren et al. 1999, Fox and Olsen 2000).

Soil-dwelling microarthropods are generally present in high numbers in both no-till and Conventional-till soil (Appendices E, M). Although different taxa frequent the two different environments, representatives of most functional feeding groups are present in both environments, and many of these functional feeding groups are characterized by the prevalence of omnivory, to include observations of nematophagy (Groffman 1986, Walter and Ikonen 1989, Mueller et al 1990, Gilmore and Potter 1993, Walter et al. 1986).

Soil-dwelling organisms are adapted to the pulsed input of resources typical of most soil environments, and can remain dormant or inactive for long periods of time (Ostfield and Keesing 2000). The application of water, as with inundative application of nematodes, can serve to activate populations of microarthropods and other organisms (Ostfield and Keesing 2000, Brown et al 2002).

Since most of the significant responses of invertebrate taxa to treatments were due primarily to the addition of water to the soil, predation upon nematodes may be more likely a result of chance encounters between EPN and nematophagous microarthropods and nematodes rather than to specific targeting of the infective juveniles. The high numbers of microarthropods and their activation resulting from an input of moisture may provide a significant enough mortality source to reduce EPN populations to a level closer to that at which they naturally occur (Kaya and Gaugler 1993). Abundance data indicates that all 6

major groups of invertebrates (the four major suborders of soil mites: Mesostigmata, Oribatida, Prostigmata and Astigmata, the Collembola, and other invertebrates responded positively to the application of the water only control to the soil, compared to the soil control. The response among these groups, however, to nematodes applied in solution versus water alone, was inconsistent (Table-2-1, Table 2-2, Table 2-3, Table 2-4).

Observed inconsistencies among these groups of soil invertebrates suggest that, while biotic factors may affect inundatively applied EPN populations, these impacts are varied (Appendices F, G and H). Whereas certain large taxonomic affiliations may appear to exhibit some slight trends, the actual interactions that are occurring between EPN and other soil invertebrate fauna may not be accurately reflected in these higher taxonomic groupings (House and Stinner 1983, Mueller et al 1990, Beare et al 1992).

Abundance

Traditional groupings of soil organisms are based on taxonomic affiliation, although emphasis on trophic or behavioral distinction rather than taxonomic affiliation is gaining in popularity (Mueller et al 1990), Abundance analyses in this chapter evaluate soil fauna interactions at the level of traditional large taxonomic groupings. Soil mites (Arachnida: Acari) were the most abundant invertebrates collected (Table-2-1, Table 2-2, Table 2-3). Traditional taxonomic categories for soil mites include the major suborders, Oribatida (Cryptostigmata), Mesostigmata, Prostigmata and Astigmata (currently contained in the Oribatida) (Edwards 1991, Coleman et al. 2002).

The second most abundant invertebrates were the collembolans, which were evaluated at the level of taxonomic order (Collembola). All other invertebrates were present in distinctly lower numbers and were analyzed collectively as “other invertebrates” in the abundance analyses. All of these categories were evaluated at finer taxonomic levels in the community composition analyses of this research.

Experimental factors

Effects of the major experimental factors such as date of experimental replicate, block, time (4 hr or 24 hr) and till (NT or CT) at the level of large taxonomic groupings, were fairly consistent with known literature regarding the biology of these invertebrate groups (Krantz 1978, Edwards et al. 1988, Perdue and Crossley 1990, Edwards 1991, Coleman and Crossley 1996).

Tillage practices are known to have significant effects on soil communities. (House and Stinner 1983, Millar and Barbercheck 2000, Hummel et al. 2002). Conservation tillage practices have been shown, generally, to result in increased abundance and diversity of all of the major groups of invertebrates except the Prostigmata, and sometimes the Astigmata (Belnap and Phillips 2001, Symondson et al. 2002).

In this experiment the major groupings of invertebrates, with the exception of the Prostigmata, were detected in higher abundance and diversity in the no-till soil than in the conventional-till soil (Appendices E, F and G).

Seasonal influences on population dynamics were also visible in the highly significant effect of date of experiment on abundance and diversity of

invertebrates (Appendices E, F and G) and reflect the temporally patchy distribution of soil organisms (Perdue and Crossley 1990).

Almost universally significant effects on abundance due to block (and interactions involving blocks) (Appendices E, F, G and H) are consistent with the tendency of soil organisms to be spatially patchy in distribution and affiliated with certain microhabitat preferences (Coleman and Crossley 1996).

Effects of sampling time (4 hours versus 24 hours), which were also fairly common and consistent, on the abundance of the major groups of invertebrates (Appendices E, F, G and H) may be directly related to the longevity of the effect of adding 15ml of water to a 5cm² area of soil. Moisture is often a limiting resource in soil systems and the addition of moisture may serve as a “pulsed resource” that activates otherwise dormant soil organisms (Ostfield and Keesing 2000). Abundance tended to be higher among all groups at 4 hours than at 24 hours, with the exception of the Collembola in conventionally-tilled soil, which exhibited higher abundance at 24 hours in all treatments (Table 2-2, Table 2-3). Collembolans are adapted to life in the soil environment. Whereas environmental characteristics, such as moisture, substrate and food resources are important factors affecting their distribution, they have been shown to exhibit strong aggregative behaviors (using aggregation pheromones) that seem to play an important role in influencing their distribution (Christiansen 1970, Barra and Christiansen 1975, Coleman and Crossley 1996). It may be that the delayed increased abundance at 24 hours resulted from a release of aggregation pheromone following the initial attraction to an introduced resource.

Treatment effects on abundance

Mesostigmata, Collembola, Oribatida, and other invertebrates responded positively to both the presence of water and of nematode treatments, although the response of oribatid mites was not significantly different between the water control and the nematode treatments. The Mesostigmata, and, particularly, the Collembola exhibited stronger positive responses to the presence of nematodes (Table 2-2, Table 2-3, Table 2-4, Table 2-5).

The Prostigmata was the only group to exhibit consistently lower abundance in nematode treatments than in the soil and water controls. Prostigmatid mites, although a very biologically diverse category, are predominantly fluid-feeders and bacterivores (Walter and Proctor 1999). They may not recognize the “cryptic” IJ as a food source (Glazer 1996). Alternatively, they may be repelled by certain chemical qualities of the IJ, or, by the increased presence of other organisms potentially attracted to the introduced resource of IJ and water.

Mesostigmatid mites, also a very biologically diverse suborder, are predominantly characterized as predators. They are highly mobile and sensitive to vibration in the soil, which they use to detect prey (Walter and Proctor 1999). An increased presence of Mesostigmata may be a direct attraction to a prey source, or, potentially an indirect attraction to some other resource or characteristic resulting from an introduced resource (Walter and Proctor 1999).

Diversity

Measures of biological diversity tend to focus on two attributes of a biological community, species richness (number of taxa present), and, evenness (the relative abundance of the various taxa present) and attempt to combine measurements of both characteristics into a descriptive value (Ludwig and Reynolds 1988). Many mathematical formulas, termed diversity indices, have been derived in an attempt to quantify these ecological characteristics (Ludwig and Reynolds 1988), although they are often difficult to interpret and rarely significant on their own when not in the context of other ecological descriptors, or used in comparison with like measurements, as a relative value. (Hurlbert 1971, Ludwig and Reynolds 1988).

All diversity measures were significantly affected by the experimental factors, such as blocks, date (seasonal fluctuations) and tillage regime. These differences are consistent with differences already depicted in abundance and are also consistent with literature descriptive of invertebrate community characteristics due to factors related to tillage practices (House and Stinner 1983 Elkschmitt and Griffiths 1998, Mueller et al. 1990 Coleman et al. 2002, Scheu, 2002).

Richness was the only measure exhibiting significant effects due to nematode treatment. Higher numbers of taxa were present in both the water treatment and in the nematode treatments versus the soil control (Table 2-11, Figure 2-1, Figure 2-2) on all sampling dates and in both tillage regimes. Soil invertebrates, which inhabit a resource-limited system, are known to exhibit

increased abundance in the presence of an introduced resource. Increased diversity is likely an incidental consequence of increased abundance (House and Stinner 1983, Mueller et al. 1990, Neher and Barbercheck 1990, Elkschmitt and Griffiths 1998, Neave and Fox 1998, Coleman et al. 2002, Scheu 2002), Elkschmitt and Griffiths (1998) characterized the difficulties in assessing effects of species richness within soil communities and described them as context-dependent. They also deduced that species richness within a trophic level works to decrease spatial and temporal functional gaps, and, that nutrient cycling processes within the decomposer food web could be enhanced by species richness within the inclusive trophic levels.

Community composition

Within the representative 49 taxonomic groupings, most exhibited a significant response to the experimental factors (block, date, till, and time) characteristic of the larger taxonomic groupings in the abundance section of this experiment. Effects due to treatment, however, among individual taxa differed from those exhibited at the level of larger taxonomic affiliations (Table 2-2, Table 2-3, Table 2-4, Table 2-8, Table 2-9, Table 2-10, Appendices F, G, H, I, J).

Whereas the Oribatida, as a large traditional grouping, did not exhibit any significant response to treatments, a number of oribatid mites, when evaluated at a lower taxonomic level, did respond to treatment. Many families of oribatid mites have records of nematophagy and even records of increased fecundity when feeding on nematodes versus fungi (Walter et.al. 1986, Walter 1987, Walter and Ikonen 1989).

Tectocepheus spp., the most abundant invertebrate collected, exhibited a significant response to treatment as did the “other oribatids” category, and to the interaction of treatment by date (Table 2-8, Table 2-10, Appendices F, G, H, I, J). Other oribatids were consistently lower in abundance in the nematode treatments versus soil control in the no-till soil, except for an occasional sporadic positive response to Hb treatment, and, consistently higher in abundance in nematode treatments versus soil control in conventionally-tilled soil (Appendix I). This type of variable response may be due to less previous resource availability in conventionally-tilled soil, particularly moisture, since the water treatment produced the highest abundance of oribatid mites followed by the nematode treatments. Alternatively, the relative low abundance in no-till soil may be indicative of some repellent quality of IJ (Kaya and Kopenhofer 1996, Smits 1996).

Immature oribatids mites also exhibited a significant response to the interaction of treatment by date. This response was primarily due to the effect of date. On May 23 2000 an exceptionally high number of immature oribatids were detected with the highest abundance detected in the Hb treatment. (Appendix V). More observations are required, however, to determine if factors related to *H. bacteriophora* IJ are attractive to immature oribatid mites.

Nothrus spp. and *Scheloribates spp.* both exhibited a significant response to the interaction of treatment by sampling time (Table 2-9, Appendices F, G, H, I, J). *Nothrus spp.* increased in abundance in the nematode treatments at the 4 hour sampling time and decreased at the 24-hour sampling time. *Scheloribates*

spp. exhibited the inverse response, i.e., they were less abundant relative to soil control in nematode treatments at 4 hours and more abundant relative to soil control at 24 hours. Morphological differences among the oribatid mites may play a role in their behavior and ecology (Walter and Proctor 1999). *Nothrus spp.* are long-legged fast moving mites, while *Schelorbates spp.* tend to be shorter-legged and more heavily sclerotized (Balogh 1972, Krantz 1978). While inferences about their behavior may be made based upon morphological characteristics, very little is known via observation about the biology of these mites (Walter and Proctor 1999).

Tectocephus spp. exhibited a particularly strong positive response to nematode treatments mainly to the application of Sc treatment in conventionally-tilled soil on two dates (Appendix v). Immature oribatid mites also exhibited a positive response to nematode treatments, particularly Sc and Rb, on a number of dates (Appendix V). Further observations are needed to determine if these taxa of oribatid mites are attracted to steinernematid species and, if so, for what reason?

Within the Prostigmata, the finer category of “other prostigmatid” mites was less informative. As in its taxonomically larger counterpart, it contained a variety of rare and unidentified prostigmatid mites. This group also exhibited a significant response to nematode treatments of the same nature as the Prostigmata in the abundance analyses (Table 2-2, Table 2-3, Table 2-5, Table 2-8, Appendix I). Abundance was significantly lower in all nematode and water treatments than in the soil control in no-till soil. In conventionally-tilled soil there

was no significant difference in abundance among the controls and treatments (Appendix I). Since all groups of invertebrates, other than the Prostigmata, tend to be less abundant in conventionally-tilled soil, it is possible that the decrease of prostigmatid mites in no-till soil is the result of an indirect effect by organisms less prevalent or absent in the conventionally-tilled soil (Polis 1994, Rosenheim et al. 1995). The lack of effect in conventionally-tilled soil also supports this possibility.

Likewise, the finer taxonomic division of Collembola in the community composition analyses (which consisted of a variety of unidentified Collembola, similar to the larger grouping in the abundance analysis) exhibited a response similar to its larger counterpart. A very strong positive response to nematode treatments versus soil control in conventionally-tilled soil could indicate aggregation behavior (Christiansen 1970, Barra and Christiansen 1975, Coleman and Crossley 1996) triggered by some factor related to the introduction of EPN. The strong negative response in no-till soil, however, in which abundance was significantly lower in all treatments versus soil control is interesting and requires further investigation.

The overall response of soil fauna to the inundative application of EPN was generally negligible, rarely differing from the response of soil fauna to the water only control. The tremendous abundance of microarthropods in the soil, however, and their activation resulting from an input of moisture may provide a significant mortality source for EPN (Kaya and Gaugler 1993). The lack of significant response of soil fauna to inundative applications of EPN may have

implications for further evaluation of non-target effects, when EPN are used as a biological control agent (Bathon 1996. Millar and Barbercheck 2002).

Further assessment of soil community interactions resulting from inundative applications of EPN, at the level of community composition, are needed to more fully evaluate both the impact of indigenous soil fauna on EPN populations and the response of soil fauna to the introduction of EPN.

References

- Andrén, O. and J. Lagerlöf.** 1983. Soil fauna (microarthropods, enchytraeids, nematodes) in Swedish agricultural cropping systems. *Acta Agricultural Scandinavia* 33: 33-52.
- Andren, O., L. Brussard, and M. Clarholm.** 1999. Soil organism influence on ecosystem-level processes – bypassing the ecological hierarchy? *Applied Soil Ecology* 11: 177-188.
- Balogh, J.** 1972. The oribatid genera of the world. *Akademiai Kiado.* Budapest. 331 pp.
- Barbercheck, M.E. and H.K. Kaya.** 1991a. Effect of host condition and soil texture on host finding by the entomogenous nematodes *Heterorhabditis bacteriophora* (Rhabditida: Heterorhabditidae) and *Steinernema carpocapsae* (Rhabditida: Steinernematidae). *Environ. Entomol.* 20: 582-589.
- Barbercheck, M.E. and H.K. Kaya.** 1991b. Competitive interactions between entomopathogenic nematodes and *Bearveria bassiana* (Deuteromycotina: Hyphomycetes) in soilborne larvae of *Spodoptera exigua* (Lepidoptera: Noctuidae). *Environ. Entomol.* 20: 707-712.
- Barbercheck, M.E. and L.C. Millar.** 2000. Environmental impacts of entomopathogenic nematodes used for biological control in soil. Chapter 17 in: *Nontarget Effects of Biological Control*. P. Follett and J. Duan, eds. Kluwer Academic Publishers.
- Barbercheck, M.E.** 1992. Effect of soil physical factors on biological control agents of soil insect pests. *Fl. Entomol.* 75: 539-548.
- Barra, J. and K. Christiansen.** 1975. Experimental study of aggregation during the development of *Psuedosinella impediens* (Collembola: Entomobryidae). *Pedobiologia* 15: 343-347.
- Bathon, H.** 1996. Impact of entomopathogenic nematodes on non-target hosts. *Biocontrol Science and Technology* (1996) 6: 421-434.
- Beare, M.H., P.Hendrix, and D. Coleman.** 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. *Ecol. Monogr.* 62: 569-591.
- Beavers, J.B., C. McCoy and D. Kaplan.** 1983. Natural enemies of subterranean *Diaprepes abbreviatus* (Coleoptera: Curculionidae) larvae in Florida. *Environ. Entomol.* 12: 840-843.
- Belnap, J. and S. L. Phillips.** 2001. Soil biota in an ungrazed grassland: Response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications*, 11 (5): 1261-1275.
- Bilgrami, A.L., Jairajpuri, M.S.** 1989a. Predatory abilities of *Mononchoides longicaudatus* and *M. fortidens* (Nematoda: Diplogasterida) and factors influencing predation. *Nematologica* 35, 475-488.
- Bilgrami, A.L., Jairajpuri, M.S.** 1989b. Resistance of prey to predation and strike rate of the predators *Mononchoides longicaudatus* and *M. fortidans* (Nematoda: Diplogasterida). *Revue de Nematologie* 12, 45-49.

- Blevins, R.L., D. Cook, S. Phillips, R. Phillips and W. Frye.** 1983. Influence of conservation tillage on soil properties. *J. Soil and Water Conserv.* 38: 301-304.
- Brown, I.M., Gaugler, R.** 1997. Temperature and humidity influence emergence and survival of entomopathogenic nematodes. *Nematologica* 43, 363-375.
- Brown, I.M., Lovett, B.J, Grewal, P.S., Gaugler, R.** 2002. Latent infection: a low temperature survival strategy in steinernematid nematodes. *Journal of Thermal Biology* 27, 531-539.
- Brust, G.E.** 1985. Tillage and soil insecticide effects on predator-black cutworm interactions in corn agroecosystems. *J. Econ. Entomol.* 78: 1389-1392.
- Brust, G.E.** 1991. Augmentation of an endemic entomogenous nematode by agroecosystem manipulation for the control of a soil pest. *Agriculture, Ecosystems and Environment.* 36: 175-184
- Campbell, J. and R. Gaugler.** 1997. Interspecific variation in entomopathogenic nematode foraging strategy: dichotomy or variation along a continuum? *Fundamental and Applied Nematology* 20: 393-398.
- Carcamo, H.A., J.K. Niemala, and J.R. Spence.** 1995. Farming and ground beetles: effects of agronomic practice on populations and community structure. *Can. Entomol.* 127:123-140.
- Carmona, D. M., and Landis, D. A.** (1999). Influence of refuge habitats and cover crops on seasonal activity-density of ground beetles (Coleoptera: Carabidae) in field crops. *Biological Control* 28: 1145-1153.
- Christiansen, K.** 1970. Experimental studies on the aggregation and dispersion of Collembola. *Pedobiologia* 10: 180-198.
- Christiansen, K.A. and B.F. Bellinger.** 1979. *The Collembola of North America North of the Rio Grande.* Grinnell College, IA.
- Cobb, N.A.** 1917. The mononchs (*Mononchus* Bastian, 1866) a genus of free-living predatory nematodes. *Soil Science* 3: 431-486.
- Coll, M. and M. Guershon.** 2002. Omnivory in terrestrial arthropods: Mixing plant and prey diets. *Annu. Rev. Entomol.* 2002. 47: 267-297.
- Coleman, D.C. and D.A. Crossley Jr.** 1996. *Fundamentals of Soil Ecology.* Academic Press. New York. 205pp.
- Crossely, D.A., Jr., Coleman D. and E. Odum.** 1992. Biodiversity of microarthropods in agricultural soils: relations to processes. *Agric. Ecosys. Environ.* 40: 37-46.
- De Goede, R.G.M. and L. Brussard.** 2002. Soil zoology: An indispensable component of integrated ecosystem studies. *European J. Soil Biology* 38 (2002): 1-6.
- Dindal, D.L.** 1990. *Soil Biology Guide.* John Wiley and Sons. New York.
- Edwards, C., B. Stinner, D. Stinner and S. Rabatan (eds).** 1988. *Biological interactions in soils.* Elsevier Science Pub. Amsterdam.
- Edwards, C.A.** 1991. The assessment of populations of soil-inhabiting invertebrates. *Agriculture, Ecosystems and Environment* 34: 145-176.

- Elkschmitt, K. and Griffiths, B.** 1998. Soil biodiversity and its implications for ecosystem functioning in a heterogeneous and variable environment. *Applied Soil Ecology* 10: 201-215.
- Ettema, C.H. and D. A. Wardle.** 2002. Spatial soil ecology. *TRENDS in Ecology and Evolution* Vol. 17. No. 4 April 2002: 177-183.
- Fox, J. and E. Olsen.** 2000. Food web structure and the strength of transient indirect effects. *Oikos* 90: 219-226.
- Georgis, R.** 1992. Present and future prospects for entomopathogenic nematode products. *Biocontrol. Sci. Tech.* 2: 83-99.
- Gilmore, S.K. and D.A. Potter.** 1993. Potential role of Collembola as biotic mortality agents for entomopathogenic nematodes. *Pedobiologia* 37: 30-38.
- Glazer, I., E. Kozodoi, L. Salame, and D. Nestel.** 1995. Spatial and temporal occurrence of natural populations of *Heterorhabditis* spp. (Nematoda: Rhabditida) in a semiarid region. *Biol. Control* 6: 130-136.
- Grewel, P., E. Lewis, J. Campbell, and R. Gaugler.** 1994. Searching behavior as a predictor of foraging strategy for entomopathogenic nematodes. *Parasitology* 108: 207-215.
- Grewel, P., R. Gaugler, and R. Georgis.** 1995. Predictors of foraging strategy in entomopathogenic nematodes. In: *Ecology and Transmission Strategies of Entomopathogenic Nematodes*. C.T. Griffin, R.L. Gwynn and J.P. Masson, eds. European Commission Luxembourg. pp 95-104.
- Hechler, H.C.** 1963. Description, developmental biology and feeding habits of *Seinura tenuicaudata* (DeMan) J.B. Goodey, (1960). (Nematoda: Aphelenchoididae) a nematode predator. *Proceedings of the Helminthological Society of Washington* 30: 182-195.
- Hendrix, P.F., R. Parmalee, R. Crossley, D. Coleman, E. Odum and P. Groffman.** 1986. Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience* 36: 374-380.
- Hill, M.** 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* 54: 427-432.
- Hooper, D., D.E. Bignell, V.K. Brown, L. Brussard, J.M. Dangerfield, D.H. Wall, D.A. Wardle, D.C. Coleman, K.E. Giller, P. Lavelle, W.H. Van der Putten, P.C. DeRuiter, J. Rusek, W.L. Silver, J.M. Tiedje, and V. Wolters.** 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: Patterns, Mechanisms, and Feedbacks. *BioScience* Vol. 50: 1049-1061.
- House, G.J. and M.D. R. Alzugaray.** 1989. Influence of cover cropping and no-tillage practices on community composition of soil arthropods in a North Carolina agroecosystem. *Environ. Entomol.* 18: 302-307.
- House, G.J. and B.R. Stinner.** 1983. Arthropods in no-tillage soybean agroeco-systems: Community composition and ecosystem interactions. *Environmental management* 7(1): 23-28.
- Hummel, R.L., J. F. Walgenbach, M.E. Barbercheck, G.G. Kennedy, G.D. Hoyt, and C. Arellano.** 2002. Effects of production practices on soil-borne entomopathogens in western North Carolina vegetable systems. *Environ. Entomol.* 31: 84-91.

- Hurlbert, S.** 1971. The non-concept of species diversity: A critique and alternative parameters. *Ecology* 52: 577-586.
- Jansson, R.K., Lecrone, S.H., Gaugler, R.** 1993. Field efficacy and persistence of entomopathogenic nematodes (*Rhabditida: Steinernematidae, Heterorhabditidae*) as biological control agents of the sweetpotato weevil (*Coleoptera: Apionidae*) in southern Florida. *J. Econ. Entomol.* 86:1055-1063.
- Kaya, H.K. and R. Gaugler.** 1993. Entomopathogenic nematodes. *Ann Rev. Entomol.* 38: 181-206.
- Kaya, H. and S. Stock.** 1997. Techniques in insect nematology in: *Manual of Techniques in Insect Pathology*. L.A. Lacey, ed. Academic Press. London. Pp. 281-324.
- Kajak, A. and H. Jakubczyk.** 1977. Experimental studies on predation in the soil-litter interface. *Ecol. Bull. (Stockholm)* 25: 493-496.
- Koppenhöfer A.M, and H. Kaya.** 1996. Coexistence of entomopathogenic nematode species (*Steinernematidae* and *Heterorhabditidae*) with different foraging behavior. *Fundamentals of Applied Nematology* 19: 175-183.
- Koppenhöfer A.M., Baur, M.E., Stock S.P., Choo H.Y., Chinnasri B., Kaya, H.K.** 1997. Survival of entomopathogenic nematodes within host cadavers in dry soil. *Applied Soil Ecology* 6, 231-240
- Krantz, G.W.,** 1978. *A Manual of Acarology*. (second edition), Oregon State University Press. Corvallis, Oregon. 509 pp.
- Laakso, J. and H. Setälä.** 1999. Population and ecosystem level effects of Predation on microbial-feeding nematodes. *Oecologia* 120: 279-286.
- Lagerlof, J. and O. Andren.** 1988. Abundance and activity of soil mites (Acari) in four cropping systems. *Pedobiologia* 32: 129-145.
- Lewis, E., R. Gaugler and R. Harrison.** 1992. Entomopathogenic nematode host finding: response to host contact cues by cruise and ambush foragers. *Parasitology* 105: 309-319.
- Lewis, E., R. Gaugler and R. Harrison.** 1993. Response of cruiser and ambusher entomopathogenic nematodes (*Steinernematidae*) to host volatile cues. *Canadian Journal of Zoology* 71: 765-769.
- Lewis, E.E., P.S. Grewal, and S. Sardanelli.** 2001. Interactions between the *Steinernema feltiae-Xenorhabdus bovienii* insect pathogen complex and the root knot nematode *Meloidogyne incognita*. *Biological control.* 21 (1). May 2001: 55-62.
- Ludwig, J. and J. Reynolds.** 1988. *Statistical Ecology*. John Wiley and sons. New York
- McCoy, C.W., Shapiro, D.I., Duncan, L.W.** 2000. Application and evaluation of entomopathogens for citrus pest control. In: Lacey, L., Kaya, H.K. (Eds.), *Field Manual of Techniques in Insect Pathology*, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 577-596.
- Menalled, F., D. Landis, J. Lee, S. White, and K. Renner.** 2000. Ecology and management of weed seed predators in Michigan agroecosystems. *MSU Extension bulletin E-2716*
- Millar, L.C. and M.E. Barbercheck.** 2002. Effects of tillage practices on Entomopathogenic nematodes in a corn agroecosystem. *Biological*

Control 25: 11-20.

Mueller, B.R., M.H. Beare and D.A. Crossley, Jr. 1990. Soil mites in detrital food webs of conventional and no-tillage agroecosystems. *Pedobiologia* 34: 389-401.

Murphy, P.W., Doncaster C.C. 1957. A culture method for soil meiofauna and its application to the study of nematode predators. *Nematologica* 2, 202-214.

Neave, P. and C.A. Fox. 1998. Response of soil invertebrates to reduced tillage systems established on a clay loam soil. *Applied Soil Ecology* 9: 423-428.

Neher, D. and M. Barbercheck. 1990. Diversity and function of soil mesofauna. *Biodiversity in Agroecosystems*. W.W. Collins and C.O. Qualset, eds. CRC Press.

Nelmes, A.J., McCulloch, J.S. 1975. Numbers of mononchid nematodes in soils sown to cereals and grasses. *Annals of Applied Biology* 79, 231-242.

Ostfield, R.S and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *TREE* Vol. 15 No. 6. June 2000: 232-238.

Parkman, J.P., Hudson, W.G., Frank, J.H., Nguyen, K.B., Smart, G.C. 1993. Establishment and persistence of *Steinernema scapterisci* (Rhabditida:Steinernematidae) in field populations of *Scapteriscus* spp. mole crickets (Orthoptera: Gryllotalpidae). *J. Entomol. Sci.* 28:182- 190.

Pimm, S.L. 1982. *Food webs*. Chapman and Hall, NY. 219 pp.

Polis, G. 1994. Food webs, trophic cascades and community structure. *Australian Journal of Ecology* (1994) 19: 121-136.

Rosenheim, J.A., H.K. Kaya, L.E. Ehler, J.J. Marois and B.A. Jaffee. 1995. Intraguild predation among biological-control agents: Theory and evidence. *Biological Control* 5: 303-335.

Scheu, Stefan. 2002. The soil food web: Structure and perspectives. *European J. of Soil Biology* 38: 11-20.

Shannon, C. and W. Weaver. 1949. *The mathematical theory of communication*. University Illinois Press, Urbana, Ill.

Shapiro, D.I., Obrycki, J.J., Lewis, L.C. and Jackson, J.J. 1999. Effects of crop residue on the persistence of *Steinernema carpocapsae*. *J. Nematol.* 31: 517-519.

Simpson, E. 1949. Measurement of diversity. *Nature* 163: 168.

Sloderbeck, P.E. and K.V. Yeargen. 1983. Green cloverworm populations in conventional and double-cropped no-till soybeans. *J. Econ. Entomol.* 76: 785-791.

Smits, P. 1996. Post-application persistence of entomopathogenic nematodes. *Biocontrol Science and Technology* 6: 379-387.

Steen, E. 1983. Soil animals in relation to agricultural practices and soil productivity. *Swedish J. Agricultural Res.* 13: 157-165.

Stinner, B.R. and G.J. House. 1990. Arthropods and other invertebrates in conservation-tillage agriculture. *Ann. Rev. Entomol.* 35: 299-318.

- Symondson, W.O.C., K.D. Sunderland and M.H. Greenstone.** 2002. Can Generalist predators be effective biocontrol agents? *Annu. Rev. Entomol.* 2002, 47: 561-594.
- Thorne, G.** 1927. The life history, habits and economic importance of some mononchs. *J. Agric. Res.* 34:265-286.
- Van de Bund, C.F.** 1970. Influence of crop and tillage on mites and springtails in arable soil. *Neth. J. Agric. Sci.* 18: 308-314.
- Van der Werf, W., et al.** 1995. Concepts and prospects for modelling the efficacy and ecology of entomopathogenic nematodes. Pp. 42-51 in Ecology and transmission strategies of entomopathogenic nematodes, **C.T. Griffen, R.L. Gwynn and J.P. Masson** (eds.) European commission , Luxembourg.
- Walter, D.E, R.A. Hudgens, and D.W. Freckman.** 1986. Consumption of nematodes by fungivorous mites, Tyrophagus spp. (Acarina: Astigmata: Acaridae). *Oecologia* (Berlin) 1970: 357-361.
- Walter, D.E.** 1987. Trophic behavior of "mycophagous" microarthropods. *Ecology* 68: 226-229.
- Walter, D.E. and E.K. Ikonen.** 1989. Species, guilds, and functional groups: taxonomy and behavior in nematophagous arthropods. *J. Nematol.* 21: 315-327.
- Walter, D.E., J.C. Moore,** and S.J. Loring. 1989. *Symphylela* sp. (Symphyla: Scolopendrellidae) predators of arthropods and nematodes in grassland Soils. *Pedobiologia* 33: 113-116.
- Walter, D.E. and D.T. Kaplan.** 1990. Feeding observations on two astigmatic mites, *Schwiebea rocketti* (acaridae) and *Histiostoma bakeri* (Histiostomatidae) associated with *Citrus* feeder roots. *Pedobiologia* 34: 281-286.
- Walter, D.E. and H. Proctor.** 1999. *Mites: Ecology, Evolution and Behaviour.* CABI Publ. New York, NY.
- Wootton, J.T.** 1994. The nature and consequences of indirect effects in ecological communities. *Annu. Rev. Ecol. Syst.* 25: 443-66.
- Yeates, G.W.** 1984. Variation in soil nematode diversity under pasture with soil and year. *Soil Biol. Biochem.* 16: 95-102

Table-2-1 Total abundance and abundance of groups of invertebrates extracted in inundation experiment. Pooled data derived from 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, water (controls), Sc=Steinernema carpocapsae, Rb=Steinernema riobrave, Hb=Heterorhabditis bacteriophora (nematode strains))

Total invertebrates	44996
Soil mites (Arachnida: Acari)	
Mesostigmata	2681
Oribatida	23295
Prostigmata	3084
Astigmata	3485
Insects	
Collembola	9582
Other insects	2869

Table 2-2 Mean (\pm std. err.) abundance of soil invertebrates in conventionally-tilled soil in inundation experiment. Invertebrates are grouped into 7 major categories (Mesostigmata, Oribatida, Prostigmata, Astigmata, Collembola, other invertebrates, total invertebrates=sum of other 6 groups). Pooled data derived from 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, water (controls), Sc=Steinernema carpocapsae, Rb=Steinernema riobrave, Hb=Heterorhabditis bacteriophora (nematode strains))

Treatment	Hb		Rb		Sc		Soil		Water	
Observations	(n=24)		(n=24)		(n=24)		(n=24)		(n=24)	
Time (hr)	4	24	4	24	4	24	4	24	4	24
Mesostigmata	4.917	4.042	4.125	3.667	5.167	4.583	4.208	3.917	4.250	5.000
	± 0.880	± 0.920	± 0.736	± 0.716	± 1.111	± 1.092	± 0.878	± 1.137	± 0.821	± 1.306
Oribatida	23.958	21.333	28.292	26.792	27.875	41.667	24.542	19.208	28.458	25.542
	± 3.673	± 3.786	± 4.370	± 5.551	± 4.342	± 13.315	± 3.284	± 3.634	± 3.400	± 4.706
Prostigmata	6.750	5.958	7.917	6.042	5.042	6.708	7.583	8.333	8.333	7.667
	± 1.851	± 1.770	± 2.637	± 1.710	± 1.135	± 1.914	± 2.029	± 2.051	± 1.626	± 1.980
Astigmata	2.333	2.167	1.667	1.583	2.833	1.625	2.292	1.125	2.208	1.458
	± 0.675	± 1.085	± 0.554	± 0.507	± 0.836	± 0.521	± 0.997	± 0.392	± 0.678	± 0.335
Collembola	20.500	22.958	13.542	25.167	15.625	16.417	9.000	10.083	17.375	16.750
	± 9.963	± 10.416	± 5.076	± 12.687	± 4.441	± 4.553	± 1.934	± 3.480	± 5.186	± 6.133
Other	4.792	3.250	4.042	4.667	4.500	3.875	3.750	3.375	3.833	5.125
invertebrates	± 1.189	± 0.819	± 0.826	± 1.134	± 1.025	± 0.858	± 0.783	± 0.926	± 1.069	± 1.411
Total	63.250	59.708	59.583	67.917	61.042	74.875	51.375	46.042	64.458	61.542
invertebrates	± 11.121	± 12.669	± 8.202	± 17.159	± 7.592	± 18.050	± 5.209	± 7.380	± 6.832	± 10.241

Table 2-3 Mean (\pm std. err.) abundance of soil invertebrates in no-till soil in inundation experiment. Invertebrates are grouped into 7 major categories (Mesostigmata, Oribatida, Prostigmata, Astigmata, Collembola, other invertebrates, total invertebrates=sum of other 6 groups). Pooled data derived from 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, water (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Treatment	Hb		Rb		Sc		Soil		Water	
Observations	(n=24)									
Time (hr)	4	24	4	24	4	24	4	24	4	24
Mesostigmata	8.458	8.125	7.250	5.333	8.375	5.583	7.750	3.458	7.458	6.042
	± 1.819	± 1.511	± 1.356	± 1.148	± 1.319	± 2.148	± 1.844	± 0.668	± 1.002	± 1.071
Oribatida	75.125	69.125	64.292	55.250	68.708	64.542	87.542	58.750	76.292	83.333
	± 10.592	± 11.235	± 15.596	± 7.672	± 9.260	± 9.968	± 9.964	± 10.258	± 10.927	± 13.918
Prostigmata	4.167	6.000	3.625	5.125	4.792	6.875	9.583	6.000	4.708	7.292
	± 0.892	± 1.926	± 0.681	± 1.307	± 1.034	± 1.877	± 2.150	± 1.477	± 1.125	± 1.239
Astigmata	11.250	40.833	5.833	7.375	13.542	4.792	12.167	11.000	7.917	11.208
	± 3.171	± 33.043	± 1.106	± 2.343	± 3.082	± 1.251	± 5.566	± 5.085	± 2.087	± 6.347
Collembola	25.125	27.292	22.792	20.250	27.250	19.583	27.042	22.208	21.500	18.792
	± 4.512	± 7.709	± 3.068	± 4.660	± 5.019	± 4.384	± 6.884	± 6.601	± 3.912	± 3.518
Other invertebrates	8.167	6.708	8.583	7.167	8.667	8.333	9.083	6.583	7.208	7.833
	± 1.069	± 1.069	± 1.479	± 1.639	± 0.988	± 1.719	± 1.315	± 1.342	± 0.946	± 1.255
Total invertebrates	132.292	158.083	112.375	100.500	131.333	109.708	153.167	108.000	125.083	134.500
	± 16.864	± 47.562	± 18.315	± 15.531	± 13.844	± 17.516	± 22.086	± 21.805	± 14.759	± 21.240

Table 2-4 F, P, and d.f. Statistics, including major factors, treatment, contrasts of treatments and interactions of large groupings of soil invertebrates in the inundation experiment. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn. Superscripts 1-17 indicate error term used for analysis see Appendix S.

Statistical measure	Total invertebrates		Collembola		Other invertebrates	
Total abund	44996		9582		2869	
abund in No-till	67.50%		58.10%		65.50%	
major factors (df)	F	P	F	P	F	P
Block ¹⁷ (3,30)	ns	ns	ns	ns	10.2	<.0001
Date ¹ (5,15)	78.21	<.0001	25.81	<.0001	9.98	0.0002
Till ² (1,3)	24.35	0.016	27.28	0.0137	44.04	0.007
Time ³ (1,30)	288.07	<.0001	87.43	<.0001	16.44	0.0003
till*date ⁴ (5,20)	6.39	<.0001	3.1	0.0096	8.01	<.0001
till*time ⁶ (1,30)	ns	ns	6.71	0.0146	ns	ns
till*trt ¹⁶ (4,30)	ns	ns	ns	ns	ns	ns
Trt ⁸ (4,24)	4.63	0.007	3.6	0.0195	ns	ns
Contrasts(1,24)	F	P	F	P	F	P
Soil*Water ⁹	11.98	0.002	5.85	0.0235	ns	ns
Soil*trt ¹⁰	4.42	0.046	11.6	0.0023	ns	ns
Water*trt ¹¹	4.56	0.043	ns	ns	ns	ns
Hb*Sc, Rb ¹²	6.41	0.018	ns	ns	ns	ns
Rb*Sc, Hb ¹³	ns	ns	ns	ns	ns	ns
Sc*Rb, Hb ¹⁴	ns	ns	ns	ns	ns	ns

Table 2-5 F, p, and df Statistics, including major factors, treatment, contrasts of treatments and interactions of large groupings of soil mites in the inundation experiment. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01)), 2 sampling times (4 or 24 h time), 2 tillage regimes (conventional tillage and no-tillage till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied to a corn field. Superscripts 1-17 indicate error term used for analysis see Appendix S.

Statistical measure	Mesostigmata		Oribatida		Prostigmata		Astigmata	
Total abund	2681		23295		3084		3485	
abund in No-till	60.7%		72.4%		45.3%		86%	
major factors (df)	F	P	F	P	F	P	F	P
Block ¹⁷ (3,30)	11.48	<.0001	7.55	<.0001	14.04	<.0001	17.23	<.0001
Date ¹ (5,15)	4.52	0.01	69.82	<.0001	4.54	0.0101	6.77	0.0017
Till ² (1,3)	ns	ns	16.43	0.0271	ns	ns	22.03	0.0183
Time ³ (1,30)	28.94	<.0001	146.6	<.0001	ns	ns	13.29	0.001
till*date ⁴ (5,20)	9.58	<.0001	11.65	<.0001	4.6	0.0005	10.03	<.0001
till*time ⁶ (1,30)	5.62	0.024	ns	ns	ns	ns	ns	ns
till*trt ¹⁶ (4,30)	ns	ns	3.69	0.0176	ns	ns	ns	ns
Trt ⁸ (4,24)	2.57	0.064	ns	ns	8.15	0.0003	3.65	0.0185
Contrasts(1,24)	F	P	F	P	F	P	F	P
Soil*Water ⁹	3.5	0.074	4.77	0.0389	0	0.9523	3.42	0.0767
Soil*trt ¹⁰	4.88	0.037	ns	ns	20.25	0.0001	11.42	0.0025
Water*trt ¹¹	ns	ns	ns	ns	19.59	0.0002	ns	ns
Hb*Sc, Rb ¹²	3.63	0.069	ns	ns	ns	ns	ns	ns
Rb*Sc, Hb ¹³	ns	ns	ns	ns	ns	ns	ns	ns
Sc*Rb, Hb ¹⁴	ns	ns	ns	ns	ns	ns	ns	ns

Table 2-6 Taxa responding significantly ($p < 0.05$) to nematode treatments in inundation experiment. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h time), 2 tillage regimes (conventional tillage and no-tillage till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied to a corn field (df = 4, 24 for all analyses)

Taxon	total	% in NT	F	P
<i>Hypoaspis spp.</i>	489	48.70%	3.53	0.0211
Oribatid immature	10161	68.80%	3.99	0.0127
Sminthuridae	124	53.20%	4.15	0.0108
Coleoptera adult	94	60.60%	6.18	0.0015

Table 2-7 Taxa (and relative abundance, of total collected, in No-till soil). Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn.

Taxon	total	% in NT
Arachnida		
Acari		
Mesostigmata		
<i>Macrocheles spp.</i>	297	83.80%
<i>Rhodacarus spp.</i>	390	82.30%
Ascidae	112	72.30%
Other Mesostigmata	1222	61.50%
<i>Hypoaspis spp.</i>	489	48.70%
<i>Protogamasellus spp.</i>	283	24.00%
Oribatida		
<i>Neonothrus spp.</i>	205	100.00%
<i>Galumna spp.</i>	452	96.20%
<i>Nothrus spp.</i>	394	96.20%
<i>Zygoribatula spp.</i>	1867	93.00%
Brachychthoniidae	353	83.30%
<i>Xylobates spp.</i>	1071	72.10%
<i>Tectocepheus spp.</i>	5022	70.50%
<i>Scheloribates spp.</i>	2444	69.80%
Oribatida immature	10161	68.80%
Other Oribatida	188	67.00%
<i>Rhysotritia spp.</i>	203	65.00%
<i>Eremobelba spp.</i>	120	60.80%
Oppiidae	537	59.00%
<i>Epilohmannia spp.</i>	278	57.90%
Prostigmata		
Tydeidae	224	87.10%
Other Prostigmata	246	76.40%
<i>Eupodes spp.</i>	446	61.40%
Cunaxidae	356	53.90%
<i>Nanorchestes spp.</i>	785	48.00%
Scutacaridae	178	39.90%
Pygmephoridae	158	24.70%

<i>Speleorchestes spp.</i>	691	8.70%
Astigmata		
<i>Sancassania spp.</i>	1095	96.70%
Acaridae	155	95.50%
Hypopi	2092	82.20%
Other Astigmata	143	66.40%
Insecta		
Collembola		
Hypogastruridae	183	90.20%
Isotomidae	605	78.80%
Onychiuridae	567	68.60%
Entomobryidae	344	57.00%
Sminthuridae	124	53.20%
Diptera immature	338	83.10%
Formicidae	41	65.90%
Japygidae	219	63.00%
Coleoptera adult	94	60.60%
Other insects	123	56.90%
Thysanoptera	124	55.60%
Mixed Collembola	7759	55.00%
Coleoptera immature	356	49.70%
Other invertebrates		
Nematoda	344	89.00%
Symphyla	407	73.00%
Chilopoda	62	58.10%
Enchytraeidae	761	55.50%

Table 2-8 Taxa significantly responding (ANOVA $P < .05$, $df = 4, 24$ to the interaction of tillage type by treatment (till*trt) f and p statistics, mean and standard error (s.e.). Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn.

Taxon	total	% in NT	F	P
<i>Tectocepheus spp.</i>	5022	70.50%	2.89	0.0436
unidentified Oribatids	188	67.00%	2.78	0.0499
Unidentified Prostigmatids	246	76.40%	3.23	0.0295
Collembola	7759	55.00%	4.13	0.0109

Table 2-9 Taxa responding significantly (ANOVA $P < .05$, $df = 4,30$) to the interaction of sampling time by treatment (time*trt) in inundation experiment. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn.

Taxon	total	% in NT	F	P
<i>Nothrus spp.</i>	394	96.20%	2.89	0.0389
<i>Scheloribates spp.</i>	2444	69.80%	5.67	0.0016
Entomobryidae	344	57.00%	2.87	0.0400
Immature Diptera	338	83.10%	2.9	0.0383

Table 2-10 Taxa responding significantly (ANOVA $P < .05$, $df = 20, 20$) to the interaction of $trt * date$ in inundation experiment. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn.

Taxon	total	% in NT	F	P
<i>Tectocepheus spp.</i>	5022	70.50%	1.81	0.0193
Immature Oribatida	10161	68.80%	1.97	0.0089
Hypopi (Acaridae)	2092	82.20%	1.88	0.0139
Sminthuridae	124	53.20%	1.77	0.0240
Adult Coleoptera	94	60.60%	2.18	0.0029

Table 2-11 f and p Statistics of diversity measures. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h time), 2 tillage regimes (conventional tillage and no-tillage till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied to a corn field

Diversity measure	Till df 1,3		Date df 5,15		Time df 1,30		Trt df 4,24	
	F	P	F	P	F	P	F	P
Shannon	105.96	0.002	9.48	0.0003	7.86	0.0088	ns	ns
Simpson	ns	ns	7.6	0.001	ns	ns	ns	ns
hill 1	118.83	0.0017	9.32	0.0003	9.91	0.0037	ns	ns
Evenness	ns	ns	10.94	0.0001	ns	ns	ns	ns
no. taxa	145.3	0.0012	3.46	0.0281	15.46	0.0005	2.91	0.0426
hill 2	ns	ns	8.48	0.0006	ns	ns	ns	ns

Figure 2-1 Total abundance of Mesostigmata, Oribatida, Prostigmata, Astigmata, Collembola and other invertebrates in blocks I – IV of inundation experiment.

Pooled data derived from 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 4 blocks, 2 sampling times (4, 24 hrs) and 5

treatments (soil, water (controls), Sc=*Steinernema carpocapsae*,

Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

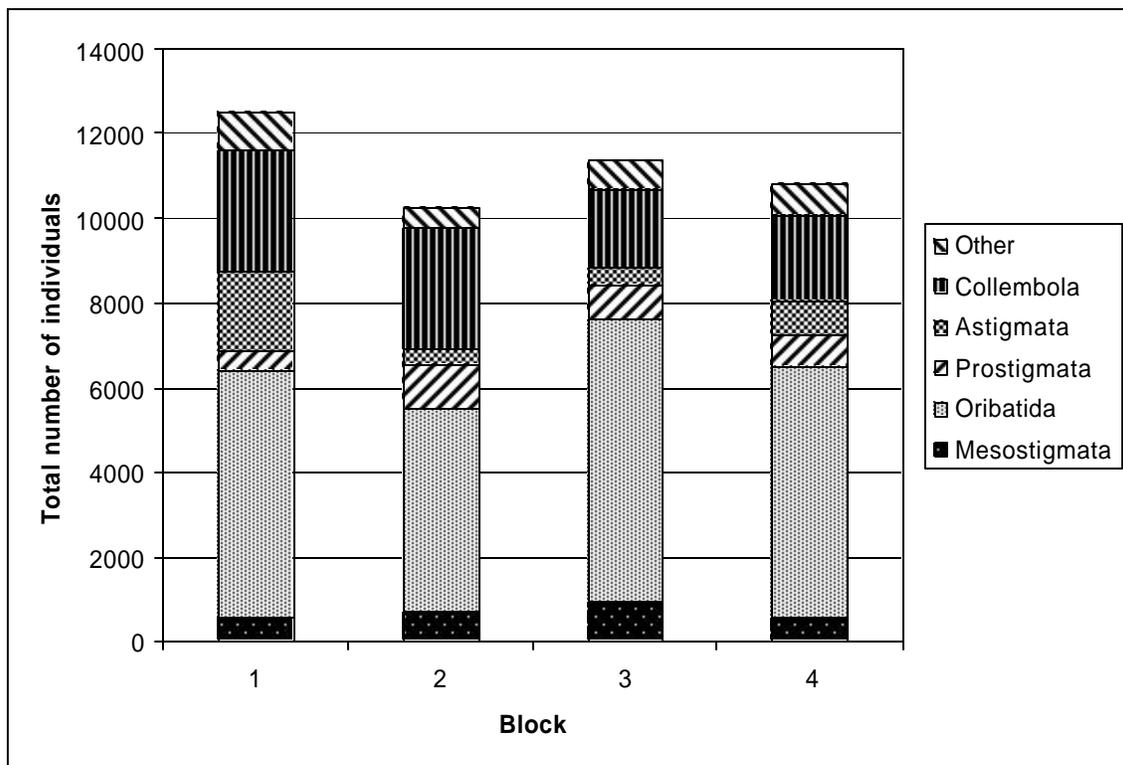


Figure 2-2 Richness (# taxa) in No-till (NT) and Conventional till (CT) soil in inundation experiment. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h time), 2 tillage regimes (conventional tillage and no-tillage till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied to a corn field

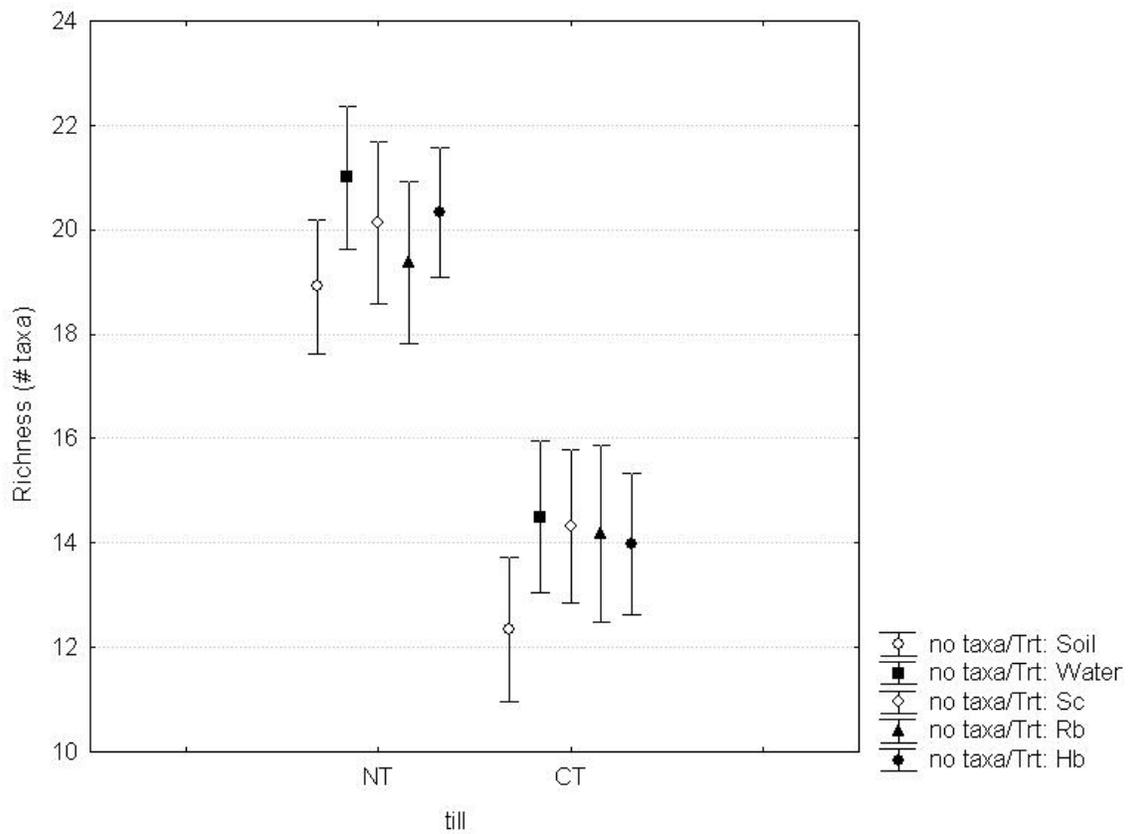
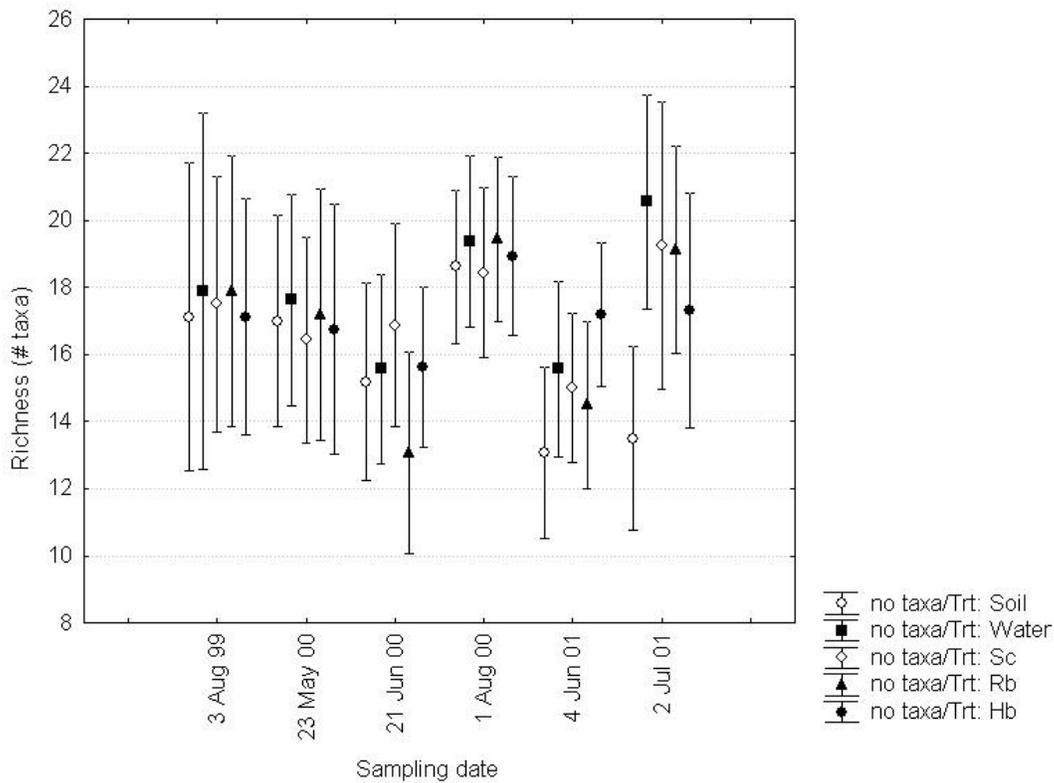


Figure 2-3 Richness (# taxa) in 6 sampling dates in inundation experiment. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01)), 2 sampling times (4 or 24 h time), 2 tillage regimes (conventional tillage and no-tillage till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied to a corn field



Chapter 3 Response of soil fauna to application of entomopathogenic nematodes via infected insect cadaver

Abstract

The impending potential loss of many traditional synthetic soil-dwelling insect pest suppression agents, which are currently undergoing federal re-evaluation, in agriculture has resulted in an increased focus on soil ecology and biological pest suppression. Entomopathogenic nematodes (EPN) in the families Steinernematidae and Heterorhabditidae occur naturally in the soil and have also been commercially produced as a soil-dwelling pest suppression agent. Evaluation of interactions between EPN and the soil community historically assess impacts resulting from commercially prescribed inundative methods of EPN application. Recent attention, however, has focused on alternative methods of EPN application using infected host cadavers as the delivery mechanism. Introduction of an EPN-infected insect cadaver to the soil community differs from the introduction of infective juveniles suspended in aqueous solution. Because these systems of EPN application are very different, responses of soil fauna may also differ from those resulting from inundative application of EPN and therefore require independent assessment.

Response of soil fauna to the application of entomopathogenic nematodes (EPN) in both no-till and conventional-till corn was evaluated at the levels of abundance, diversity and community composition. Entomopathogenic nematodes

were applied to the soil via an infected *Galleria mellonella* cadaver. The experiment was designed as a stripped split split plot over four blocks. Nematodes were applied on 6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00. Variables included: 6 application dates x 4 blocks x 2 tillage regimes x 2 sampling times (4 hours and 24 hours after nematode application) x 5 treatments = 480 observations. The treatments included: three nematode species treatments *Heterorhabditis bacteriophora* (CEFS strain), *Steinernema riobrave* (commercially available but does not naturally occur in NC), and *Steinernema carpocapsae* (CEFS strain) and two control treatments, soil only and a dead insect control. Response of soil fauna was measured at the levels of abundance (large traditional taxonomic affiliations of soil invertebrates), diversity, and community composition based on the finest level of taxonomic identification of invertebrates collected.

Experimental factors including sampling date and time, tillage regime, and blocks, and their interactions, significantly affected abundance, diversity and community composition of soil invertebrates at all levels. Significant changes in abundance due to the effect of treatment were also found both in large taxonomic groupings as well as in the finer taxonomic categories. Responses of soil fauna due to nematode treatment were found to differ within different tillage regimes, within different blocks, and at different sampling times and different sampling dates. Certain taxa decreased in abundance in the presence of EPN while others increased. Large taxonomic groupings of invertebrates exhibited responses that differed significantly from the responses of individual taxa within those large

groupings. Therefore, while evaluation of the response of large taxonomic groupings to EPN application is informative to some extent, evaluation of individual taxa within the large groupings is needed to accurately determine specific interactions between EPN and other members of the soil community.

Introduction

With a growing emphasis on agriculturable sustainability has come the need for a more in-depth understanding of the various components of agroecosystems (Beare et al. 1982, Andren and Lagerlof 1983, Blevins et al. 1983, House and Alzugaray 1989, Barbercheck and Millar 2000, Wardle et al, 2000, Jackson and Jackson 2002). One integral component of agroecology that has received more recent attention is that of soil ecology and biology, and the need for more thorough assessments biological interactions within the soil community (Mueller et al. 1990, Edwards 1991, deGoede and Brussard 2002, Schue 2002).

Soil organisms provide a host of vital ecosystem services to all terrestrial ecosystems, including agricultural systems. These services include nutrient cycling, decomposition, bioremediation, promotion of plant health and diversity, suppression of soil-dwelling insect pests, and physical structuring of soil (Steen 1983, Neher and Barbercheck 1990, Crossley et al. 1992, Coleman and Crossley 1996, Pfiffner and Niggli 1996, Neave and Fox 1998, Laakso and Setala 1999, Coll and Guershon 2002). The soil community is integral to overall soil quality, and inextricably linked to the abiotic factors that also contribute to soil quality

(Van de bund 1970, House and Stinner 1983, Coleman and Crossley 1996, Ettema and Wardle 2002).

Within the realm of ecosystem services offered by soil fauna, suppression of soil-dwelling insect pests is of particular interest in the pursuit of sustainable agriculture, particularly as many currently used soil insecticides are currently undergoing federal re-evaluation and may no longer be available in the future. Therefore, growers will require alternative biological and cultural pest management strategies to manage soil-dwelling insect pests (Jackson and Jackson 2002, Millar and Barbercheck 2002).

Beneficial soil organisms, including soil-dwelling predators and pathogens of insects provide a natural source of biological control for agricultural pests (Rosenheim et al. 1995, Symondson et al. 2002). Entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae serve as a naturally-occurring biological control agent, in the soil, have been isolated from a wide range of both natural and disturbed habitats and have a worldwide distribution (Brust 1991, Kaya and Gaugler 1993).

Entomopathogenic nematodes (EPN) exist in an obligate symbiotic association with genus-specific species and strains of bacteria (*Xenorhabdus spp.* in the Steinernematidae and *Photorhabdus spp.* in the Heterorhabditidae). The only free-living form of these nematodes is the infective juvenile (IJ). The IJ dwell in the soil and employ various host-searching behaviors. Once an arthropod host is found the IJ enter through natural openings. In the host's body, the IJ release their bacterial symbiont. The bacteria kill the insect host and

provide a nutrient source for the nematodes as they complete their life cycle (Kaya and Gaugler 1993).

Several species and strains of EPN have been isolated and produced commercially. Prescribed application of commercial strains is typically via inundation (IJ suspended in aqueous solution) at the rate of 2.5 billion per hectare. Efficacy of commercially available strains, with prescribed application, has proven, however, to be inconsistent (Kajak and Jakubczyk 1977, Jansson et al. 1993, Kaya and Stock 1997). Population densities of EPN, at the commercial rate of application, are low in comparison to other soil fauna, and have been observed to decrease rapidly. Recoveries directly following application can be less than 50% (Van der Werf et al. 1995, Smits 1996, Laakso and Setala 1999) even under optimal abiotic environmental conditions.

Other potential factors impacting populations of EPN may include biotic interactions such as predation. The high numbers of soil-inhabiting invertebrates and their predisposition for omnivory (and nematophagy) makes predation by natural enemies an obvious consideration (Gilmore 1970, Walter 1987, Walter and Ikonen 1989, Walter and Moore 1989, Mueller et al. 1990, Walter and Kaplan 1990, Gilmore and Potter 1993, Glazer et al. 1995, Smits 1996).

Nematode behavior, and the method by which they are introduced into the soil, may play an integral role in the extent to which predation impacts EPN populations (Lewis et al. 1992, Lewis et al. 1993, Grewel et al 1994, Campbell and Gaugler 1997).

Traditional EPN application has been inundative through the application of IJ in solution. Recent interest, however has focused on the use of EPN-infected cadavers a method of applying EPN to soil (Kaya and Kopenhofer 1996, Shapiro and Lewis 1999, McCoy et al. 2000, Shapiro-ilan et al. 2003). EPN applied in this fashion enter the soil as a nematode-bacteria complex with the insect cadaver housing large quantities of EPN, bacteria and bacterial metabolites (Shapiro and Glazer 1996, Brown and Gaugler 1997, Kopenhofer et al. 1997).

Here we report the results of an experiment in which entomopathogenic nematodes were introduced to the soil via infected insect cadavers to two different tillage regimes to determine the response of soil organisms to the introduction of the EPN-infected insect cadaver complex.

This research also examines how soil fauna respond to different environmental factors, including seasonal and spatial fluctuations, varying tillage regimes and interactions between environmental factors and introduction of EPN. The specific objectives of this research are to answer the questions:

What is the response of soil invertebrate fauna to the presence of an insect infected with native or introduced entomopathogenic nematodes (simulates a natural infection)?

How do tillage practices affect soil invertebrate fauna, and in particular, potential predators of native and introduced entomopathogenic nematodes?

Materials and methods

Field site

This research was conducted in conjunction with a larger reasearch project designed to evaluate effects of different tillage practices within a 5-crop rotation (Appendices A and B) in the tillage unit at the Center for Environmental Farming Systems (CEFS) near Goldsboro, North Carolina. Research within the tillage unit was organized as a randomized complete block design experiment containing both no-till and conventional-till rotations. Conventional-till plots were chisel plowed and disked in the fall and disked in the spring. This experiment took place in the 0.15 hectare no-till and conventional-till corn fields present in the four blocks of the five-crop rotation in the tillage unit (Appendix B). Portions of the field used for this study were treated with fertilizer and herbicides, but were not treated with insecticides. Soil type at the site is predominantly Wickham fine sandy loam.

Production of entomopathogenic nematodes

All nematodes used in this study were reared in the laboratory using *Galleria mellonella* larvae according to Kaya and Stock (1997). Three nematode strains belonging to two families, Steinernematidae and Heterorhabditidae, were used. Two of the strains, *Heterorhabditidae bacteriophora*, CEFS strain and *Steinernema carpocapsae* CEFS strain were indigenous strains isolated from the research site. The third strain, *Steinernema riobrave*, is a commercially available

strain originating in Texas. Nematodes were maintained in culture at 10° C for no longer than two weeks before use.

G. mellonella were exposed to IJ in petri dishes one week prior for *Steinernematid spp.* and ten days prior for *Heterorhabditis spp.* to application of cadavers in the field. One day before application single infected cadavers were placed in plastic biopsy cassettes (25 x 30 mm, Fisher Scientific), with the remaining volume of the cassette filled with microwave “pasteurized” soil (Ferriss 1984, Barbercheck & Kaya 1991ab). A control treatment, for the presence of a dead insect, consisted of a dead *G. mellonella* killed by freezing in a biopsy cassette.

Introduction of nematode-infected insect cadavers

Cages were placed vertically in the soil with minimal disturbance at a depth of 40mm, at 10 randomly assigned locations within 3 randomly chosen corn rows with one corn row between each treatment row and no closer than 1m from other cages within each tillage treatment of each block. Each application site was flagged with different colors indicating different nematode and time treatments. Sufficient cages were buried in each tillage treatment so that half could be sampled 4 and 24 hrs after application, respectively. 4 blocks x 2 tillage treatments x 5 treatments x 2 sampling times X 6 sampling dates = 480 observations.

The soil sample collected consisted of one soil core containing the entire contents of the soil (50 ml soil) directly surrounding the buried biopsy cassette, with the cassette included in the soil sample and placed in the bag with the soil.

Each soil and cage sample was placed in a zip-lock bag, labeled and protected from heat and light for transit to the laboratory for extraction of microarthropods.

Extraction of microarthropods from soil

Soil plus contents of the cassette were placed in modified Tullgren funnels under 20 watt incandescent bulbs for five days during which soil microarthropods collected in 70% alcohol in vials attached to the bottom of the funnels. Complete specimens from alcohol were enumerated and mounted on microscope slides for identification in Berlese's fluid (8g gum acacia, 8 ml distilled water, 5 ml glycerol, 70 g chloral hydrate, 3 ml glacial acetic acid). Taxonomy follow keys in Dindal (1990), Christiansen & Bellinger (1979), Balogh (1972) and materials from the Summer Program in Acarology at the Ohio State University.

Statistical analysis

This experiment was designed as a split split plot in four blocks, with whole plot factor tillage (NT=no-till soil and CT=conventional-till soil), subplot factor treatment (soil and dead insect controls, 3 nematode treatments, Sc = *Steinernema carpocapsae*, Rb = *Steinernema riobrave*, and Hb = *Heterorhabditis bacteriophora*), sub-sub-plot factor time (4 and 24 hour). Soil fauna were extracted from different locations within each whole plot at three times in each of 2 years, hence "date" is regarded as a stripped factor.

Abundance

Invertebrates were identified and taxonomically grouped into large traditional taxonomic affiliations (Krantz 1978, Lagerlof and Andren 1988, Mueller et al. 1990, Walter and Kaplan 1990, Crossley et al. 1992, deGoede and

Brussard 2002). Soil mites (Arachnida: Acari) were the most abundant invertebrates collected (Table 3-1). Soil mites were grouped into four suborders, Mesostigmata, Oribatida, Prostigmata and Astimata (currently contained within the Oribatida). The second most abundant of the invertebrates collected were the Collembola. The Collembola were collectively grouped into a fifth category. The remaining invertebrates consisted of other soil insects, predatory nematodes, segmented worms, such as annelids and enchytraeids, and myriapods. These were grouped into a 6th category designated “other invertebrates.” The sum of all individuals contained in these 6 categories constituted a seventh category entitled “total invertebrates” (Table 3-1). All seven categories were subjected to statistical analysis using ANOVA and the General Linear Model procedure (PROC GLM, SAS Institute 1996), and means were separated with the least significant difference (LSD, SAS Institute 1996).

Invertebrates collected were identified to genus or family (Appendix M). Tillage type preference was also documented for all invertebrates at this level. The total number of each taxon collected, and the proportion of the total found in either no-till soil or conventional-till soil.

Experimental factors taken into account when evaluating the response of soil fauna to EPN application included: date (sampling date), block (four), time (length of time after nematode application that soil was sampled, 4 hours or 24 hours), tillage type (no-till=NT and conventional-till=CT corn fields), and nematode treatment (soil only and dead insect cadaver controls, Sc

=*Steinernema carpocapsae* CEFS strain, Rb=*Steinernema riobrave* (commercial strain), and Hb=*Heterorhabditis bacteriophora* CEFS strain).

When significant effects on abundance due to treatment were detected, contrasts within treatments were made to further evaluate how individual taxa responded to specific treatments. Controls were contrasted against each other and against nematode treatments, and nematode treatments were contrasted against each other. All analyses of experimental factors, interactions and contrasts, and corresponding error terms are shown in the generic GLM model (Appendix S).

Diversity

Invertebrate taxa were evaluated for various measures of diversity relative both to experimental factors. Taxonomic richness (S) was determined for all treatments, using identifications made to the finest taxonomic level (Appendix M). Computed evenness among the taxa was evaluated for all experimental factors. Calculated diversity indices included: Simpson's index (Simpson 1949), Shannon's index (Shannon and Weaver 1949), and Hill's diversity numbers (1 and 2) (Hill 1973, Ludwig and Reynolds 1988). The following formulas were used:

$$\text{Simpson's index } D = \frac{\sum_{i=1}^S n_i(n_i-1)}{n(n-1)}$$

$$\text{Shannon's index } H' = -\sum_{i=1}^S \left[\left(\frac{n_i}{n} \right) \ln \left(\frac{n_i}{n} \right) \right]$$

$$\text{Evenness} = \ln(N^2) / \ln S$$

Hill's 1 = $N1 = e^H$

Hill's 2 = $N2 = 1/D$

Number of taxa = S

Number of taxa in each sample = n

All measures of diversity by major factors, treatments and interactions of major factors and treatment were also subjected to statistical analysis using ANOVA and the General Linear Model procedure (PROC GLM, SAS Institute 1996), and means were separated with the least significant difference (LSD SAS Institute 1996).

Community composition

Invertebrate taxa collected were identified to family or genus (Appendix M). Responses of soil fauna at this level of identification were measured within all 5 treatments.

When significant effects on abundance due to treatment were observed contrasts within treatments were made to further evaluate how individual taxa responded to specific treatments. Controls were contrasted against each other and against nematode treatments, and nematode treatments were contrasted against each other.

All analyses of experimental factors, interactions and contrasts, and corresponding error terms are exhibited in the generic GLM model (Appendix S).

45,606 Invertebrates were collected. They were identified to 134 different taxa. Many of these taxa were represented by only one or a few individuals.

Therefore, they were collapsed into 55 representative categories (each category

containing at least 100 individuals) for statistical analyses, using ANOVA and the General Linear Model procedure (PROC GLM, SAS Institute 1996). When a significant F was obtained, means were separated with the least significant difference (LSD, SAS Institute 1996). Most groups were maintained at the genus or family level. Unidentified adult male mesostigmatid mites, and rare (less than a total of 100 individuals collected over all replicate dates), or unidentified mesostigmatid mites were grouped into the category “other mesostigmatids.” In the Oribatida, Astigmata and Prostigmata, the categories “other oribatids,” “other astigmatids” and “other prostigmatids,” respectively, contained rare and unidentified adults within the respective suborder. Untransformed data are presented in all tables and figures.

Results

We collected a total of 45,606 individuals summed over 6 dates, four blocks, two sampling times in the two tillage regimes. These individuals were identified to 134 taxa (Appendix M).

Abundance

Significant effects on abundance due to tillage were detected in all seven groups except mesostigmatid and prostigmatid mites. All groups except Astigmata exhibited significant effects due to sampling time. All groups except Astigmata and Mesostigmata exhibited significant effects due to date. Block effects were universally significant in all groups at the 95% confidence level (Table 3-2, Table 3-3, Table 3-4, Table 3-5). All categories except the

Prostigmata were more abundant in no-till than in conventional-till corn. Invertebrate abundance varied among the four blocks (Table 3-6). All groups increased from 4-hour to 24-hour sampling time, with the exception of the Collembola in no-till corn, where abundance in all nematode treatments decreased except for the dead insect control (Table 3-2, Table 3-3, Table 3-4, Table 3-5).

Nematode treatment effects

Significant effects on abundance due to nematode treatment were detected in the total invertebrates, Prostigmata, Astigmata, Collembola and in the other invertebrates group (Table 3-2, Table 3-3, Table 3-4, Table 3-5). Total invertebrates were most abundant in the Rb, Sc, dead insect and soil controls, and Hb treatments in no-till soil respectively (Table 3-2, Table 3-3, Table 3-4, Table 3-5). In conventional-till soil, Total invertebrates were most abundant in dead insect control, Rb, Hb, Soil control and Sc treatments respectively. Both the Collembola and the “other invertebrates” were lower in abundance in the soil control in both tillage types, and higher in abundance in the dead insect control in both tillage types with abundance in the nematode treatments being intermediate (Table 3-2, Table 3-3, Table 3-4, Table 3-5). The Prostigmata were most abundant in the Rb, Sc, Dead, Hb, and soil treatments in conventionally-tilled soil, respectively. In no-till soil the Prostigmata were more abundant in the dead insect control, Rb, Sc, Soil and Hb treatments respectively. The Astigmata were more abundant in the Rb and Hb treatments in both tillage types (Table 3-2, Table 3-3, Table 3-4, Table 3-5).

Interactions

Interactions involving date, block, till and time were evident in many of the invertebrate groups (Table 3-2, Table 3-3, Table 3-4, Table 3-5). Several taxa also exhibited significant responses to interactions involving nematode treatments. Collembola exhibited a significant response to the interaction between time and nematode treatment (time*trt), in which abundance increased in all treatments from 4-hour to 24-hour time (Table 3-2, Table 3-3, Table 3-4, Table 3-5, Appendix S). Total invertebrates, Mesostigmata, Oribatida and Prostigmata also reflect significant interactions between sampling date and treatment (Table 3-2, Table 3-3, Table 3-4, Table 3-5, Appendix S).

Diversity

All diversity indices exhibited significant effects due to experimental variables. All indices, except Hill's diversity number 2 exhibited significant effects due to block. Shannon's index, Hill's diversity number 1 and richness all exhibited significant response to date and time. Shannon's index, Hill's diversity number 1, evenness and richness exhibited significant effects due to tillage type (Table 3-6). Evenness (df 4,30 F3.3, P0.0274) and richness (df 4,30, F 5.62, P0.0025) also exhibited effects due to nematode treatment and effects due to Interactions involving treatment. (Figure 3-2, Figure 3-3).

Community composition

Of the 55 taxa collected, 41 exhibited significant effects due to blocks (Appendix P), 28 taxa exhibited significant effects due to sampling date (Appendix P), 25 taxa exhibited significant effects due to sampling time

(Appendix P) and 14 taxa exhibited significant effects due to tillage type (Appendix P). Ten taxa responded significantly to treatments (Table 3-8, Appendix P).

Community composition effects due to treatment

Specific taxa exhibited a variety of significant responses to nematode treatments in the bait experiment (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, Q,R,S,T). Individuals in the “other Mesostigmata” tended to have greater abundance (than in the soil control) in the dead insect control, followed by the Sc and Rb, and less abundance in the Hb treatment (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendix T).

Galumna spp. exhibited a positive response (overall) to nematode treatments in conventionally-tilled soil and a negative response to nematode treatments in no-till soil. The positive responses they exhibited tended to be more prominent at the 4-hour sampling time than at the 24-hour sampling time (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, R, S, T). *Scheloribates spp.* exhibited a fairly consistent response with relative abundance highest in dead insect control, Rb and Sc treatments in both no-till and conventional-till. In no-till soil Hb was lower in abundance, in conventional-till soil the soil control was lower than the Hb treatment (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, Q, R, S, T). *Eupodes spp.* also exhibited a fairly consistent response, being more abundant in dead insect control, Sc and Rb treatments than in the soil control, but less abundant in

the Hb treatment in almost all cases (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, R, S, T). Abundance of Histiostomatidae was generally sporadic among dates, times and tillage regimes. In most cases, however, abundance tended to be higher in the Rb treatment and lower in the Hb treatment (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, R, S, T).

Entomobryidae exhibited a strong positive response to the dead insect control overall and generally a positive response to nematode treatments as well. The response to Hb treatment was generally either a very low positive response, however, or a negative response compared to the soil control (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, R, S, T).

Response within the Pauropoda was highly variable and very low numbers of individuals were detected on certain dates. On the dates that the largest numbers of Pauropods were collected they exhibited a strong positive response to the dead insect control, with response to nematode treatments varying from very negative to slightly positive (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, R, S, T). Symphylans exhibited a (varying) positive response to all nematode treatments and the dead insect control, with a general increase in abundance from 4 to 24 hours (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, R, S, T). Abundance of immature Diptera was high in the Rb and Hb treatments and increased significantly from 4 to 24 hours (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, R, S, T). Formicidae

exhibited a varying positive response to all nematode treatments and the dead insect control. The response was more pronounced in the conventionally-tilled soil than in the no-till soil (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, R, S, T).

Statistical contrasts between treatments distinguished significant differences in how some of the taxa that were responsive to treatment, responded within the various treatments (Table 3-7, Table 3-10 Appendix N).

Three taxa responded significantly when the two controls were contrasted against each other. Entomobryidae (df=1,24 F 23.04, $P<.0001$), Symphyla (df=1,24 F=8.69, $P=0.007$), and Formicidae (df =1,24 F=12.13 $P=0.0019$) were all significantly more abundant in the dead control than in the soil control (Appendix N). Entomobryidae, Symphyla and immature Diptera were also more abundant in the dead insect control and nematode treatments than in the soil control, particularly in no-till soil. Immature Diptera exhibited a positive response to Rb and Hb nematode treatments in both no-till and conventional-till soil (Appendix N).

Interactions

Interactions among the most significant experimental factors were also predominantly significant. All taxa significantly responded to the interaction of block by date (block*date). Of the 55 taxa evaluated, 34 responded significantly to tillage type by date (till*date), 23 responded significantly to the interaction of sampling time by date (time*date) and 7 taxa responded significantly to the interaction of tillage type by time (till*time) (Appendices S and Q).

Certain taxa also exhibited significant responses to effects due to interactions of experimental factors and nematode treatment. Six taxa responded significantly to the interaction of nematode treatment by date (trt*date)(Table 3-11. Of these six taxa two exhibited disproportionately high abundance on just one sample date. Both the Stigmaeidae and the immature Diptera were generally present in low numbers with the exception of one sampling date. High numbers of Stigmaeidae occurred only on 21 August 1999, particularly in the Sc treatment, while a high abundance of immature Diptera was detected, in the Rb and Hb treatments on 26 July 1999 (Table 3-11, Appendices P, U).

Ascidae were more abundant on 8 June 2000 and exhibited a general positive response to the Rb and Sc treatments on most dates (Table 3-11, Appendices P, U).

Scheloribates spp. were more abundant during the year 2000 than in 1999. They generally exhibited very little or negative response to nematode treatments on dates in 1999. In 2000 they occasionally exhibited a positive response to Sc or Rb treatments but generally a negative response to the Hb treatment (Table 3-11, Appendices P, U). *Tectocephus spp.* were very abundant on all dates in both 1999 and 2000. The response to nematode treatments, however, varied and did not exhibit any particular trend (Table 3-11, Appendices P, U).

Sancassania spp. were more prevalent during 2000 than during 1999, with the exception of one date, 26 July 1999, when they occurred in large numbers in the Sc treatment only. Their abundance was generally greater in 2000 but

response to specific nematode treatments varied. On dates in July and August they exhibited a positive response to nematode treatments, while on 8 June 2000 they exhibited a negative response to nematode treatments versus the soil only control (Table 3-11, Appendices P, U).

Six taxa responded significantly to the interaction of tillage type by nematode treatment (till*trt) (Table 3-12, Appendices P, Q). *Gamasellodes spp.* increased in abundance in the Rb and Hb treatments when compared with the soil only control in no-till soil and responded positively to dead insect control, Sc and Hb treatments versus soil control in conventionally-tilled soil (Table 3-12, Appendices P, Q). Both *Macrocheles spp.* and Phytoseidae exhibited a positive response to all nematode treatments and the dead insect control in no-till soil and a negative response to all treatments versus soil only control in conventional-till soil. *Macrocheles spp.*, however, were more prevalent in no-till soil than in conventional-till soil (Table 3-12, Appendices P, Q).

Galumna spp. exhibited a decrease abundance in all treatments in comparison to the soil only control in both no-till and conventional-till soil, but were present in much higher numbers in no-till soil (Table 3-12, Appendices P, Q).

Both *Eupodes spp.* and *Nanorchestes spp.* exhibited a negative response to all nematode treatments, but a positive response to the dead insect control in comparison to the soil only control in no-till soil. In conventional-till soil *Eupodes spp.* exhibited a positive response to all nematode treatments versus soil control, except the Hb treatment and *Nanorchestes spp.* exhibited a positive response to

all nematode treatments versus the soil only control (Table 3-12, Appendices P, Q).

Two taxa exhibited significant effects due to the interaction of time by nematode treatment (time*trt) (Table 3-13, Appendices P, R). One taxonomic group, the immature Diptera, was disproportionately abundant on one date, 26 July 1999, in the Rb and Hb treatments. The response in Brachychthoniidae, however, contrasted sharply between tillage regimes. A positive response to all nematode treatments versus soil control was indicated in no-till soil and a strong negative response to all nematode treatments versus soil control in conventional-till soil (Table 3-12, Appendices P, Q).

Discussion

The biology of introducing a relatively large insect cadaver full of tens of thousands of pre-emerging juvenile nematodes suspended in billions of their symbiotic bacteria and its host of chemical compounds is a much more complex system than the simple introduction of infective juveniles in a simple aqueous solution to the soil (Kaya and Gaugler 1993, Shapiro and Glazer 1996, Kaya and Stock 1997, Kopenhofer et al. 1997, Shapiro-ilan et al. 2003). This experiment included an uninfected insect cadaver as a control, but it is important to note that the EPN-infected cadaver was treated as a single unit, i.e., there were no isolating controls for the bacteria or their chemical compounds. Responses of the soil fauna are considered to be in relation to the entire bacteria-nematode-exudate complex, even though there may be specific factors within the complex

responsible for different soil fauna responses. Further in-depth studies are required to determine which factors influenced which responses.

This study incorporated the effects of two different families of entomopathogenic nematodes. The two species, *Steinernema carpocapsae* and *S. riobrave* belong to the family Steinernematidae, which is associated with *Xenorhabdus spp.* of bacteria. *Heterorhabditis bacteriophora*, in the family Heterorhabditidae is associated with *Photorhabdus spp.* of bacteria. This, in turn results in two different types nematode-bacteria complex because each strain of bacteria has its own corresponding chemical compounds (Kaya and Gaugler 1993, Kaya and Kopenhofer 1996). Therefore, we concluded that, to more accurately assess the different effects of each nematode-bacteria complex we should incorporate a contrast between the nematode genera in the statistical analysis (Appendix S). Because the two controls used in this experiment were also strikingly different from each other, one being just soil, while the other being an uninfected insect cadaver which represents a significant nutrient source, the controls were also contrasted against each other (Appendices C, D, L and S).

The nematode-bacteria complex within the insect cadaver appears to have varying effects on different soil-dwelling microarthropod taxa. Some taxa appear to be repelled, their numbers are lower than those of the control, and some taxa appear to respond positively to the different complexes

Abundance

The major physical experimental factors of this experiment, date, block, time and tillage regime, played a significant role in determining abundance of soil

organisms (Crossley et al. 1992, Carcamo et al. 1995, Carmona and Landis 1999, deGoede and Brussard 2002). The significance of these environmental factors was evident in the prevalence of response among all of the major groups of invertebrates. Universal effects on abundance due to blocks demonstrates the need for repetition (blocks) when evaluating soil community interactions, as well as, the patchiness in distribution and affinity for certain microhabitats among these organisms (Coleman and Crossley 1996, Hummel et al. 2002).

Soil communities exhibit a great deal of seasonal fluctuation (Coleman and Crossley 1996, Perdue and Crossley 1990) and it would be expected that date and even time (a difference of one day) would significantly change the abundance of certain groups of invertebrates, which was evident with a couple exceptions. Date and time did not significantly effect the abundance of Astigmata (currently contained within the Oribatida), although they did exhibit a positive response to Hb and Rb treatments overall (Table 3-2, Table 3-3, Table 3-4, Table 3-5). Astigmatid mites were present in low numbers with sporadic but inconsistent proliferations. They are characterized, biologically, as opportunists who proliferate rapidly in the presence of a food resource (O'Connor, B. 1994, Walter and Proctor 1999), this type of life history pattern is supported by results reported here.

The Mesostigmata also did not exhibit significant changes in abundance due to date (Table 3-2, Table 3-3, Table 3-4, Table 3-5). This taxonomic grouping contains a diverse assemblage of primarily long-legged mobile, long-lived

predatory mites with a wide range of morphological and behavioral adaptations to many different types of habitat (Walter and Proctor 1999).

Behavior within the Collembola, often contrary to that of the other major groups, may be complicated by their tendency for aggregation (Christiansen 1970, Barra and Christiansen 1975, Christiansen et al. 1992). Laboratory observations indicated that behavioral responses due to the release of aggregation pheromones play a more significant role in influencing distribution and abundance of collembolans than does the presence of moisture or food resources (Christiansen 1970, Barra and Christiansen 1975, Christiansen et al. 1992). In this experiment, collembolans were the only major group to decrease in abundance from the 4-hour to the 24-hour sampling time in no-till soil, in all treatments except the dead insect control, but increase in abundance in all treatments compared to the soil only control) in conventionally-tilled soil (Table 3-2, Table 3-3, Table 3-4, Table 3-5). It is difficult to ascertain what factors may be directly or indirectly (Polis 1994, Wootton 1994, Fox and Olsen 2000) influencing this response, and requires further investigation.

Prostigmatid mites were the only major group to exhibit higher abundances in conventionally-tilled soil than in no-till soil. They also demonstrated a consistent positive response to nematode treatments and the dead insect control in both tillage regimes (Table 3-2, Table 3-3, Table 3-4, Table 3-5). In all cases the response to Hb treatment was the lowest except for the soil only control) which may indicate properties of the Hb nematode-bacteria complex

that are less attractive or repellent compared with that of the other nematode complexes (Kaya and Kopenhofer 1996).

Diversity

Diversity was assessed in this research, as the number of taxa (at the finest level identified – Appendix M), or “richness” in each observation, subjected to major experimental factors and treatments. Additional assessments of diversity included evenness (the relative species abundance among the observed taxa), as well as a number of indices intended to evaluate combined properties of richness and evenness. The indices used to make these evaluations included Shannon’s index (Shannon and Weaver 1949), Simpsons’s index (Simpson 1949) and Hill’s diversity numbers 1 and 2 (Hill 1973). None of these indices exhibited any significant effects on abundance due to treatments (Table 3-6, Figure 3-2, Figure 3-3).

Both taxonomic richness and evenness, however, exhibited significant responses due to treatments. Evenness decreased in all treatments except the soil only control in both tillage regimes with the exception of the Sc treatment in no-till soil (Table 3-6, Figure 3-2, Figure 3-3). The fluctuations in abundance among observed taxa in all treatments indicate that assessment at the level of community composition is required to accurately ascertain how each taxon is responding to the presence of the infected cadavers, and dead insect control.

Taxonomic richness varied significantly among sampling dates. The dead insect control and Sc treatment were consistently higher in richness compared with the soil only control on all dates, except one. The Rb treatment was higher in

richness on all sampling dates. The Hb treatment was lower in species richness compared with the soil only control on 3 dates and higher on 3 dates (Table 3-6, Figure 3-2, Figure 3-3). This may also be a reflection of properties of the Hb nematode-bacteria complex that are less attractive or repellent compared with the other treatments (Kaya and Kopenhofer 1996).

The significance of species richness as a community characteristic is subject to controversy (Hurlbert 1971). It is generally only considered to be useful in assessing the effects within soil communities if used “in context” with other descriptors (Elkschmitt and Griffiths 1998). Elkschmitt and Griffiths (1998) did indicate, however, that higher species richness within trophic levels of the decomposer food web could aid nutrient cycling processes by decreasing spatial and temporal functional gaps.

Community composition

As in the larger taxonomic groupings, many of the individual taxa also reflected significant effects on abundance due to the experimental factors of sampling date, sampling time, tillage regime, blocks and interactions thereof.

Responses to treatment, however, were varied in both response type and magnitude (Table 3-8, Table 3-7, Table 3-10, Table 3-11, Table 3-12, Table 3-13, Appendices N, P, R, S, T).

The generally decreased abundance relative to soil only control of many taxa (*Scheloribates spp.*, *Eupodes spp.*, other Mesostigmata, *Galumna spp.* in no-till soil, Pauropoda and Entomobryidae) within the Hb treatment (Figure 3-2,

Figure 3-3, Table 3-10, Table 3-11, Table 3-13, Table 3-12, Appendices N, Q, R, T, U) could be reflective of laboratory observations of Kaya and Kopenhöfer (1996) of certain repellent properties of the nematode-bacteria complex (and its metabolites). This trend could also be the result of a less quantifiable indirect effect resulting from the multitude of interactions occurring in proximity to the disturbance represented by the placement and presence of the infected insect cadaver (Polis 1994, Wootton 1994, Elkschmitt and Griffiths 1998, Fox and Olsen 2000). Further experimentation is required to ascertain the cause and nature of this response.

Other taxa exhibited a response somewhat contrary to that mentioned above. Immature Diptera increased in abundance significantly in both the Rb and Hb treatments compared with both controls and the Sc treatment from 4 to 24 hours. This apparent attraction to the Rb and Hb nematode-bacteria complex also warrants further investigation. Large numbers of adult Phorid flies were observed near the Rb and Hb cadavers both in the lab and in the field (Greenwood, unpubl. Data)

Responses among individual taxa belonging to the same large taxonomic grouping also varied significantly, further confirming the need to evaluate soil community interactions at the level of community composition. Within the Mesostigmata, *Gamasellodes spp.* increased in abundance in nematode treatments and dead insect control compared with the soil only control in conventionally-tilled soil. *Macrocheles spp.* and Phytoseidae, however, decreased in abundance in all nematode treatments and dead insect control

relative to the soil only control in conventionally-tilled soil, and increased in abundance in all nematode treatments and dead insect control (relative to soil control) in no-till soil (Figure 3-2, Figure 3-3, Table 3-10, Table 3-11, Table 3-13, Table 3-12, Appendices N, Q, R,T, U).

The Prostigmata, consistently increased in abundance in all nematode treatments and dead insect control relative to soil only control in both tillage regimes. In community composition analyses, however, certain taxa responded differently than the larger taxonomic affiliation. *Eupodes spp.* and *Nanorchestes spp.* decreased in abundance in all nematode treatments relative to soil control, except for the dead insect control in no-till soil. Both, however, increased in abundance Sc and Rb treatments and dead insect control relative to the soil only control in conventionally-tilled soil (Figure 3-2, Figure 3-3, Table 3-10, Table 3-12, Appendices N, Q, R,T, U).

The larger grouping of Oribatida exhibited no significant response in abundance due to treatment (in the abundance section). Certain oribatid taxa, however, exhibited significant responses in abundance due to treatment. Some of the most abundant soil invertebrates collected (Appendix M), *Tectocephus spp.* and *Scheloribates spp.* exhibited significant increases in abundance, particularly within the Sc and Rb treatments (Figure 3-2, Figure 3-3, Table 3-10, Table 3-12, Appendices N, P, Q, T).

Detailed examination of soil fauna responses to the introduction of EPN-infected insect cadavers reveals a very diverse and complicated range of interactions (Barbercheck and Kaya 1991a and b). The soil community system in

general is extremely complex. The high abundance and diversity of the community (Mueller et al. 1990, Barbercheck 1992, Hansen and Coleman 1998, Laakso and Setälä 1999, Barbercheck and Millar 2000, Scheu 2002), the physical heterogeneity of the soil environment (Hooper et al. 2000, Fox and Olsen 2000, Ettema and Wardle 2002), and the adaptations of soil organisms to the pulsed input of resources (Polis 1994, Andren et al. 1999, Ostfield and Keesing 2000) contribute to an ecosystem that can be extremely difficult to assess.

Therefore, based on findings of this research, further, in-depth evaluations of the response of soil fauna to the introduction of EPN are needed to ascertain specific interactions related to potential impacts on population dynamics of EPN, and to potential non-target effects on soil fauna resulting from nematode application. More detailed information regarding the biology and ecology of soil fauna at finer taxonomic designations is required to accurately assess interactions. Different vehicles of EPN delivery should be evaluated. Physical and experimental factors should be taken into account. Response of soil fauna should be assessed at the finest taxonomic level possible to ensure the most accurate reflection of specific biological interactions.

References

- Andrén, O. and J. Lagerlöf.** 1983. Soil fauna (microarthropods, enchytraeids, nematodes) in Swedish agricultural cropping systems. *Acta Agricultural Scandinavia* 33: 33-52.
- Andren, O., L. Brussard, and M. Clarholm.** 1999. Soil organism influence on ecosystem-level processes – bypassing the ecological hierarchy? *Applied Soil Ecology* 11: 177-188.
- Balogh, J.** 1972. The oribatid genera of the world. *Akademiai Kiado.* Budapest. 331 pp.
- Barbercheck, M.E. and H.K. Kaya.** 1991a. Effect of host condition and soil texture on host finding by the entomogenous nematodes *Heterorhabditis bacteriophora* (Rhabditida: Heterorhabditidae) and *Steinernema carpocapsae* (Rhabditida: Steinernematidae). *Environ. Entomol.* 20: 582-589.
- Barbercheck, M.E. and H.K. Kaya.** 1991b. Competitive interactions between entomopathogenic nematodes and *Bearveria bassiana* (Deuteromycotina: Hyphomycetes) in soilborne larvae of *Spodoptera exigua* (Lepidoptera: Noctuidae). *Environ. Entomol.* 20: 707-712.
- Barbercheck, M.E. and L.C. Millar.** 2000. Environmental impacts of entomopathogenic nematodes used for biological control in soil. Chapter 17 in: *Nontarget Effects of Biological Control*. P. Follett and J. Duan, eds. Kluwer Academic Publishers.
- Barbercheck, M.E.** 1992. Effect of soil physical factors on biological control agents of soil insect pests. *Fl. Entomol.* 75: 539-548.
- Barra, J. and Christiansen, K.** 1975. Experimental study of aggregation during the development of *Psuedosinella impediens* (Collembola: Entomobryidae). *Pedobiologia* 15: 343-347.
- Bathon, H.** 1996. Impact of entomopathogenic nematodes on non-target hosts. *Biocontrol Science and Technology* (1996) 6: 421-434.
- Beare, M.H., P.Hendrix, and D. Coleman.** 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. *Ecol. Monogr.* 62: 569-591.
- Belnap, J. and S. L. Phillips.** 2001. Soil biota in an ungrazed grassland: Response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications*, 11 (5): 1261-1275.
- Bilgrami, A.L., Jairajpuri, M.S.** 1989a. Predatory abilities of *Mononchoides longicaudatus* and *M. fortidens* (Nematoda: Diplogasterida) and factors influencing predation. *Nematologica* 35, 475-488.
- Bilgrami, A.L., Jairajpuri, M.S.** 1989b. Resistance of prey to predation and strike rate of the predators *Mononchoides longicaudatus* and *M. fortidans* (Nematoda: Diplogasterida). *Revue de Nematologie* 12, 45-49.
- Brown, I.M., Gaugler, R.** 1997. Temperature and humidity influence emergence and survival of entomopathogenic nematodes. *Nematologica* 43, 363-375.
- Brust, G.E.** 1991. Augmentation of an endemic entomogenous nematode by agroecosystem manipulation for the control of a soil pest. *Agric. Ecosyst.*

Environ. 36: 175-184

Campbell, J. and R. Gaugler. 1997. Interspecific variation in entomopathogenic nematode foraging strategy: dichotomy or variation along a continuum?

Fundamental and Applied Nematology 20: 393-398.

Carcamo, H.A., J.K. Niemala, and J.R. Spence. 1995. Farming and ground beetles: effects of agronomic practice on populations and community structure.

Can. Entomol. 127:123-140.

Carmona, D. M., and Landis, D. A. (1999). Influence of refuge habitats and cover crops on seasonal activity-density of ground beetles (Coleoptera:

Carabidae) in field crops. *Biological Control* 28: 1145-1153.

Christiansen, K. 1970. Experimental studies on the aggregation and dispersion of Collembola. *Pedobiologia* 10: 180-198.

Christiansen, K.A. and B.F. Bellinger. 1979. *The Collembola of North America North of the Rio Grande.* Grinnell College, IA.

Christiansen, K.A., K. Doyle, M. Kahlert, D. Gobaleza. 1992. Interspecific interactions between collembolan populations in culture. *Pedobiologia* 36: 274-286.

Cobb, N.A. 1917. The mononchs (*Mononchus* Bastian, 1866) a genus of free-living predatory nematodes. *Soil Science* 3: 431-486.

Coll, M. and M. Guershon. 2002. Omnivory in terrestrial arthropods: Mixing plant and prey diets. *Annu. Rev. Entomol.* 2002. 47: 267-297.

Coleman, D.C. and D.A. Crossley Jr. 1996. *Fundamentals of Soil Ecology.* Academic Press. 205pp.

Crossely, D.A., Jr., Coleman D. and E. Odum. 1992. Biodiversity of microarthropods in agricultural soils: relations to processes. *Agric. Ecosys. Environ.* 40: 37-46.

De Goede, R.G.M. and L. Brussard. 2002. Soil zoology: An indispensable component of integrated ecosystem studies. *European J. Soil Biology* 38 (2002): 1-6.

Dindal, D.L. 1990. *Soil Biology Guide.* New York: John Wiley and Sons.

Edwards, C., B. Stinner, D. Stinner and S. Rabatan (eds). 1988. *Biological interactions in soils.* Elsevier Science Pub. Amsterdam

Edwards, C.A. 1991. The assessment of populations of soil-inhabiting invertebrates. *Agriculture, Ecosystems and Environment* 34: 145-176.

Elkshmitt, K. and Griffiths, B. 1998. Soil biodiversity and its implications for ecosystem functioning in a heterogeneous and variable environment. *Applied Soil Ecology* 10: 201-215

Ettema, C.H. and D. A. Wardle. 2002. Spatial soil ecology. *TRENDS in Ecology and Evolution* Vol. 17. No. 4 April 2002: 177-183.

Ferriss, R.S. 1984. Effects of microwave oven treatment on microorganisms in soil. *Phytopathology* 74: 121-126.

Fox, J. and E. Olsen. 2000. Food web structure and the strength of transient indirect effects. *Oikos* 90: 219-226.

Georgis, R. 1992. Present and future prospects for entomopathogenic nematode products. *Biocontrol. Sci. Tech.* 2: 83-99.

Gilmore, S.K. and D.A. Potter. 1993. Potential role of Collembola as biotic

mortality agents for entomopathogenic nematodes. *Pedobiologia* 37: 30-38.

Glazer, I., E. Kozodoi, L. Salame, and D. Nestel. 1995. Spatial and temporal occurrence of natural populations of *Heterorhabditis* spp. (Nematoda: Rhabditida) in a semiarid region. *Biol. Control* 6: 130-136.

Grewel, P., E. Lewis, J. Campbell, and R. Gaugler. 1994. Searching behavior as a predictor of foraging strategy for entomopathogenic nematodes. *Parasitology* 108: 207-215.

Hansen, R. and D. Coleman. 1998. Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acari: Oribatida) in litterbags. *Applied Soil Ecology* 9: 17-23.

Hendrix, P.F., R. Parmalee, R. Crossley, D. Coleman, E. Odum and P. Groffman. 1986. Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience* 36: 374-380.

Hill, M. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* 54: 427-432.

Hooper, D., D.E. Bignell, V.K. Brown, L. Brussard, J.M. Dangerfield, D.H. Wall, D.A. Wardle, D.C. Coleman, K.E. Giller, P. Lavelle, W.H. Van der Putten, P.C. DeRuiter, J. Rusek, W.L. Silver, J.M. Tiedje, and V. Wolters. 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: Patterns, Mechanisms, and Feedbacks. *BioScience* Vol. 50 No. 12: 1049-1061.

House, G.J. and M.D. R. Alzugaray. 1989. Influence of cover cropping and no-tillage practices on community composition of soil arthropods in a North Carolina agroecosystem. *Environ. Entomol.* 18: 302-307.

House, G.J. and B.R. Stinner. 1983. Arthropods in no-tillage soybean agroeco-systems: Community composition and ecosystem interactions. *Environmental management* 7(1): 23-28.

Hummel, R.L., J. F. Walgenbach, M.E. Barbercheck, G.G. Kennedy, G.D. Hoyt, and C. Arellano. 2002. Effects of production practices on soil-borne entomopathogens in western North Carolina vegetable systems. *Environ. Entomol.* 31 (1): 84-91.

Jackson, D. and L. Jackson (eds). 2002. *The Farm as Natural Habitat*. Island Press. Washington.

Jansson, R.K., Lecrone, S.H., Gaugler, R. 1993. Field efficacy and persistence of entomopathogenic nematodes (*Rhabditida: Steinernematidae, Heterorhabditidae*) as biological control agents of the sweetpotato weevil (*Coleoptera: Apionidae*) in southern Florida. *J. Econ. Entomol.* 86:1055-1063.

Kaya, H.K. and R. Gaugler. 1993. Entomopathogenic nematodes. *Ann Rev. Entomol.* 38: 181-206.

Kaya, H. and S. Stock. 1997. Techniques in insect nematology in: *Manual of Techniques in Insect Pathology*. L.A. Lacey, ed. Academic Press. London. Pp. 281-324.

Kajak, A. and H. Jakubczyk. 1977. Experimental studies on predation in the soil-litter interface. *Ecol. Bull.* (Stockholm) 25: 493-496.

- Koppenhöfer A.M, and H. Kaya.** 1996. Coexistence of entomopathogenic nematode species (Steinernematidae and Heterorhabditidae) with different foraging behavior. *Fundamentals of Applied Nematology* 19: 175-183.
- Koppenhöfer A.M., Baur, M.E., Stock S.P., Choo H.Y., Chinnasri B., Kaya, H.K.** 1997. Survival of entomopathogenic nematodes within host cadavers in dry soil. *Applied Soil Ecology* 6, 231-240
- Krantz, G.W.,** 1978. *A Manual of Acarology.* (second edition), Oregon State University Press. Corvallis, Oregon. 509 pp.
- Laakso, J. and H. Setälä.** 1999. Population and ecosystem level effects of Predation on microbial-feeding nematodes. *Oecologia* 120: 279-286.
- Lagerlof, J. and O. Andren.** 1988. Abundance and activity of soil mites (Acari) in four cropping systems. *Pedobiologia* 32: 129-145.
- Lewis, E., R. Gaugler and R. Harrison.** 1992. Entomopathogenic nematode host finding: response to host contact cues by cruise and ambush foragers. *Parasitology* 105: 309-319.
- Lewis, E., R. Gaugler and R. Harrison.** 1993. Response of cruiser and ambusher entomopathogenic nematodes (Steinernematidae) to host volatile cues. *Canadian Journal of Zoology* 71: 765-769
- Ludwig, J. and J. Reynolds.** 1988. *Statistical Ecology.* John Wiley and sons. New York
- Mikola, Juha and H. Setälä.** 1998. No evidence of trophic cascades in an Experimental microbial-based soil food web. *Ecology* 79(1): 153-164.
- Millar, L.C. and M.E. Barbercheck.** 2002. Effects of tillage practices on Entomopathogenic nematodes in a corn agroecosystem. *Biological Control* 25: 11-20.
- Mueller, B.R., M.H. Beare and D.A. Crossley, Jr.** 1990. Soil mites in detrital food webs of conventional and no-tillage agroecosystems. *Pedobiologia* 34: 389-401.
- Murphy, P.W., Doncaster C.C.** 1957. A culture method for soil meiofauna and its application to the study of nematode predators. *Nematologica* 2, 202-214.
- Neave, P. and C.A. Fox.** 1998. Response of soil invertebrates to reduced tillage systems established on a clay loam soil. *Applied Soil Ecology* 9: 423-428.
- Neher, D. and M. Barbercheck.** 1990. Diversity and function of soil mesofauna. Chapter 3 of: *Biodiversity in Agroecosystems.* W.W. Collins and C.O. Qualset, eds. CRC Press.
- Nelmes, A.J., McCulloch, J.S.** 1975. Numbers of mononchid nematodes in soils sown to cereals and grasses. *Annals of Applied Biology* 79, 231-242.
- O'Connor, B.** 1994. Life-history modifications in astigmatid mites, in *Mites: Ecological and Evolutionary Analyses of Life-History Patterns.* M.A. Houck, ed. Chapman and Hall. New York. Pp354-381.
- Ostfield, R.S and F. Keesing.** 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *TREE* Vol. 15 No. 6. June 2000: 232-238.
- Parkman, J.P., Hudson, W.G., Frank, J.H., Nguyen, K.B., Smart, G.C.** 1993. Establishment and persistence of *Steinernema scapterisci*

- (Rhabditida:Steinernematidae) in field populations of *Scapteriscus spp.* mole crickets (Orthoptera: Gryllotalpidae). *J. Entomol. Sci.* 28:182- 190.
- Perdue, J. and D. Crossley.** 1990. Seasonal abundance of soil mites (Acari) in experimental agroecosystems: Effects of drought in no-tillage and conventional tillage soil. *Soil and Tillage Res.* 25: 145-156.
- Pfiffner, L. and U. Niggli.** 1996. Effects of bio-dynamic, organic and conventional farming on ground beetles (Colembola: Carabidae) and other epigaeic arthropods in winter wheat. *Biol. Agric. Hort.* 12: 353-364.
- Pimm, S.L.** 1982. *Food webs.* Chapman and Hall, NY. 219 pp.
- Polis, G.** 1994. Food webs, trophic cascades and community structure. *Australian Journal of Ecology* (1994) 19: 121-136
- Raulston, J.R. et al.** 1992. Prepupal and pupal parasitism of *Helicoverpa zea* and *Spodoptera frugiperda* (Lepidoptera: Noctuidae) by *Steinernema sp.* in cornfields in the lower Rio Grande valley. *J. Econ. Entomol.* 85: 1666-1670.
- Rosenheim, J.A., H.K. Kaya, L.E. Ehler, J.J. Marois and B.A. Jaffee.** 1995. Intraguild predation among biological-control agents: Theory and evidence. *Biological Control* 5: 303-335.
- Scheu, Stefan.** 2002. The soil food web: Structure and perspectives. *European J. of Soil Biology* 38: 11-20.
- Shannon, C. and W. Weaver.** 1949. *The mathematical theory of communication.* University Illinois Press, Urbana, Ill.
- Shapiro-Ilan, D.I., Gaugler, R.** 2002. Production technology for entomopathogenic nematodes and their bacterial symbionts. *J. Ind. Microbiol. Biot.* 28: 137-146.
- Shapiro, D. I., Glazer, I.** 1996. Comparison of entomopathogenic nematode dispersal from infected hosts versus aqueous suspension. *Environ. Entomol.* 25: 1455-1461.
- Shapiro D.I., Lewis E.E.** 1999. Comparison of entomopathogenic nematode infectivity from infected hosts versus aqueous suspension. *Environ. Entomol.* 28: 907-911.
- Shapiro-ilan, D., E.E. Lewis, S.W. Youngsoo, and L. Tedders.** 2003. Superior efficacy observed in entomopathogenic nematodes applied in infected host cadavers compared with application in aqueous suspension. *J. of Invertebrate Pathology* 83 (3) July 2003: 270-272.
- Simpson, E.** 1949. Measurement of diversity. *Nature* 163: 168
- Smits, P.** 1996. Post-application persistence of entomopathogenic nematodes *Biocontrol Science and Technology* 6: 379-387.
- Steen, E.** 1983. Soil animals in relation to agricultural practices and soil productivity. *Swedish J. Agricultural Res.* 13: 157-165.
- Stinner, B.R. and G.J. House.** 1990. Arthropods and other invertebrates in conservation-tillage agriculture. *Ann. Rev. Entomol.* 35: 299-318.
- Symondson, W.O.C., K.D. Sunderland and M.H. Greenstone.** 2002. Can Generalist predators be effective biocontrol agents? *Annu. Rev. Entomol.* 2002, 47: 561-594.
- Van de Bund, C.F.** 1970. Influence of crop and tillage on mites and springtails

in arable soil. *Neth. J. Agric. Sci.* 18: 308-314.

Van der Werf, W., et al. 1995. Concepts and prospects for modelling the efficacy and ecology of entomopathogenic nematodes. Pp. 42-51 in

Ecology and transmission strategies of entomopathogenic nematodes,

Walter, D.E., R.A. Hudgens, and D.W. Freckman. 1986. Consumption of nematodes by fungivorous mites, *Tyrophagus* spp. (Acarina: Astigmata: Acaridae). *Oecologia* (Berlin) 1970: 357-361.

Walter, D.E. 1987. Trophic behavior of "mycophagous" microarthropods. *Ecology* 68(1): 226-229.

Walter, D.E. and E.K. Ikonen. 1989. Species, guilds, and functional groups: taxonomy and behavior in nematophagous arthropods. *J. Nematol.* 21: 315-327.

Walter, D.E., J.C. Moore, and S.J. Loring. 1989. *Symphylela* sp. (Symphyla: Scolopendrellidae) predators of arthropods and nematodes in grassland Soils. *Pedobiologia* 33: 113-116.

Walter, D.E. and D.T. Kaplan. 1990. Feeding observations on two astigmatic mites, *Schwiebea rocketti* (acaridae) and *Histiostoma bakeri* (Histiostomatidae) associated with *Citrus* feeder roots. *Pedobiologia* 34: 281-286.

Walter, D.E. and H. Proctor. 1999. *Mites: Ecology, Evolution and Behaviour.* CABI Publ. New York, NY.

Wootton, J.T. 1994. The nature and consequences of indirect effects in ecological communities. *Annu. Rev. Ecol. Syst.* 25: 443-66

Table 3-1 Total number of invertebrates collected, grouped into 6 categories (Mesostigmata, Oribatida, Prostigmata, Astigmata, Collembola and other invertebrates) with the sum of all 6 categories constituting "Total invertebrates." Pooled data derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 tillage regimes (NT=no-till CT=conventional-till), 2 sampling times (4 and 24 hours) and 5 treatments (Soil, Dead=dead uninfected insect, Sc(=*G.mellonella* larva infected with *S. carpocapsae* nematodes), Rb(=*G.mellonella* larva infected with *S. riobrave* nematodes), Hb(=*G.mellonella* larva infected with *H. bacteriophora* nematodes))

Total invertebrates	45606
Soil mites (Arachnida: Acari)	
Mesostigmata	4267
Oribatida	21184
Prostigmata	3373
Astigmata	3059
Insects	
Collembola	7787
Other invertebrates	5936

Table 3-2 f, df, and p statistics for 6 dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), two tillage regimes (no-till and conventional till, 5 treatments (Soil, Dead=dead uninfected insect, Sc(=*G.mellonella* larva infected with *S. carpocapsae* nematodes), Rb(=*G.mellonella* larva infected with *S. riobrave* nematodes), Hb(=*G.mellonella* larva infected with *H. bacteriophora* nematodes)) and two sampling times (4 and 24 hours). Superscripts 1 -17 indicate error terms used for analysis, see Appendix S.

	total invertebrates		Collembola		other invertebrates	
Total abund	45606		7787		5936	
% in No-till	63.40%		61.80%		50.70%	
major factors(df)	F	Pr<F	F	Pr<F	F	Pr<F
Date ¹ (5,15)	14.81	<.0001	11.99	<.0001	4.94	0.0072
Till ² (1,3)	40.18	0.0079	15.64	0.0289	37.49	0.0088
Time ³ (1,30)	63.31	<.0001	75.02	<.0001	33.89	<.0001
till*date ⁴ (5,20)	22.56	<.0001	6.56	<.0001	6.82	<.0001
time*date ⁵ (5,20)	5.98	<.0001	ns	ns	2.68	0.0219
till*time ⁶ (1,30)	10.10	0.0034	26.41	<.0001	ns	ns
tr*date ⁷ (20,20)	2.05	0.0056	ns	ns	ns	ns
Trt ⁸ (4,24)	6.07	0.0016	ns	ns	3.97	0.0131
Contrasts(1,24)	F	Pr<F	F	Pr<F	F	Pr<F
Soil*Dead ⁹	14.84	0.0008	ns	ns	11.31	0.0026
Soil*trt ¹⁰	8.12	0.0088	ns	ns	ns	ns
Dead*trt ¹¹	ns	ns	ns	ns	4.33	0.0482
Hb*Sc, Rb ¹²	8.52	0.0075	ns	ns	4.54	0.0436
Rb*Sc, Hb ¹³	4.35	0.0477	ns	ns	ns	ns
Sc*Rb, Hb ¹⁴	ns	ns	ns	ns	ns	ns

Table 3-3 f, df, and p statistics for major factors, interactions and contrasts of abundance data. Pooled data is derived from 6 dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), two tillage regimes (no-till and conventional till), 5 treatments (Soil, Dead=dead uninfected insect, Sc(=*G.mellonella* larva infected with *S. carpocapsae* nematodes), Rb(=*G.mellonella* larva infected with *S. riobrave* nematodes), Hb(=*G.mellonella* larva infected with *H. bacteriophora* nematodes)) and two sampling times (4 and 24 hours). Superscripts 1-17 indicate error terms used for analysis, see Appendix S.

	Mesostigmata		Oribatida		Prostigmata		Astigmata	
Total abund	4267		21184		3373		3059	
% in No-till	49.90%		72.20%		42.40%		73.90%	
major factors(df)	F	Pr<F	F	Pr<F	F	Pr<F	F	Pr<F
Date ¹ (5,15)	ns	ns	6.61	0.0019	43.22	<.0001	ns	ns
Till ² (1,3)	ns	ns	27.34	0.0136	ns	ns	44.1	0.007
Time ³ (1,30)	78.3	<.0001	16.6	0.0003	58.34	<.0001	ns	ns
till*date ⁴ (5,20)	8.6	<.0001	ns	ns	2.58	0.0263	12.52	<.0001
time*date ⁵ (5,20)	6.51	<.0001	ns	ns	9.13	<.0001	18.9	<.0001
till*time ⁶ (1,30)	16.82	0.0003	ns	ns	6.12	0.0193	14.58	0.0006
tr*date ⁷ (20,20)	1.7	0.0331	1.83	0.0178	1.86	0.0154	ns	ns
Trt ⁸ (4,24)	ns	ns	ns	ns	ns	ns	ns	ns
Contrasts(1,24)	F	Pr<F	F	Pr<F	F	Pr<F	F	Pr<F
Soil*Dead ⁹	ns	ns	ns	ns	ns	ns	ns	ns
Soil*trt ¹⁰	ns	ns	ns	ns	ns	ns	ns	ns
Dead*trt ¹¹	ns	ns	ns	ns	ns	ns	ns	ns
Hb*Sc, Rb ¹²	ns	ns	ns	ns	8.26	0.0084	ns	ns
Rb*Sc, Hb ¹³	ns	ns	ns	ns	ns	ns	ns	ns
Sc*Rb, Hb ¹⁴	ns	ns	ns	ns	ns	ns	8.21	0.0085

Table 3-4 Mean (\pm std. err.) abundance of soil invertebrates in conventionally-tilled soil in bait experiment. Invertebrates are grouped into 7 major categories (Mesostigmata, Oribatida, Prostigmata, Astigmata, Collembola, other invertebrates, total invertebrates=sum of other 6 groups). Pooled data derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, dead (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Treatment	Hb		Rb		Sc		Soil		Dead	
Observations	(n=24)		(n=24)		(n=24)		(n=24)		(n=24)	
Time (hr)	4	24	4	24	4	24	4	24	4	24
Mesostigmata	4.833	10.625	4.833	14.000	7.250	12.333	5.208	10.500	5.417	14.083
	± 0.870	± 1.497	± 1.116	± 2.537	± 1.158	± 2.445	± 0.858	± 1.866	± 0.878	± 1.919
Oribatida	18.667	25.375	22.417	26.042	24.042	24.375	20.875	29.583	25.500	28.875
	± 2.545	± 2.890	± 4.041	± 4.110	± 3.773	± 3.556	± 3.480	± 5.139	± 3.250	± 4.463
Prostigmata	6.667	7.167	7.083	11.208	6.458	12.667	4.500	9.083	5.833	10.333
	± 1.857	± 1.068	± 1.816	± 1.733	± 1.328	± 2.726	± 0.907	± 1.260	± 1.801	± 1.825
Astigmata	2.458	4.542	2.167	3.583	2.167	3.583	3.333	4.042	2.875	4.542
	± 0.561	± 1.021	± 0.384	± 0.766	± 0.677	± 0.812	± 0.906	± 0.869	± 0.830	± 0.978
Collembola	6.917	15.750	7.917	19.375	7.458	17.625	7.958	11.958	8.958	19.958
	± 1.100	± 2.700	± 2.073	± 3.002	± 1.404	± 3.318	± 1.440	± 2.454	± 1.523	± 3.543
Other invertebrates	9.292	13.708	6.917	13.000	8.500	24.958	6.875	5.750	15.250	17.667
	± 5.149	± 6.402	± 1.635	± 3.109	± 2.835	± 11.614	± 1.684	± 0.897	± 5.517	± 5.637
Total invertebrates	48.833	77.167	51.333	87.208	55.875	95.542	48.750	70.917	63.833	95.458
	± 7.644	± 7.843	± 6.520	± 7.820	± 6.315	± 11.074	± 6.024	± 8.227	± 8.002	± 10.903

Table 3-5 Mean (\pm std. err.) abundance of soil invertebrates in no-till soil in bait experiment. Invertebrates are grouped into 7 major categories (Mesostigmata, Oribatida, Prostigmata, Astigmata, Collembola, other invertebrates, total invertebrates=sum of other 6 groups). Pooled data derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, dead (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Treatment	Hb		Rb		Sc		Soil		Dead	
Observations	(n=24)									
Time (hr)	4	24	4	24	4	24	4	24	4	24
Mesostigmata	7.875	8.208	8.625	10.750	8.750	11.042	6.792	8.042	7.833	10.792
	± 1.266	± 1.124	± 1.443	± 1.805	± 1.657	± 0.984	± 1.278	± 1.177	± 1.061	± 2.025
Oribatida	53.625	64.333	66.333	76.542	56.875	64.583	55.000	65.958	63.542	70.125
	± 6.870	± 8.970	± 7.354	± 10.090	± 6.754	± 8.005	± 9.297	± 6.230	± 7.940	± 9.540
Prostigmata	3.375	5.083	4.958	7.125	4.292	6.833	4.042	9.375	6.250	8.208
	± 0.610	± 0.907	± 1.272	± 1.514	± 0.820	± 1.240	± 0.726	± 2.878	± 1.149	± 1.760
Astigmata	13.917	9.292	15.875	9.500	9.667	5.083	9.708	4.167	7.833	9.125
	± 7.179	± 2.785	± 7.694	± 2.552	± 3.243	± 1.427	± 3.370	± 0.981	± 2.070	± 2.597
Collembola	17.000	16.333	20.208	26.000	18.750	21.250	20.042	17.250	16.583	27.167
	± 3.795	± 2.153	± 3.401	± 4.902	± 3.671	± 2.924	± 5.318	± 2.160	± 2.068	± 3.027
Other	7.333	9.625	10.042	28.042	10.083	14.750	7.542	9.667	9.500	18.833
invertebrates	± 0.851	± 1.380	± 1.368	± 6.225	± 1.315	± 2.530	± 0.929	± 1.398	± 0.832	± 3.182
Total	103.125	112.875	126.042	157.958	108.417	123.542	103.125	114.458	111.542	144.250
invertebrates	± 15.969	± 13.242	± 18.394	± 14.535	± 14.530	± 11.467	± 18.906	± 10.028	± 11.506	± 13.523

Table 3-6 f, df, and p statistics for experimental factors, interactions and contrasts of abundance data. Pooled data is derived from 6 dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), two tillage regimes (no-till and conventional till), 5 treatments (Soil, Dead=dead uninfected insect, Sc(=*G.mellonella* larva infected with *S. carpocapsae* nematodes), Rb(=*G.mellonella* larva infected with *S. riobrave* nematodes), Hb(=*G.mellonella* larva infected with *H. bacteriophora* nematodes)) and two sampling times (4 and 24 hours) (df = 4,30 for all analyses)

Diversity measure	Till df = 1,3		Block df = 3,30		Time df = 1,30		Date df = 5,15		Trt df = 4,24	
	F	P	F	P	F	P	F	P	F	trt
Shannon's index	9.09	0.057	9.94	<.0001	28.4	<.0001	5.09	0.0063	ns	ns
Simpson's index	ns	ns	3.54	0.0152	ns	ns	ns	ns	ns	ns
Hill's diversity number 1	18.73	0.0227	7.86	<.0001	31.78	<.0001	7.03	0.0014	ns	ns
evenness	46.43	0.0065	3.14	0.0258	ns	ns	ns	ns	3.3	0.0274
No. taxa (richness)	61.73	0.0043	7.32	<.0001	75.36	<.0001	15.85	<.0001	5.62	0.0025
Hill's diversity number 2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 3-7 Representative taxonomic groups of invertebrates collected, total abundance and proportion found in No-till (NT) soil (versus Conventional-till soil). Pooled data derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, dead (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Taxon	total	% in NT
Arachnida		
Acari		
Mesostigmata		
Ascidae	166	73.50%
<i>Gamasellodes spp.</i>	138	46.40%
<i>Protogamasellus spp.</i>	765	6.50%
<i>Hypoaspis spp.</i>	647	47.60%
<i>Macrocheles spp.</i>	441	91.40%
Parasitidae	43	93.00%
Phytoseidae	120	65.80%
<i>Rhodacarus spp.</i>	411	66.40%
Uropodidae	96	62.50%
Other Mesostigmata	375	61.90%
Mesostigmata immature	1065	46.80%
Oribatida		
Brachychthoniidae	308	81.80%
<i>Epilohmannia spp.</i>	605	28.90%
<i>Eremobelba spp.</i>	233	49.80%
<i>Rhysotritia spp.</i>	489	67.50%
<i>Galumna spp.</i>	504	84.90%
<i>Nothrus spp.</i>	270	98.50%
Oppiidae	826	53.50%
<i>Zygoribatula spp.</i>	2247	96.20%
<i>Scheloribates spp.</i>	3035	71.40%
<i>Tectocepheus spp.</i>	5001	82.30%
<i>Xylobates spp.</i>	1500	52.00%
Other Oribatida	256	53.90%
Oribatida immature	5910	66.20%
Prostigmata		
Cunaxidae	334	42.80%

Cunaxidae immature	292	46.20%
<i>Eupodes spp.</i>	1032	49.00%
<i>Nanorchestes spp.</i>	413	43.60%
<i>Speleorchestes spp.</i>	537	11.00%
Pygmephoridae	156	46.20%
Scutacaridae	215	31.20%
Stigmaeidae	108	75.00%
Tydeidae	168	76.80%
Other Prostigmata	118	48.30%
Astigmata		
<i>Sancassania spp.</i>	509	78.80%
Histiostomatidae	287	44.60%
Other Astigmata	102	78.40%
Hypopi	2161	76.40%
Insecta		
Collembola		
Entomobryidae	1573	47.00%
Hypogastruridae	797	87.00%
Isotomidae	2225	56.60%
Onychiuridae	2005	72.10%
Sminthuridae	263	39.20%
Mixed Collembola	924	62.00%
Japygidae	384	61.50%
Coleoptera immature	411	60.80%
Coleoptera adult	166	48.80%
Diptera immature	1355	62.50%
Formicidae	1317	18.60%
Other insects	306	52.60%
Other invertebrates		
Enchytraeidae	1035	52.40%
Chilopoda	75	64.00%
Paupoda	89	55.10%
Symphyla	530	66.40%
Nematoda	268	74.30%

Table 3-8 Taxa exhibiting significant response (ANOVA $P < .05$, $df = 4,24$) due to treatment in bait experiment. Pooled data derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, dead (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Taxon	total	% in NT	F	P
Other Mesostigmata	375	61.90%	3.52	0.0213
<i>Galumna spp.</i>	504	84.90%	3.25	0.029
<i>Scheloribates spp.</i>	3035	71.40%	2.72	0.0533
<i>Eupodes spp.</i>	1032	49.00%	6.66	0.0009
Histiostomatidae	287	44.60%	4.13	0.011
Entomobryidae	1573	47.00%	7.14	0.0006
Pauropoda	89	55.10%	3.01	0.0382
Symphyla	530	66.40%	2.73	0.0529
Diptera immature	1355	62.50%	13.94	<.0001
Formicidae	1317	18.60%	3.93	0.0136

Table 3-9 Taxa with significant response (ANOVA $P < .05$, $df = 1,24$) to the contrast of Hb (*Heterorhabditis bacteriophora*) nematode treatment against Sc (*Steinernema carpocapsae*) and Rb (*Steinernema riobrave*) nematode treatments in bait experiment. Total= total individuals collected. %in NT= proportion of total found in No-till soil (versus Conventional till soil).

Taxon	total	% in NT	F	P
Other Mesostigmata	375	61.90%	8.38	0.008
<i>Scheloribates spp.</i>	3035	71.40%	5.7	0.0251
<i>Eupodes spp.</i>	1032	49.00%	21.67	<.0001
Histiostomatidae	287	44.60%	7.82	0.01
Entomobryidae	1573	47.00%	4.84	0.0376
Diptera immature	1355	62.50%	18.7	0.0002

Table 3-10 Taxa with significant response (ANOVA $P < .05$, $df = 1, 24$) to the contrast of Rb (*Steinernema riobrave*) nematode treatment against Sc (*Steinernema carpocapsae*) and Hb (*Heterorhabditis bacteriophora*) nematode treatments in bait experiment. Total = total individuals collected. % in NT = proportion of total found in No-till soil (versus Conventional till soil)

Taxon	total	% in NT	F	P
Other Mesostigmata	375	61.90%	4.78	0.0388
<i>Eupodes spp.</i>	1032	49.00%	10.38	0.0036
Histiostomatidae	287	44.60%	14.02	0.001
Diptera immature	1355	62.50%	38.68	<.0001

Table 3-11 Taxa exhibiting a significant response (ANOVA $P < .05$, $df = 20,20$) to effects due to the interaction of treatment by sampling date (trt*date). Pooled data derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, dead (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Taxon	total	% in NT	F	P
Ascidae	166	73.50%	1.71	0.0312
<i>Scheloribates</i> spp.	3035	71.40%	2.04	0.0061
<i>Tectocephus</i> spp.	5001	82.30%	1.85	0.0161
Stigmaeidae	108	75.00%	1.98	0.0084
<i>Sancassania</i> spp.	509	78.80%	1.79	0.0215
Diptera immature	1355	62.50%	3.02	<.0001

Table 3-12 Taxa exhibiting a significant response (ANOVA $P < .05$, $df = 4,24$) to effects due to the interaction of tillage type by treatment (till*trt). Pooled data derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, dead (controls), Sc=Steinernema carpocapsae, Rb=Steinernema riobrave, Hb=Heterorhabditis bacteriophora (nematode strains))

Taxon	total	% in NT	F	P
<i>Gamasellodes spp.</i>	138	46.40%	4.75	0.0058
<i>Macrocheles spp.</i>	441	91.40%	3.1	0.0344
Phytoseidae	120	65.80%	2.85	0.046
<i>Galumna spp.</i>	504	84.90%	3.89	0.0142
<i>Eupodes spp.</i>	1032	49.00%	3.02	0.0375
<i>Nanorchestes spp.</i>	413	43.60%	3.89	0.0142

Table 3-13 Taxa exhibiting a significant response (ANOVA $P < .05$, $df = 4,20$) to effects due to the interaction of sampling time by treatment (time*trt). Pooled data derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, dead (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Taxon	total	% in NT	F	P
Brachychthoniidae	308	81.80%	3.95	0.0108
Diptera immature	1355	62.50%	4.17	0.0084

Figure 3-1 Total abundance of soil invertebrates in blocks 1-4 of bait experiment. Invertebrates are grouped into 7 major categories (Mesostigmata, Oribatida, Prostigmata, Astigmata, Collembola, other invertebrates, total invertebrates=sum of other 6 groups). Pooled data derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, dead (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

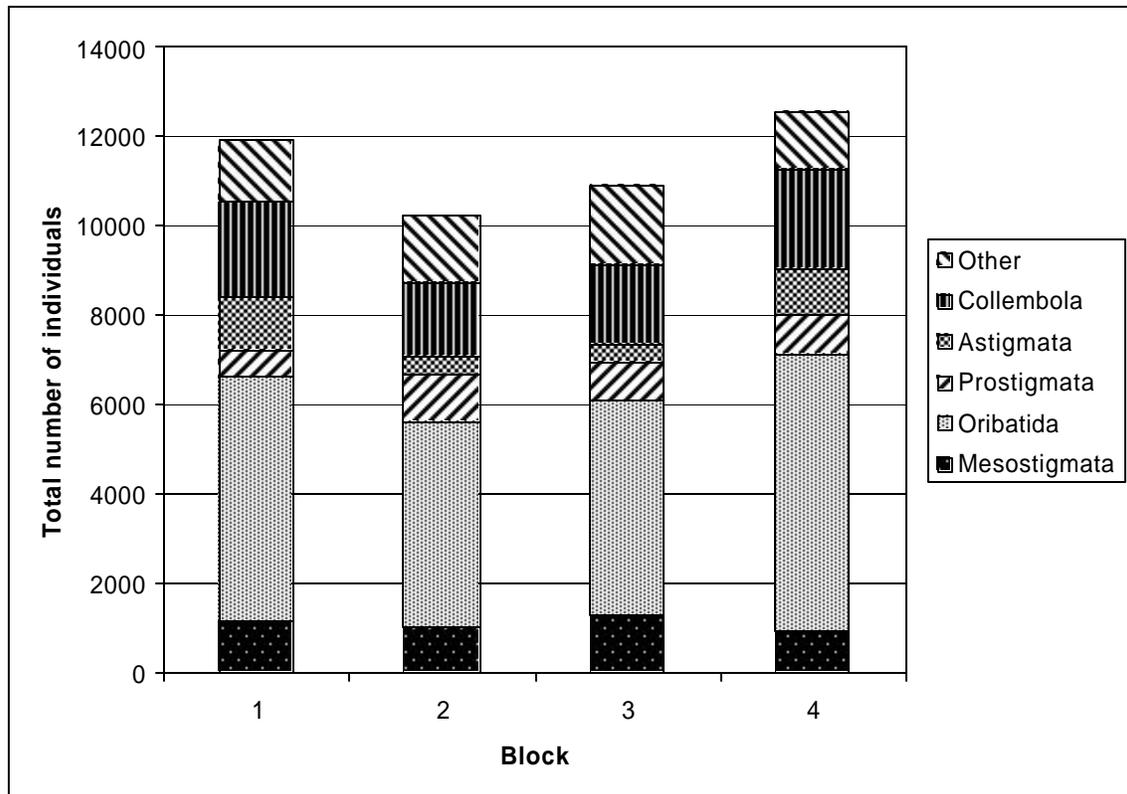


Figure 3-2 Interaction of treatment by sampling date (trt*date) in Richness bait experiment. Pooled data is derived from 6 dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), two tillage regimes (no-till and conventional till), 5 treatments (Soil, Dead=dead uninfected insect, Sc(= *G.mellonella* larva infected with *S. carpocapsae* nematodes), Rb(= *G.mellonella* larva infected with *S. riobrave* nematodes), Hb(= *G.mellonella* larva infected with *H. bacteriophora* nematodes)) and two sampling times (4 and 24 hours)

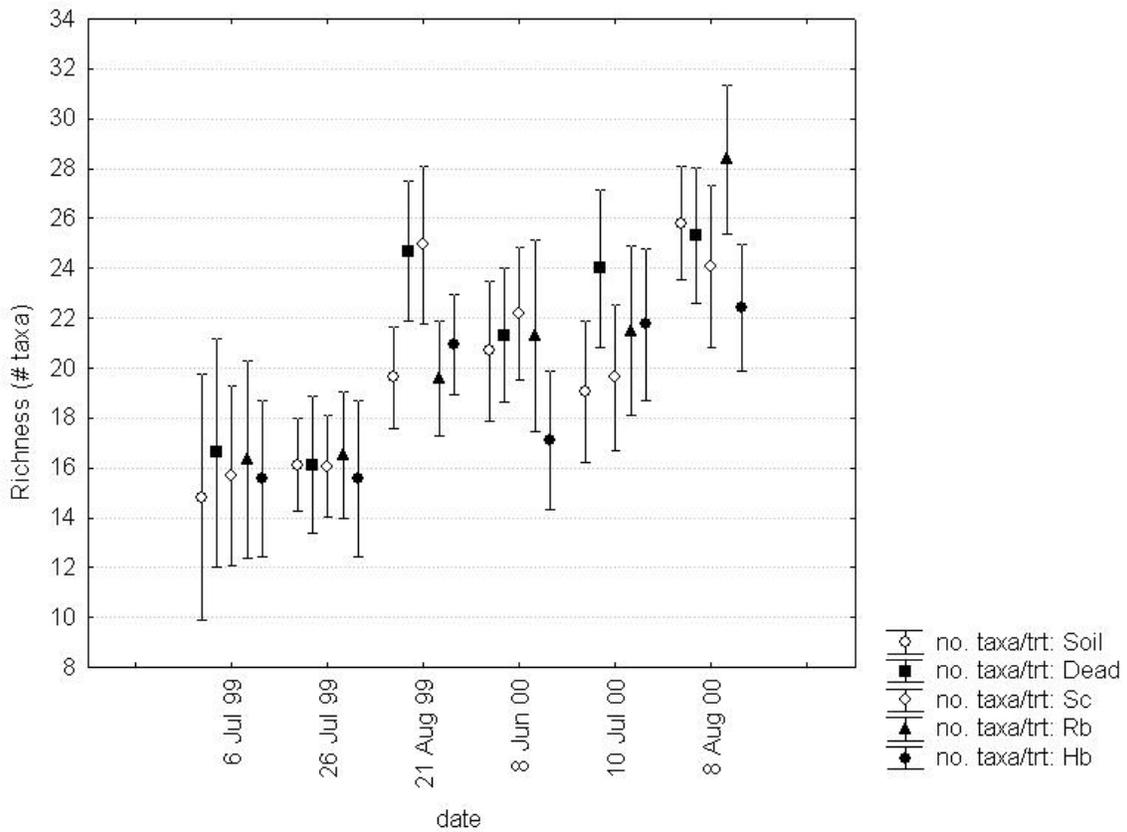
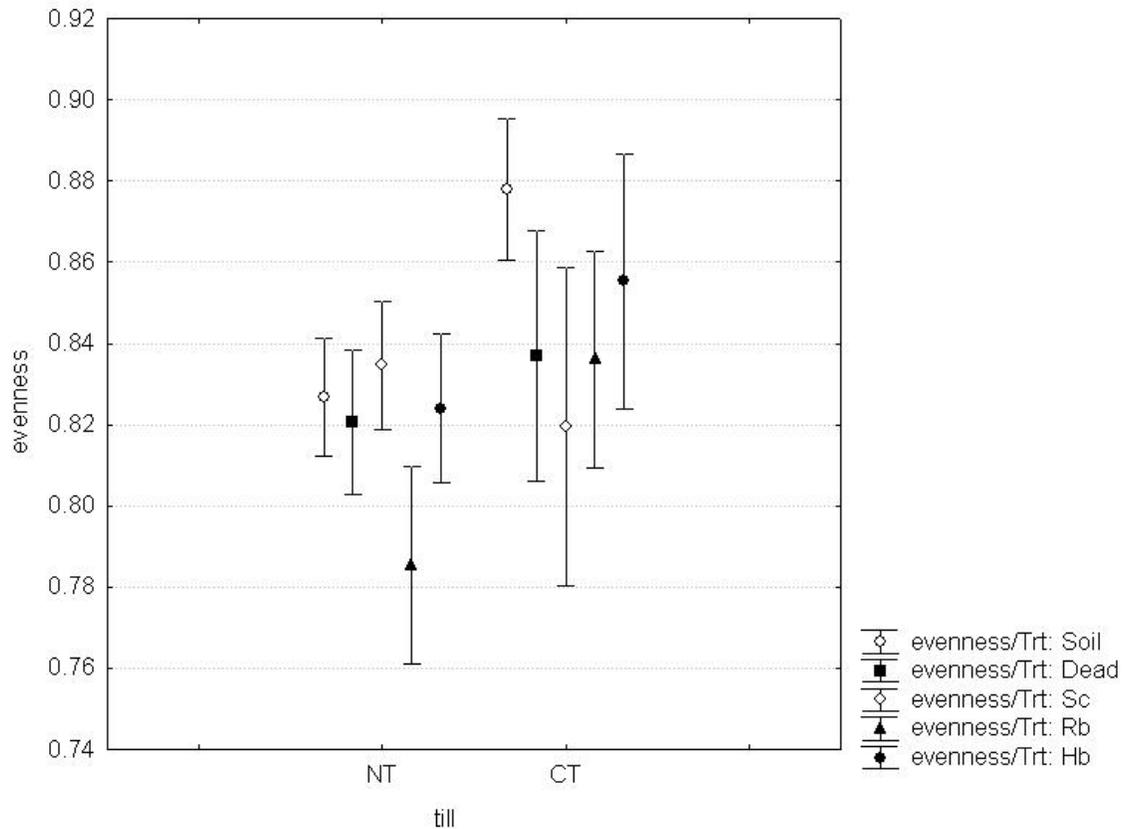


Figure 3-3 interaction of tillage type by treatment (till*trt) in evenness where EPN applied as infected insect cadaver in bait experiment. Pooled data is derived from 6 dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), two tillage regimes (no-till and conventional till), 5 treatments (Soil, Dead=dead uninfected insect, Sc(=*G.mellonella* larva infected with *S. carpocapsae* nematodes), Rb(=*G.mellonella* larva infected with *S. riobrave* nematodes), Hb(=*G.mellonella* larva infected with *H. bacteriophora* nematodes)) and two sampling times (4 and 24 hours)



Appendix A Experimental designs for bait and inundation experiments

Bait experiment

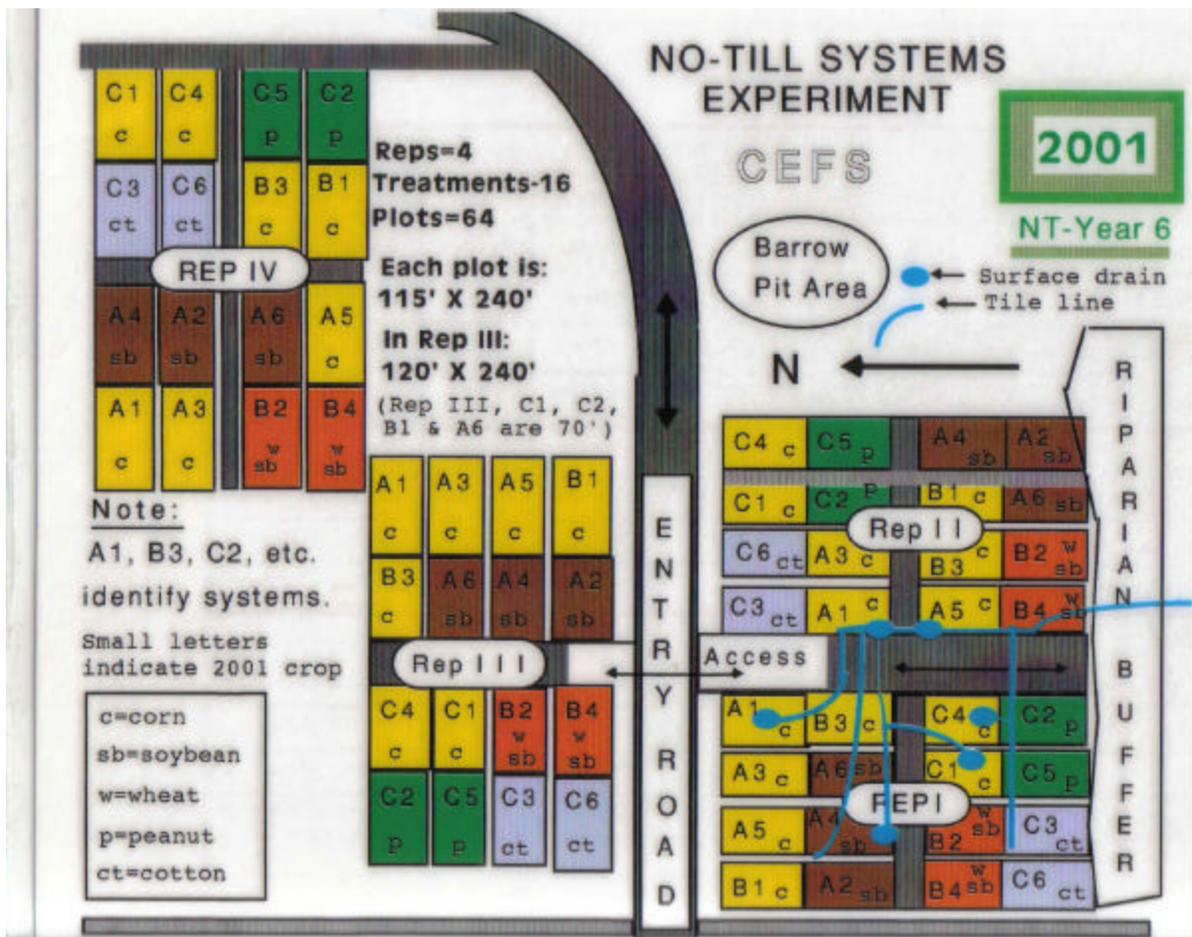
		Blocks							
		I					II	III	IV
		Soil	Dead	Sc	Rb	Hb			
NT	4hr								
	24hr								
CT									

Inundation experiment

		Blocks							
		I					II	III	IV
		Soil	Water	Sc	Rb	Hb			
NT	4hr								
	24hr								
CT									

Appendix B Diagram of the tillage unit at the Center for Environmental Farming Systems (CEFS)

This research (both bait and inundation experiment) was conducted in A1 and A3 plots (c=corn) of Reps (blocks) I-IV for 2001 and plots corresponding to the normal crop rotation for 1999 and 2000.



Appendix C SAS Code for contrasted ANOVA

All data were analyzed using the general linear model procedure (PROC GLM, SAS Institute 1996), and means were separated with the least significant difference (LSD SAS Institute 1996) SAS code for inundation experiment.

```
PROC IMPORT OUT= WORK.b
            DATAFILE= "F:\Copy of
PhD_data_masterSASversion_11feb04.XLS"
            DBMS=EXCEL2000 REPLACE,
            RANGE="Ind$",
            GETNAMES=YES,
RUN,
proc print data=b, run,

data a, set b,
time=time__hrs_,
date=julian_date,
sqcoll=sqrt(total_col), sqprost=sqrt(total_prostig),
sqmeso=sqrt(total_mesos),
sqmites=sqrt(total_mites), sqorib=sqrt(total_orib),
ltot=log10(total+.5), lmites=log10(mites+.5),
lother=log10(total_other+.5),
lastig=log10(total_astig+.5), lorib=log10(total_orib+.5),
lcoll=log10(total_col+.5),
drop julian_date time__hrs_ F70-F79,
options ls=78,
proc sort data=a, by total,
proc print data=a, run,

*** USE lsd's if appropriate *****,
proc glm, class block till time trt date,
model sqmeso lorib lastig sqprost lcoll lother ltot=
      block|till trt|time|till block*trt(till)
block*time(trt*till)
      date|till|time|trt date*block/ss3,
test h=till e=block*till,
test h=trt trt*till e=block*trt(till),
test h=time trt*time time*till trt*time*till
e=block*time(trt*till),
test h=date e=block*date,
contrast 'Soil vs water' trt 0 0 0 -1 1/e=block*trt(till),
```

```

contrast 'Soil vs nemas' trt  -1 -1 -1 3 0/
e=block*trt(till),
contrast 'water vs nemas' trt  -1 -1 -1 0 3/
e=block*trt(till),
contrast 'Hb vs Sc,Rb' trt  -1 .5 .5 0 0/
e=block*trt(till),
contrast 'Hb,Rb vs Sc' trt  .5 .5 -1 0 0/ e=block*trt(till),
contrast 'Hb,Sc vs Rb' trt  .5 -1 .5 0 0/
e=block*trt(till),
means till*trt till*time*trt date date*till date*time,
means trt/lsd e=block*trt(till),
output out=p p= pmeso porib pastig pprost pcoll pother
ptot
r=rmeso rorib rastig rprost rcoll rother rtot,
proc plot, plot rmeso*pmeso rorib*porib rastig*pastig
          rprost*pprost rcoll*pcoll rother*pother
          rtot*ptot/vref=0,
run,

proc sort data=a, by till trt,
proc means data=a n mean stderr min max, by till trt,
var total coll mites,
run,

proc sort data=a, by till date,
proc means data=a n mean stderr min max, by till date,
var total coll mites,
run,
proc glm, class block time trt date, by till,
model sqmeso lorib lastig sqprost lcoll lother ltot=
      block|trt trt|time block*time(trt)
      date|time|trt date*block/ss3,
test h=trt e=block*trt,
test h=time trt*time e=block*time(trt*till),
test h=date e=block*date,
contrast 'Soil vs water' trt  0 0 0 -1 1/e=block*trt,
contrast 'Soil vs nemas' trt  -1 -1 -1 3 0/ e=block*trt,
contrast 'water vs nemas' trt  -1 -1 -1 0 3/ e=block*trt,
contrast 'Hb vs Sc,Rb' trt  -1 .5 .5 0 0/ e=block*trt,
contrast 'Hb,Rb vs Sc' trt  .5 .5 -1 0 0/ e=block*trt,
contrast 'Hb,Sc vs Rb' trt  .5 -1 .5 0 0/ e=block*trt,
means time*trt date date*time,
means trt/lsd e=block*trt,
run,

data a, set a,
sqascid=sqrt(ascid),

```

```

sqOthermesos=sqrt(Othermesos),
lprotoga = log10(protoga+.5),
lhypoasp = log10(hypoasp+.5),
lmacroch = log10(macroch+.5),
lrhoda = log10(rhoda+.5), lBrachychthoniidae=
log10(Brachychthoniidae+.5),
lneonothrus=log10(neonothrus+.5),
lepilohm=log10(epilohm+.5), leremob=log10(eremob+.5),
lrhysot=log10(rhysot+.5), lgalumn=log10(galumn+.5),
lnothrus=log10(nothrus+.5), loppiid=log10(oppiid+.5),
lzygor=log10(zygor+.5), lschelor=log10(schelor+.5),
ltecto=log10(tecto+.5), lxylo=log10(xylo+.5),
lotherorib=log10(otherorib+.5), loribimm=log10(oribimm+.5),
lcunax=log10(cunax+.5), leupod=log10(eupod+.5),
lnanorch=log10(nanorch+.5), lspeleo=log10(speleo+.5),
lpygme=log10(pygme+.5),
lscutac=log10(scutac+.5), ltydeidae=log10(tydeidae+.5),
lotherprostig=log10(otherprostig+.5),
lacarid=log10(acarid+.5),
lsancass=log10(sancass+.5),
lotherastig=log10(otherastig+.5), lhypopi=log10(hypopi+.5),
lentomob=log10(entomob+.5),
lhypogas=log10(hypogas+.5), liso=log10(iso+.5),
lonych=log10(onych+.5), lsminth=log10(sminth+.5),
lunidcoll=log10(unidcoll+.5),
lchilo=log10(chilo+.5), lsymph=log10(symph+.5),
ljapyg=log10(japyg+.5), lthrips=log10(thrips+.5),
lant=log10(ant+.5),
lnema=log10(nema+.5), lenchy=log10(enchy+.5),
lcoleopimm=log10(coleopimm+.5),
lcoleopad=log10(coleopad+.5),
ldiptimm=log10(diptimm+.5),
lotherinsects=log10(otherinsects+.5),
proc glm data=a, class block till time trt date,
model sqascid lprotoga lhypoasp lmacroch lrhoda
      sqOthermesos lBrachychthoniidae lNeonothrus
      lepilohm
leremob lrhysot lgalumn lnothrus loppiid lzygor
      lschelor ltecto lxylo lotherorib
loribimm lcunax leupod lNanorch lSpeleo lPygme
      lScutac lTydeidae lotherprostig lacarid
lsancass lOtherastig lHypopi lentomob lhypogas liso
      lonych lsminth lunidcoll lchilo
lsymph ljapyg lThrips lant lnema lenchy
      lColeopimm lColeopad lDiptimm
lotherinsects=

```

```

    block|till trt|time|till block*trt(till)
block*time(trt*till)
    date|till|time|trt date*block/ss3,
test h=till e=block*till,
test h=trt trt*till e=block*trt(till),
test h=time trt*time time*till trt*time*till
e=block*time(trt*till),
test h=date e=block*date,
contrast 'Soil vs water' trt  0 0 0 -1 1/e=block*trt(till),
contrast 'Soil vs nemas' trt  -1 -1 -1 3 0/
e=block*trt(till),
contrast 'water vs nemas' trt  -1 -1 -1 0 3/
e=block*trt(till),
contrast 'Hb vs Sc,Rb' trt  -1 .5 .5 0 0/
e=block*trt(till),
contrast 'Hb,Rb vs Sc' trt  .5 .5 -1 0 0/ e=block*trt(till),
contrast 'Hb,Sc vs Rb' trt  .5 -1 .5  0 0/
e=block*trt(till),
means till*trt till*time*trt date date*till date*time,
means trt/lsd e=block*trt(till),
output out=p p= pascid porib pastig pprost pcoll pother
ptot
r=rascid rorib rastig rprost rcoll rother  rtot,

proc plot, plot rascid*pascid rorib*porib rastig*pastig
          rprost*pprost rcoll*pcoll rother*pother
          rtot*ptot/vref=0,

run,
proc glm, class block  time trt date, by till,
model sqascid lprotoga lhypoasp lmacroch lrhoda
      sqOthermesos  lBrachychthoniidae
lNeonothrus  lepilohm
leremob  lrhysot  lgalumn  lnothrus  loppiid  lzygor
      lschelor  ltecto  lxylo  lotherorib
loribimm  lcunax  leupod  lNanorch  lSpeleo  lPygme
      lScutac  lTydeidae lotherprostig
lacarid  lsancass  lOtherastig  lHypopi  lentomob
      lhypogas  liso  lonych  lsminth  lunidcoll
lchilo  lsymph  ljapyg  lThrips  lant  lnema
      lenchy  lColeopimm  lColeopad  lDiptimm
lotherinsects=
    block|trt trt|time  block*time(trt)
    date|time|trt date*block/ss3,
test h=trt  e=block*trt,
test h=time trt*time  e=block*time(trt*till),
test h=date e=block*date,
contrast 'Soil vs water' trt  0 0 0 -1 1/e=block*trt,

```

```

contrast 'Soil vs nemas' trt -1 -1 -1 3 0/ e=block*trt,
contrast 'water vs nemas' trt -1 -1 -1 0 3/ e=block*trt,
contrast 'Hb vs Sc,Rb' trt -1 .5 .5 0 0/ e=block*trt,
contrast 'Hb,Rb vs Sc' trt .5 .5 -1 0 0/ e=block*trt,
contrast 'Hb,Sc vs Rb' trt .5 -1 .5 0 0/ e=block*trt,
means time*trt date date*time,
means trt/lsd e=block*trt,
run,
*** untransformed *****,
proc glm data=a, class block till time trt date,
model ascid protoqa hypoasp macroch rhoda
      Othermesos Brachychthoniidae Neonothrus
      epilohm
eremob rhysot galumn nothrus oppiid zygor
      schelor tecto xylo otherorib
oribimm cunax eupod Nanorch Speleo Pygme
      Scutac Tydeidae otherprostig acarid
sancass Otherastig Hypopi entomob hypogas iso
      onych sminth unidcoll chilo
sympH japyg Thrips ant nema enchy Coleopimm
      Coleopad Diptimm otherinsects=
      block|till time|till block*time(till) trt|time|till
block*trt(time*till)
      date|till|time|trt /ss3,
test h=till e=block*till,
test h=time time*till e=block*time(till),
test h=trt trt*time trt*till trt*time*till
e=block*trt(time*till),
contrast 'Soil vs Water' trt 0 0 0 1 -1
/e=block*trt(time*till),
contrast 'Hb vs Sc,Rb' trt -1 .5 .5 0 0/
e=block*trt(time*till),
means till*trt till*time*trt,
means trt/lsd e=block*trt(time*till),
output out=p p= pmeso porib pastig pprost pcoll pother
ptot
r=rmeso rorib rastig rprost rcoll rother rtot,

proc plot, plot rmeso*pmeso rorib*porib rastig*pastig
      rprost*pprost rcoll*pcoll rother*pother
      rtot*ptot/vref=0,
run,

```

Appendix D Contrasted ANOVA

All data were analyzed using the general linear model procedure (PROC GLM, SAS Institute 1996), and means were separated with the least significant difference (LSD SAS Institute 1996) SAS code for diversity indices (both bait and inundation experiments).

```
PROC IMPORT OUT= WORK.A
      DATAFILE= "F:\ST data indices by sample values
for stats.xls"
      DBMS=EXCEL2000 REPLACE,
      RANGE="'ind indices for sas$'",
      GETNAMES=YES,
RUN,
proc print data=a,
run,
data b, set a, if year=. then delete,
options ls=78,
proc print data=b,
proc glm data=b, class block till time trt year date,
model shannon simpson hill2 hill1 evenness no_taxa =
      block|till trt|time|till block*trt(till)
block*time(trt*till)
      date|till|time|trt date*block/ss3,
test h=till e=block*till,
test h=trt trt*till e=block*trt(till),
test h=time trt*time time*till trt*time*till
e=block*time(trt*till),
test h=date e=block*date,
contrast 'Soil vs dead' trt 1 0 0 0 -1 /e=block*trt(till),
contrast 'Soil vs nemas' trt 0 -1 -1 -1 3 /
e=block*trt(till),
contrast 'Dead vs nemas' trt 3 -1 -1 -1 0 /
e=block*trt(till),
contrast 'Hb vs Sc,Rb' trt 0 -1 .5 .5 0 /
e=block*trt(till),
contrast 'Hb,Rb vs Sc' trt 0 .5 .5 -1 0 /
e=block*trt(till),
contrast 'Hb,Sc vs Rb' trt 0 .5 -1 .5 0 /
e=block*trt(till),
means till*trt till*time*trt date date*till date*time time,
means trt/lsd e=block*trt(till) lines,
run,
```

Appendix E Invertebrates collected in the inundation experiment

All Invertebrates extracted in inundation experiment, identified to the lowest taxonomic level, showing relative prevalence (% of total collected) in no-till (NT) and conventional-till (CT) soil. Pooled data derived from 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, water (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Taxa	Total # Ind	Total # in CT	% in CT	Total # in NT	% in NT
Arachnida					
Acari					
Mesostigmata					
Asca	1	0	0.0%	1	100.0%
Digamasellidae	1	0	0.0%	1	100.0%
Parasitidae	1	0	0.0%	1	100.0%
<i>Vulgarogamasus spp.</i>	11	0	0.0%	11	100.0%
<i>Amblyseius spp.</i>	11	1	9.1%	10	90.9%
Uropodidae	57	6	10.5%	51	89.5%
<i>Lasioseius spp.</i>	9	1	11.1%	8	88.9%
<i>Macrocheles spp.</i>	297	48	16.2%	249	83.8%
<i>Rhodacarus spp.</i>	390	69	17.7%	321	82.3%
<i>Cheiroseius spp.</i>	73	13	17.8%	60	82.2%
Phytoseiidae	72	15	20.8%	57	79.2%
<i>Gamasellodes spp.</i>	63	20	31.7%	43	68.3%
Unidentified Mesostigmata	244	103	42.2%	141	57.8%
Immature Mesostigmata	745	315	42.3%	430	57.7%
Ascidae	22	11	50.0%	11	50.0%
<i>Rhodacarellus spp.</i>	2	1	50.0%	1	50.0%
Ologamasidae	2	1	50.0%	1	50.0%
<i>Hypoaspis spp.</i>	489	251	51.3%	238	48.7%
<i>Veigaia spp.</i>	14	8	57.1%	6	42.9%
<i>Protogamasellus spp.</i>	283	215	76.0%	68	24.0%
<i>Arctoseius spp.</i>	5	5	100.0%	0	0.0%

Laelapidae	1	1	100.0%	0	0.0%
Oribatida					
<i>Neonothrus</i> spp.	205	0	0.0%	205	100.0%
<i>Haplochthonius</i> spp.	1	0	0.0%	1	100.0%
<i>Haplozetes</i> spp.	2	0	0.0%	2	100.0%
<i>Lohmannia</i> spp.	1	0	0.0%	1	100.0%
<i>Lamellobates</i> spp.	1	0	0.0%	1	100.0%
<i>Suctobelbella</i> spp.	2	0	0.0%	2	100.0%
<i>Eremobelba</i> #2 spp.	39	1	2.6%	38	97.4%
<i>Galumna</i> spp.	452	17	3.8%	435	96.2%
<i>Nothrus</i> spp.	394	15	3.8%	379	96.2%
<i>Lauroppia</i> spp.	21	1	4.8%	20	95.2%
<i>Zygoribatula</i> spp.	1867	130	7.0%	1737	93.0%
<i>Liochthonius</i> spp.	131	12	9.2%	119	90.8%
<i>Poecilochthonius</i> spp.	170	27	15.9%	143	84.1%
<i>Rostrozetes</i> spp.	153	41	26.8%	112	73.2%
<i>Xylobates</i> spp.	1071	299	27.9%	772	72.1%
<i>Tectocepheus</i> spp.	5022	1480	29.5%	3542	70.5%
<i>Schelorbates</i> spp.	2444	738	30.2%	1706	69.8%
Immature Oribatida	10161	3169	31.2%	6992	68.8%
<i>Rhysotritria</i> spp.	203	71	35.0%	132	65.0%
<i>Brachychthonius</i> spp.	52	20	38.5%	32	61.5%
<i>Oppiella</i> spp.	493	205	41.6%	288	58.4%
<i>Epilohmannia</i> spp.	278	117	42.1%	161	57.9%
<i>Eremobelba</i> #1 spp.	81	46	56.8%	35	43.2%
<i>Ramusella</i> spp.	17	10	58.8%	7	41.2%
<i>Multioppia</i> spp.	6	4	66.7%	2	33.3%
<i>Berlesezetes</i> spp.	22	15	68.2%	7	31.8%
<i>Mochlozetes</i> spp.	2	2	100.0%	0	0.0%
<i>Podoribates</i> spp.	1	1	100.0%	0	0.0%
<i>Pterochthoniidae</i> spp.	1	1	100.0%	0	0.0%
Unidentified Oribatida	2	2	100.0%	0	0.0%
Prostigmata					
Cheyletidae	1	0	0.0%	1	100.0%
<i>Terpnacarus</i> spp.	14	0	0.0%	14	100.0%
<i>Stigmaeus</i> spp.	94	1	1.1%	93	98.9%
Tydeidae	224	29	12.9%	195	87.1%
Neocunaxidae	5	1	20.0%	4	80.0%
Lordalycidae	18	5	27.8%	13	72.2%
<i>Eupodes</i> spp.	446	172	38.6%	274	61.4%
<i>Dactyloscirus</i> spp.	33	13	39.4%	20	60.6%
Tarsonemidae	43	17	39.5%	26	60.5%
<i>Puleaus</i> spp.	17	7	41.2%	10	58.8%
Immature Prostigmata	29	12	41.4%	17	58.6%
Immature Cunaxidae	221	96	43.4%	125	56.6%
<i>Rhagidia</i> spp.	37	17	45.9%	20	54.1%
<i>Nanorchestes</i> spp.	785	408	52.0%	377	48.0%

Unidentified Prostigmata	9	5	55.6%	4	44.4%
<i>Coleoscirus spp.</i>	77	45	58.4%	32	41.6%
<i>Scutacarus spp.</i>	178	107	60.1%	71	39.9%
<i>Neoscirula spp.</i>	3	2	66.7%	1	33.3%
Pygmephoridae	158	119	75.3%	39	24.7%
<i>Speleorchestes spp.</i>	689	629	91.3%	60	8.7%
<i>Oeserchestes spp.</i>	2	2	100.0%	0	0.0%
<i>Raphignathus spp.</i>	1	1	100.0%	0	0.0%
Astigmata					
<i>Rhizoglyphus spp.</i>	2	0	0.0%	2	100.0%
<i>Sancassania spp.</i>	1095	36	3.3%	1059	96.7%
Acaridae	155	7	4.5%	148	95.5%
Unidentified Astigmata	57	7	12.3%	50	87.7%
Immature hypopi	1881	269	14.3%	1612	85.7%
Histiostomatidae	84	41	48.8%	43	51.2%
Immature Astigmata	211	103	48.8%	108	51.2%
Insecta					
Collembola					
Hypogastruridae	183	18	9.8%	165	90.2%
Isotomidae	605	128	21.2%	477	78.8%
Onychiuridae	567	178	31.4%	389	68.6%
Entomobryidae	344	148	43.0%	196	57.0%
Unidentified Collembola	7759	3488	45.0%	4271	55.0%
Sminthuridae	124	58	46.8%	66	53.2%
Other insects					
Chrysomelidae adult	1	0	0.0%	1	100.0%
Elateridae adult	1	0	0.0%	1	100.0%
Scarabaeidae larvae	4	0	0.0%	4	100.0%
Scarabaeidae adult	1	0	0.0%	1	100.0%
Phoridae larvae	1	0	0.0%	1	100.0%
Tipulidae larvae	1	0	0.0%	1	100.0%
Unidentified Hymenoptera	1	0	0.0%	1	100.0%
Hymenoptera adult	1	0	0.0%	1	100.0%
Hemiptera	40	4	10.0%	36	90.0%
Unidentified Diptera larvae	309	45	14.6%	264	85.4%
Elateridae larvae	6	1	16.7%	5	83.3%
Carabidae larvae	21	4	19.0%	17	81.0%
Staphylinidae adult	53	13	24.5%	40	75.5%
Cecidomyiidae larvae	8	2	25.0%	6	75.0%
Homoptera	7	2	28.6%	5	71.4%
Eosentomidae	9	3	33.3%	6	66.7%
Chrysomelidae larvae	6	2	33.3%	4	66.7%
Carabidae adult	12	4	33.3%	8	66.7%
Chironomidae larvae	3	1	33.3%	2	66.7%
Formicidae	41	14	34.1%	27	65.9%
Japygidae	219	81	37.0%	138	63.0%
Cecidomyiidae adult	10	4	40.0%	6	60.0%

Thysanoptera	124	55	44.4%	69	55.6%
Unidentified Diptera adult	18	8	44.4%	10	55.6%
Pselaphidae adult	2	1	50.0%	1	50.0%
Mycetophilidae larvae	2	1	50.0%	1	50.0%
Mycetophilidae adult	2	1	50.0%	1	50.0%
Tipulidae adult	2	1	50.0%	1	50.0%
Unidentified Coleoptera	286	149	52.1%	137	47.9%
Ceratopogonidae larvae	14	8	57.1%	6	42.9%
Staphylinidae larvae	29	19	65.5%	10	34.5%
Unidentified Coleoptera	23	18	78.3%	5	21.7%
Liposcelis	10	9	90.0%	1	10.0%
Aphidae	1	1	100.0%	0	0.0%
Pselaphidae larvae	3	3	100.0%	0	0.0%
Scydmaenidae adult	1	1	100.0%	0	0.0%
Sciaridae adult	1	1	100.0%	0	0.0%
Heteroceridae larvae	1	1	100.0%	0	0.0%
Mymaridae adult	2	2	100.0%	0	0.0%
Other invertebrates					
Nematoda	344	38	11.0%	306	89.0%
Unidentified Symphyla	407	110	27.0%	297	73.0%
Unidentified Chilopoda	62	26	41.9%	36	58.1%
Enchytraeidae	761	339	44.5%	422	55.5%
Unidentified Annelida	6	5	83.3%	1	16.7%
Unidentified Paupoda	19	17	89.5%	2	10.5%

Appendix F Means tables for inundation experiment

Mean (\pm std. error) abundance of 49 representative taxa (44,996 total individuals) collected in no-till soil in inundation experiment. Pooled data derived from 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, water (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Inundation/No Till	NT									
Time	4hr	24hr								
Treatment	Hb	Hb	Rb	Rb	Sc	Sc	Soil	Soil	Water	Water
Arachnida										
Acari										
Mesostigmata										
Ascidae	0.208	0.500	0.333	0.167	0.375	0.583	0.458	0.208	0.333	0.208
	± 0.104	± 0.313	± 0.167	± 0.115	± 0.254	± 0.225	± 0.199	± 0.104	± 0.130	± 0.120
<i>Protogamasellus spp.</i>	0.333	0.458	0.042	0.500	0.458	0.292	0.375	0.208	0.125	0.042
	± 0.223	± 0.351	± 0.042	± 0.241	± 0.313	± 0.252	± 0.189	± 0.120	± 0.069	± 0.042
<i>Hypoaspis spp.</i>	1.708	1.542	1.042	0.667	1.292	0.500	0.583	0.208	1.833	0.542
	± 0.755	± 0.571	± 0.285	± 0.349	± 0.436	± 0.147	± 0.216	± 0.120	± 0.513	± 0.208
<i>Macrocheles spp.</i>	1.042	1.167	0.875	0.792	1.417	0.458	1.708	0.417	1.625	0.875
	± 0.410	± 0.424	± 0.278	± 0.421	± 0.458	± 0.225	± 0.922	± 0.240	± 0.564	± 0.363
<i>Rhodacarus spp.</i>	1.583	1.000	1.500	1.125	2.125	1.542	1.792	0.500	1.083	1.125
	± 0.983	± 0.558	± 0.689	± 0.585	± 0.826	± 1.371	± 0.938	± 0.181	± 0.371	± 0.635
Other Mesostigmata (immature and male)	3.792	3.958	3.792	2.250	3.083	2.792	3.292	2.125	2.792	3.458
	± 0.836	± 0.848	± 0.764	± 0.455	± 0.702	± 0.608	± 0.824	± 0.423	± 0.558	± 0.759
Oribatida										
Brachychthoniidae	0.417	0.917	0.458	0.667	0.667	3.500	0.750	1.333	1.208	2.333
	± 0.133	± 0.351	± 0.170	± 0.238	± 0.187	± 2.053	± 0.250	± 0.554	± 0.408	± 0.968
<i>Neonothrus spp.</i>	2.833	0.375	0.667	0.542	0.667	0.333	0.417	0.208	1.583	0.917
	± 2.748	± 0.261	± 0.586	± 0.500	± 0.667	± 0.333	± 0.340	± 0.170	± 1.346	± 0.645
<i>Epilohmannia spp.</i>	0.542	0.542	1.333	0.583	0.708	0.583	0.667	0.750	0.500	0.500
	± 0.225	± 0.217	± 0.384	± 0.180	± 0.321	± 0.199	± 0.231	± 0.405	± 0.241	± 0.170
<i>Eremobelba spp.</i>	0.250	0.250	0.125	0.208	0.250	0.208	0.250	0.250	0.292	0.958
	± 0.138	± 0.211	± 0.069	± 0.104	± 0.124	± 0.134	± 0.124	± 0.109	± 0.127	± 0.624
<i>Rhysotritia spp.</i>	1.500	0.250	0.458	0.250	0.958	0.333	0.542	0.208	0.875	0.125
	± 1.078	± 0.173	± 0.262	± 0.138	± 0.576	± 0.130	± 0.289	± 0.104	± 0.382	± 0.069
<i>Galumna spp.</i>	1.375	2.083	1.542	1.333	1.833	1.125	3.292	2.000	1.833	1.708
	± 0.521	± 0.923	± 0.558	± 0.524	± 0.848	± 0.309	± 1.705	± 1.175	± 0.677	± 0.585
<i>Nothrus spp.</i>	5.083	1.917	2.167	1.417	0.792	1.042	1.000	0.125	0.333	1.917
	± 2.618	± 1.129	± 1.083	± 1.058	± 0.417	± 0.576	± 0.590	± 0.069	± 0.130	± 1.306
Oppiidae	1.500	1.542	0.750	1.792	1.792	1.292	0.792	1.208	0.792	1.750
	± 0.587	± 0.704	± 0.326	± 0.496	± 0.654	± 0.327	± 0.262	± 0.395	± 0.269	± 0.435

<i>Zygoribatula</i> spp.	5.667	6.458	11.167	4.458	5.208	7.750	9.708	8.708	5.625	7.625
	±1.763	±2.423	±6.900	±1.225	±1.543	±2.757	±2.782	±3.846	±1.515	±2.552
<i>Schelorbates</i> spp.	6.750	6.250	5.542	5.958	6.083	5.875	13.333	5.167	8.500	7.625
	±0.923	±0.975	±1.118	±0.933	±1.034	±1.122	±2.502	±1.218	±1.823	±1.396
<i>Tectocephus</i> spp.	15.833	16.417	13.375	12.167	15.125	15.292	17.375	11.958	17.125	12.917
	±2.944	±3.145	±2.418	±1.968	±3.890	±3.181	±2.905	±2.369	±3.121	±2.188
<i>Xylobates</i> spp.	3.958	3.792	3.208	2.333	2.958	3.292	2.500	2.333	3.542	4.250
	±1.249	±1.043	±0.608	±0.656	±0.839	±0.733	±0.590	±0.595	±0.697	±1.086
Unidentified Oribatida (male and unidentified)	1.208	0.542	0.083	0.375	0.375	0.458	0.917	0.375	0.583	0.333
	±0.645	±0.217	±0.058	±0.118	±0.157	±0.190	±0.394	±0.157	±0.262	±0.206
Unidentified Oribatida (immature)	28.208	27.792	23.417	23.167	31.292	23.458	36.000	24.125	33.500	40.375
	±4.096	±5.851	±5.988	±5.194	±5.552	±5.184	±5.416	±5.213	±6.363	±9.679
Prostigmata										
Cunaxidae	0.708	0.625	0.500	0.625	0.792	0.708	1.667	0.500	0.708	1.167
	±0.259	±0.239	±0.170	±0.232	±0.289	±0.292	±0.534	±0.200	±0.195	±0.389
<i>Eupodes</i> spp.	1.042	0.750	0.542	0.958	0.833	2.250	1.833	0.583	0.750	1.875
	±0.359	±0.264	±0.170	±0.591	±0.389	±1.048	±0.667	±0.225	±0.243	±0.906
<i>Nanorchestes</i> spp.	1.333	3.000	1.125	1.500	0.875	1.833	1.833	1.500	1.292	1.417
	±0.807	±1.637	±0.456	±0.634	±0.315	±0.983	±0.998	±0.868	±0.741	±0.631
<i>Speleorchestes</i> spp.	0.250	0.292	0.125	0.125	0.458	0.083	0.417	0.208	0.208	0.333
	±0.138	±0.153	±0.092	±0.092	±0.159	±0.083	±0.208	±0.120	±0.104	±0.143
Pygmephoridae	0.167	0.042	0.250	0.292	0.125	0.083	0.125	0.083	0.375	0.083
	±0.078	±0.042	±0.138	±0.175	±0.092	±0.058	±0.092	±0.058	±0.224	±0.058
Scutacaridae	0.083	0.208	0.125	0.417	0.125	0.458	0.250	0.500	0.208	0.583
	±0.058	±0.085	±0.069	±0.208	±0.092	±0.208	±0.138	±0.255	±0.120	±0.190
Tydeidae	0.333	0.750	0.500	0.833	0.417	1.042	1.583	0.750	0.750	1.167
	±0.143	±0.284	±0.262	±0.359	±0.146	±0.415	±0.531	±0.336	±0.320	±0.547
Unidentified Prostigmata	0.250	0.333	0.458	0.375	1.167	0.417	1.875	1.875	0.417	0.667
	±0.124	±0.115	±0.180	±0.254	±0.607	±0.180	±1.047	±0.921	±0.133	±0.420
Astigmata										
Acaridae	0.667	0.042	1.083	0.333	1.333	0.375	0.875	0.042	1.333	0.083
	±0.317	±0.042	±0.561	±0.167	±0.667	±0.300	±0.591	±0.042	±0.667	±0.083
<i>Sancassania</i> spp.	1.583	33.250	0.125	1.042	0.542	0.292	1.667	2.792	0.208	2.625
	±1.214	±32.903	±0.069	±0.550	±0.330	±0.221	±1.539	±2.457	±0.085	±2.582
Unidentified Astigmata	0.708	0.458	0.208	0.083	0.583	0.042	0.417	0.500	0.417	0.542
	±0.285	±0.262	±0.104	±0.058	±0.240	±0.042	±0.169	±0.269	±0.158	±0.318
Hypopi	8.292	7.083	4.417	5.917	11.083	4.083	9.208	7.667	5.958	7.958
	±2.347	±2.241	±1.111	±2.234	±3.060	±1.110	±4.380	±3.279	±1.910	±3.960
Insecta										
Japygidae	0.667	0.625	0.750	0.458	0.417	0.458	0.667	0.417	0.875	0.417
	±0.238	±0.179	±0.257	±0.159	±0.133	±0.170	±0.223	±0.158	±0.320	±0.146
Thysanoptera	0.375	0.167	0.250	0.208	0.208	0.500	0.292	0.167	0.292	0.417
	±0.145	±0.098	±0.173	±0.085	±0.104	±0.248	±0.213	±0.078	±0.127	±0.169
Formicidae	0.125	0.000	0.042	0.042	0.333	0.000	0.042	0.083	0.458	0.000
	±0.069	±0.000	±0.042	±0.042	±0.253	±0.000	±0.042	±0.058	±0.248	±0.000
Coleoptera immature	0.792	0.708	0.833	0.500	0.667	0.583	0.750	0.625	1.125	0.792
	±0.295	±0.310	±0.305	±0.225	±0.177	±0.180	±0.227	±0.198	±0.303	±0.518
Coleoptera adult	0.167	0.083	0.042	0.167	0.375	0.292	0.125	0.167	0.500	0.458
	±0.078	±0.058	±0.042	±0.098	±0.101	±0.127	±0.069	±0.078	±0.159	±0.159
Diptera immature	1.083	1.458	0.917	1.583	0.917	1.125	2.000	0.458	1.083	1.083
	±0.345	±0.521	±0.408	±0.775	±0.329	±0.363	±0.496	±0.159	±0.306	±0.421
Other insects	0.083	0.375	0.167	0.167	0.083	1.292	0.125	0.250	0.083	0.292
	±0.058	±0.145	±0.078	±0.078	±0.058	±1.120	±0.069	±0.138	±0.058	±0.175

Collembola										
Entomobryidae	0.250	1.542	0.125	1.000	0.792	2.375	0.875	0.333	0.292	0.583
	±0.109	±1.126	±0.069	±0.599	±0.590	±1.649	±0.671	±0.167	±0.185	±0.345
Hypogastruridae	0.083	2.042	0.458	1.042	0.208	0.500	0.125	0.708	0.250	1.458
	±0.083	±1.296	±0.248	±0.533	±0.085	±0.255	±0.092	±0.369	±0.173	±0.596
Isotomidae	2.458	4.000	1.542	1.792	2.708	1.792	0.750	1.833	1.083	1.917
	±1.144	±2.034	±0.702	±0.504	±1.585	±0.876	±0.284	±0.656	±0.507	±0.730
Onychiuridae	1.375	2.250	2.208	1.542	1.375	1.292	0.917	1.083	1.333	2.833
	±0.749	±0.703	±0.881	±0.766	±0.567	±0.494	±0.371	±0.421	±0.667	±1.033
Sminthuridae	0.167	0.583	0.208	0.125	0.375	0.375	0.125	0.167	0.292	0.333
	±0.098	±0.300	±0.085	±0.069	±0.198	±0.189	±0.069	±0.167	±0.153	±0.155
Unidentified Collembola	20.792	16.875	18.250	14.750	21.792	13.250	24.250	18.083	18.250	11.667
	±4.993	±7.982	±3.716	±5.064	±5.520	±4.505	±7.206	±6.976	±4.323	±3.903
Other invertebrates										
Chilopoda	0.292	0.042	0.042	0.333	0.167	0.083	0.083	0.083	0.250	0.125
	±0.095	±0.042	±0.042	±0.130	±0.098	±0.083	±0.058	±0.058	±0.109	±0.069
Symphyla	1.583	1.208	1.625	1.000	1.750	1.208	1.250	0.958	0.583	1.208
	±0.625	±0.351	±0.586	±0.307	±0.443	±0.361	±0.302	±0.252	±0.146	±0.346
Nematoda	0.667	1.125	1.750	1.333	1.333	1.125	1.500	1.917	0.458	1.542
	±0.187	±0.387	±0.467	±0.379	±0.398	±0.353	±0.399	±0.782	±0.147	±0.466
Enchytraeidae	2.333	0.917	2.167	1.375	2.417	1.667	2.250	1.458	1.500	1.500
	±0.477	±0.169	±0.604	±0.485	±0.521	±0.465	±0.687	±0.605	±0.399	±0.458
Total	132.292	158.083	112.375	100.500	131.333	109.708	153.167	108.000	125.083	134.500
	±16.864	±47.562	±18.315	±15.531	±13.844	±17.516	±22.086	±21.805	±14.759	±21.240

Mean (\pm std. error) abundance of 49 representative taxa (44,996 total individuals) collected in conventional till soil in inundation experiment. Pooled data derived from 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, water (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Inundation/Conv Till	CT									
Time	4hr	24hr								
Treatment	Hb	Hb	Rb	Rb	Sc	Sc	Soil	Soil	Water	Water
Arachnida										
Acari										
Mesostigmata										
Ascidae	0.125	0.208	0.167	0.042	0.167	0.083	0.042	0.042	0.250	0.167
	±0.069	±0.104	±0.130	±0.042	±0.078	±0.058	±0.042	±0.042	±0.138	±0.130
<i>Protogamasellus spp.</i>	0.875	0.958	1.000	0.958	1.125	0.750	0.875	0.500	0.625	1.292
	±0.284	±0.460	±0.446	±0.401	±0.526	±0.400	±0.498	±0.376	±0.323	±0.523
<i>Hypoaspis spp.</i>	1.500	0.458	1.042	0.542	1.417	1.417	0.833	1.042	1.250	0.958
	±0.805	±0.180	±0.476	±0.307	±0.974	±0.558	±0.344	±0.547	±0.443	±0.636

<i>Macrocheles spp.</i>	0.167	0.375	0.208	0.167	0.208	0.208	0.042	0.083	0.250	0.292
	±0.167	±0.232	±0.120	±0.115	±0.104	±0.170	±0.042	±0.058	±0.109	±0.165
<i>Rhodacarus spp.</i>	0.208	0.208	0.333	0.208	0.417	0.458	0.292	0.042	0.292	0.417
	±0.104	±0.134	±0.155	±0.134	±0.158	±0.262	±0.185	±0.042	±0.127	±0.262
Other Mesostigmata (immature and male)	2.167	2.042	1.542	1.792	2.000	1.750	2.167	2.250	1.833	2.042
	±0.449	±0.464	±0.282	±0.511	±0.450	±0.352	±0.491	±0.618	±0.441	±0.533
Oribatida										
Brachychthoniidae	0.167	0.125	0.417	0.292	0.250	0.500	0.167	0.042	0.125	0.375
	±0.098	±0.069	±0.199	±0.141	±0.109	±0.241	±0.098	±0.042	±0.092	±0.168
<i>Neonothrus spp.</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
<i>Epilohmannia spp.</i>	0.792	0.167	0.750	0.417	1.083	0.292	0.667	0.208	0.417	0.083
	±0.413	±0.078	±0.308	±0.169	±0.583	±0.141	±0.253	±0.104	±0.240	±0.058
<i>Eremobelba spp.</i>	0.208	0.167	0.625	0.083	0.083	0.125	0.208	0.042	0.250	0.167
	±0.104	±0.078	±0.300	±0.058	±0.058	±0.069	±0.104	±0.042	±0.138	±0.167
<i>Rhysotritia spp.</i>	0.250	0.000	0.208	0.042	0.958	0.292	0.458	0.250	0.333	0.167
	±0.138	±0.000	±0.085	±0.042	±0.663	±0.141	±0.307	±0.124	±0.187	±0.098
<i>Galumna spp.</i>	0.042	0.083	0.042	0.042	0.000	0.042	0.125	0.000	0.125	0.208
	±0.042	±0.058	±0.042	±0.042	±0.000	±0.042	±0.092	±0.000	±0.092	±0.147
<i>Nothrus spp.</i>	0.250	0.000	0.125	0.250	0.000	0.000	0.000	0.000	0.000	0.000
	±0.250	±0.000	±0.125	±0.250	±0.000	±0.000	±0.000	±0.000	±0.000	±0.000
Oppiidae	1.250	0.750	0.917	0.833	1.167	1.000	0.708	0.875	0.667	1.000
	±0.367	±0.302	±0.275	±0.374	±0.912	±0.361	±0.338	±0.265	±0.214	±0.319
<i>Zygoribatula spp.</i>	0.208	0.375	0.417	1.292	0.458	0.375	0.583	0.458	0.750	0.500
	±0.134	±0.118	±0.199	±0.658	±0.233	±0.157	±0.356	±0.170	±0.250	±0.217
<i>Scheloribates spp.</i>	3.375	3.292	3.000	3.250	2.917	3.292	3.625	2.083	3.208	2.708
	±0.953	±1.067	±0.862	±0.629	±0.656	±0.888	±0.876	±0.571	±0.528	±0.533
<i>Tectocephus spp.</i>	3.958	5.208	4.667	4.875	4.333	17.375	4.042	4.500	5.417	7.292
	±0.846	±0.940	±0.863	±1.321	±0.876	±11.673	±0.701	±1.205	±0.794	±1.625
<i>Xylobates spp.</i>	1.625	0.667	1.667	1.125	1.917	1.458	1.458	0.583	1.083	0.875
	±0.548	±0.197	±0.741	±0.382	±0.805	±0.538	±0.481	±0.225	±0.356	±0.431
Unidentified Oribatida (male and unidentified)	0.208	0.208	0.417	0.167	0.500	0.083	0.167	0.083	0.542	0.208
	±0.104	±0.170	±0.262	±0.098	±0.241	±0.058	±0.167	±0.058	±0.241	±0.120
Unidentified Oribatida (immature)	11.625	10.292	15.042	14.125	14.208	16.833	12.333	10.083	15.542	11.958
	±2.128	±2.533	±3.165	±3.770	±2.249	±3.939	±2.182	±2.156	±2.432	±2.734
Prostigmata										
Cunaxidae	0.792	0.500	0.625	0.458	0.542	0.958	0.792	0.792	0.917	0.458
	±0.233	±0.181	±0.232	±0.159	±0.233	±0.423	±0.233	±0.217	±0.262	±0.170
<i>Eupodes spp.</i>	0.458	1.000	0.625	0.792	0.750	0.792	0.208	1.375	0.458	0.708
	±0.134	±0.276	±0.224	±0.282	±0.284	±0.356	±0.120	±0.488	±0.190	±0.221
<i>Nanorchestes spp.</i>	2.125	0.917	2.917	1.375	1.583	0.458	3.333	1.333	1.792	1.167
	±1.224	±0.458	±1.508	±0.714	±0.789	±0.262	±1.687	±0.627	±0.830	±0.557
<i>Speleorchestes spp.</i>	2.167	2.167	2.958	2.208	1.458	2.750	2.417	3.708	2.750	3.708
	±1.129	±1.007	±1.168	±1.328	±0.438	±1.360	±0.985	±1.566	±1.087	±1.393
Pygmephoridae	0.500	0.417	0.292	0.333	0.292	0.958	0.125	0.208	1.375	0.458
	±0.269	±0.146	±0.153	±0.130	±0.141	±0.713	±0.069	±0.104	±1.164	±0.180
Scutacaridae	0.292	0.583	0.292	0.583	0.208	0.417	0.250	0.583	0.542	0.708
	±0.185	±0.294	±0.127	±0.208	±0.134	±0.146	±0.150	±0.240	±0.225	±0.304
Tydeidae	0.083	0.167	0.000	0.042	0.000	0.208	0.250	0.083	0.292	0.083
	±0.058	±0.098	±0.000	±0.042	±0.000	±0.170	±0.138	±0.083	±0.141	±0.058
Unidentified Prostigmata	0.333	0.208	0.208	0.250	0.208	0.167	0.208	0.250	0.208	0.375
	±0.214	±0.134	±0.104	±0.124	±0.134	±0.078	±0.134	±0.173	±0.120	±0.168
Astigmata										

Acaridae	0.000	0.000	0.042	0.083	0.000	0.000	0.042	0.000	0.125	0.000
	±0.000	±0.000	±0.042	±0.058	±0.000	±0.000	±0.042	±0.000	±0.092	±0.000
<i>Sancassania spp.</i>	0.458	0.042	0.042	0.208	0.083	0.000	0.000	0.083	0.458	0.125
	±0.417	±0.042	±0.042	±0.134	±0.083	±0.000	±0.000	±0.058	±0.458	±0.092
Unidentified Astigmata	0.167	0.208	0.083	0.167	0.250	0.333	0.167	0.083	0.250	0.292
	±0.078	±0.134	±0.058	±0.130	±0.138	±0.214	±0.098	±0.083	±0.109	±0.112
Hypopi	1.708	1.917	1.500	1.125	2.500	1.292	2.083	0.958	1.375	1.042
	±0.563	±1.035	±0.525	±0.363	±0.819	±0.460	±0.983	±0.353	±0.437	±0.321
Insecta										
Japygidae	0.208	0.208	0.375	0.500	0.625	0.292	0.333	0.208	0.208	0.417
	±0.134	±0.085	±0.132	±0.181	±0.345	±0.153	±0.115	±0.104	±0.120	±0.158
Thysanoptera	0.125	0.250	0.042	0.292	0.167	0.417	0.042	0.208	0.083	0.667
	±0.092	±0.173	±0.042	±0.127	±0.098	±0.169	±0.042	±0.085	±0.058	±0.384
Formicidae	0.042	0.042	0.167	0.042	0.083	0.083	0.083	0.000	0.000	0.042
	±0.042	±0.042	±0.167	±0.042	±0.058	±0.058	±0.083	±0.000	±0.000	±0.042
Coleoptera immature	0.792	0.708	1.042	1.125	0.417	0.375	0.250	0.542	0.958	1.250
	±0.225	±0.272	±0.304	±0.835	±0.103	±0.145	±0.124	±0.262	±0.516	±0.679
Coleoptera adult	0.167	0.083	0.167	0.083	0.208	0.333	0.000	0.042	0.167	0.292
	±0.078	±0.058	±0.078	±0.058	±0.085	±0.130	±0.000	±0.042	±0.078	±0.213
Diptera immature	0.208	0.125	0.208	0.208	0.542	0.167	0.167	0.208	0.125	0.417
	±0.104	±0.092	±0.120	±0.170	±0.255	±0.098	±0.115	±0.104	±0.069	±0.180
Other insects	0.167	0.208	0.250	0.167	0.292	0.208	0.375	0.167	0.083	0.292
	±0.078	±0.104	±0.109	±0.098	±0.095	±0.085	±0.179	±0.167	±0.058	±0.112
Collembola										
Entomobryidae	0.250	1.250	0.250	0.917	0.125	0.875	0.500	0.333	0.583	1.083
	±0.150	±0.748	±0.109	±0.446	±0.092	±0.515	±0.269	±0.187	±0.255	±0.836
Hypogastruridae	0.000	0.375	0.042	0.042	0.000	0.000	0.042	0.167	0.042	0.042
	±0.000	±0.300	±0.042	±0.042	±0.000	±0.000	±0.042	±0.098	±0.042	±0.042
Isotomidae	0.458	0.958	0.042	0.792	0.417	0.792	0.042	1.042	0.208	0.583
	±0.295	±0.582	±0.042	±0.295	±0.208	±0.381	±0.042	±0.588	±0.120	±0.306
Onychiuridae	1.083	1.125	0.792	1.042	0.583	1.167	0.292	0.250	0.417	0.667
	±0.551	±0.588	±0.340	±0.491	±0.356	±0.625	±0.153	±0.124	±0.240	±0.274
Sminthuridae	0.083	0.292	0.042	0.708	0.167	0.333	0.000	0.000	0.250	0.542
	±0.058	±0.112	±0.042	±0.480	±0.098	±0.155	±0.000	±0.000	±0.150	±0.417
Unidentified Collembola	18.625	18.958	12.375	21.667	14.333	13.250	8.125	8.292	15.875	13.833
	±10.076	±10.622	±5.178	±12.900	±4.585	±4.832	±2.064	±3.584	±5.355	±6.303
Other invertebrates										
Chilopoda	0.000	0.042	0.083	0.042	0.167	0.292	0.125	0.208	0.042	0.083
	±0.000	±0.042	±0.058	±0.042	±0.130	±0.112	±0.069	±0.120	±0.042	±0.058
Symphyla	0.375	0.375	0.542	0.458	0.417	0.542	0.750	0.292	0.417	0.417
	±0.157	±0.118	±0.217	±0.170	±0.180	±0.241	±0.336	±0.141	±0.158	±0.180
Nematoda	0.292	0.083	0.208	0.167	0.208	0.000	0.167	0.042	0.167	0.250
	±0.112	±0.058	±0.120	±0.078	±0.085	±0.000	±0.098	±0.042	±0.078	±0.124
Enchytraeidae	2.417	1.125	0.958	1.583	1.375	1.167	1.458	1.458	1.583	1.000
	±1.092	±0.612	±0.401	±0.450	±0.645	±0.473	±0.662	±0.568	±0.686	±0.532
Total	63.250	59.708	59.583	67.917	61.042	74.875	51.375	46.042	64.458	61.542
	±11.121	±12.669	±8.202	±17.159	±7.592	±18.050	±5.209	±7.380	±6.832	±10.241

Appendix G Taxa from inundation experiment that exhibit significant effects

Taxa from inundation experiment that exhibit significant effects ($p < 0.05$) due to major factors (date, block, time and tillage type). Pooled data is derived from 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h time), 2 tillage regimes (conventional tillage and no-tillage till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied to a corn field

Taxa with significant effects ($p < .05$) due to sampling date				
Taxon	total	% freq in NT	F	P
Ascidae	112	72.30%	7.54	0.001
<i>Hypoaspis spp.</i>	489	48.70%	8.54	0.0005
<i>Macrocheles spp.</i>	297	83.80%	8.52	0.0005
Other Mesostigmata	1222	61.50%	5.61	0.0041
Brachychthoniidae	353	83.30%	6.83	0.0017
<i>Epilohmannia spp.</i>	278	57.90%	4.17	0.0142
<i>Nothrus spp.</i>	394	96.20%	4.88	0.0075
Opriidae	537	59.00%	5.54	0.0044
<i>Zygoribatula spp.</i>	1867	93.00%	6.73	0.0018
<i>Scheloribates spp.</i>	2444	69.80%	32.26	<.0001
<i>Tectocepheus spp.</i>	5022	70.50%	11.77	<.0001
<i>Xylobates spp.</i>	1071	72.10%	3.81	0.02
Oribatida immature	10161	68.80%	35.88	<.0001
Cunaxidae	356	53.90%	3.2	0.0366
<i>Speleorchestes spp.</i>	691	8.70%	3.26	0.0343
Scutacaridae	178	39.90%	10.76	0.0002
Acaridae	155	95.50%	2.99	0.0455
Other Astigmata	143	66.40%	3.73	0.0215
Hypopi	2092	82.20%	5.59	0.0042
Entomobryidae	344	57.00%	14.78	<.0001
Hypogastruridae	183	90.20%	8.21	0.0007
Isotomidae	605	78.80%	22.46	<.0001
Onychiuridae	567	68.60%	27.38	<.0001
Sminthuridae	124	53.20%	23.37	<.0001

Collembola	7759	55.00%	186.74	<.0001
Japygidae	219	63.00%	7.53	0.001
Thysanoptera	124	55.60%	7.2	0.0013
Nematoda	344	89.00%	3.29	0.0335
Enchytraeidae	761	55.50%	13.34	<.0001
Coleoptera immature	356	49.70%	3.97	0.0171
Coleoptera adult	94	60.60%	4.76	0.0084
Diptera immature	338	83.10%	4.1	0.0152
Other insects	123	56.90%	3.86	0.0189

Taxa with significant effects (p<.05) due to block

Taxon	total	% freq in NT	F	P
Ascidae	112	72.30%	4.64	0.0035
<i>Protogamasellus spp.</i>	283	24.00%	26.96	<.0001
<i>Hypoaspis spp.</i>	489	48.70%	5.56	0.001
<i>Macrocheles spp.</i>	297	83.80%	16.84	<.0001
<i>Rhodacarus spp.</i>	390	82.30%	60.06	<.0001
Other Mesostigmata	1222	61.50%	3.58	0.0144
Brachychthoniidae	353	83.30%	10.4	<.0001
<i>Epilohmannia spp.</i>	278	57.90%	8.67	<.0001
<i>Eremobelba spp.</i>	120	60.80%	5.54	0.001
<i>Rhysotritia spp.</i>	203	65.00%	9.65	<.0001
<i>Galumna spp.</i>	452	96.20%	54.24	<.0001
Oppiidae	537	59.00%	8.92	<.0001
<i>Zygoribatula spp.</i>	1867	93.00%	20.52	<.0001
<i>Scheloribates spp.</i>	2444	69.80%	3.48	0.0164
Other Oribatida	188	67.00%	17.47	<.0001
Oribatida immature	10161	68.80%	19.58	<.0001
Cunaxidae	356	53.90%	7.79	<.0001
<i>Eupodes spp.</i>	446	61.40%	4.89	0.0025
<i>Nanorchestes spp.</i>	785	48.00%	5.99	0.0006
<i>Speleorchestes spp.</i>	691	8.70%	6.08	0.0005
Tydeidae	224	87.10%	13.93	<.0001
Other Prostigmata	246	76.40%	5.59	0.001
Acaridae	155	95.50%	10.92	<.0001
<i>Sancassania spp.</i>	1095	96.70%	6.15	0.0005
Other Astigmata	143	66.40%	2.79	0.0406
Hypopi	2092	82.20%	9.15	<.0001
Entomobryidae	344	57.00%	10.42	<.0001
Hypogastruridae	183	90.20%	4.04	0.0078
Isotomidae	605	78.80%	4.9	0.0025
Onychiuridae	567	68.60%	4.77	0.0029
Sminthuridae	124	53.20%	4.57	0.0038
Collembola	7759	55.00%	11.68	<.0001
Symphyla	407	73.00%	8.02	<.0001
Thysanoptera	124	55.60%	7.35	<.0001

Nematoda	344	89.00%	7.03	0.0001
Enchytraeidae	761	55.50%	15.71	<.0001
Coleoptera adult	94	60.60%	5.57	0.001

Taxa with significant effects (p<.05) due to tillage regime (NT= no-till vs. CT=conventional-till)

Taxon	total	% in NT	F	P
<i>Protogamasellus spp.</i>	283	24.00%	40.83	0.0078
<i>Nothrus spp.</i>	394	96.20%	39.75	0.0081
<i>Zygoribatula spp.</i>	1867	93.00%	12.56	0.0383
<i>Scheloribates spp.</i>	2444	69.80%	38.98	0.0083
Oribatid immature	10161	68.80%	18.47	0.0232
<i>Speleorchestes spp.</i>	691	8.70%	20.09	0.0207
Other Prostigmatids	246	76.40%	47.67	0.0062
Hypopi	2092	82.20%	16.37	0.0272
Hypogastruridae	183	90.20%	17.27	0.0253
Isotomidae	605	78.80%	19.08	0.0222
Onychuridae	567	68.60%	10.88	0.0458
Symphylan	407	73.00%	38.76	0.0084
Japygidae	219	63.00%	27.76	0.0133
Nematoda	344	89.00%	53.91	0.0052
Enchytraeidae	761	55.50%	22.29	0.018
Coleoptera adult	94	60.60%	318.52	0.0004
Diptera immature	338	83.10%	39.43	0.0082

Taxa with significant effects (p<.05) due to sampling time (4hrs vs. 24hrs)

Taxon	total	% in NT	F	P
<i>Hypoaspis spp.</i>	489	48.70%	17.23	0.0003
<i>Macrocheles spp.</i>	297	83.80%	8.88	0.0057
<i>Rhodacarus spp.</i>	390	82.30%	16.29	0.0003
<i>Epilohmannia spp.</i>	278	57.90%	7.06	0.0125
<i>Rhysotritia spp.</i>	203	65.00%	10.71	0.0027
<i>Nothrus spp.</i>	394	96.20%	6.86	0.0137
<i>Scheloribates spp.</i>	2444	69.80%	13.52	0.0009
<i>Xylobates spp.</i>	1071	72.10%	4.97	0.0335
Oribatid immature	10161	68.80%	51.96	<.0001
ScutAcaridaeae	178	39.90%	11.53	0.0019
Acaridae	155	95.50%	15.66	0.0004
Hypopi	2092	82.20%	4.95	0.0338
Entomobryidae	344	57.00%	13.52	0.0009
Hypogastruridae	183	90.20%	17.24	0.0003
Isotomidae	605	78.80%	33.18	<.0001
Onychuridae	567	68.60%	6.02	0.0202

Sminthuridae	124	53.20%	4.42	0.0439
Collembola	7759	55.00%	542.92	<.0001
Thrips	124	55.60%	7.14	0.0121
Formicidae	41	65.90%	4.24	0.0484
Enchytraeidae	761	55.50%	10.88	0.0025

Appendix H Taxa in inundation experiment exhibiting significant effects due to interactions of major factors

Taxa in inundation experiment exhibiting significant effects due to interactions (date, block, time, till = tillage type and trt = nematode treatment).

Pooled data derived from 6 sampling dates (3Aug99, 23May00, 21Jun00,

1Aug00, 4Jun01, 2Jul01), 4 blocks, 2 sampling times (4, 24 hrs) and 5

treatments (soil control, water control, Sc=*Steinernema carpocapsae*,

Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Taxa exhibiting significant effects (p<0.05) due to the interaction of tillage type by date sampled (till*date) in inundation experiment				
Taxon	total	% freq in NT	F	P
Ascidae	112	72.30%	5.81	<.0001
<i>Hypoaspis spp.</i>	489	48.70%	4.72	0.0004
<i>Macrocheles spp.</i>	297	83.80%	3.07	0.0102
<i>Rhodacarus spp.</i>	390	82.30%	5.34	0.0001
Other Mesostigmata	1222	61.50%	6.49	<.0001
Brachychthoniidae	353	83.30%	9.73	<.0001
<i>Epilohmannia spp.</i>	278	57.90%	7.12	<.0001
<i>Eremobelba spp.</i>	120	60.80%	2.6	0.0256
<i>Galumna spp.</i>	452	96.20%	3.92	0.0019
<i>Nothrus spp.</i>	394	96.20%	6.72	<.0001
Oppiidae	537	59.00%	11	<.0001
<i>Zygoribatula spp.</i>	1867	93.00%	4.96	0.0002
<i>Scheloribates spp.</i>	2444	69.80%	11.44	<.0001
<i>Tectocepheus spp.</i>	5022	70.50%	4.37	0.0008
<i>Xylobates spp.</i>	1071	72.10%	11.99	<.0001
Other Oribatida	188	67.00%	5.95	<.0001
Oribatida immature	10161	68.80%	9.24	<.0001
Cunaxidae	356	53.90%	3.27	0.0069
<i>Nanorchestes spp.</i>	785	48.00%	2.62	0.0246
<i>Speleorchestes spp.</i>	691	8.70%	7.29	<.0001
Scutacaridae	178	39.90%	7.17	<.0001
Tydeidae	224	87.10%	9.67	<.0001
Other Prostigmata	246	76.40%	3.49	0.0044
Acaridae	155	95.50%	8.48	<.0001
Hypopi	2092	82.20%	8.81	<.0001

Hypogastruridae	183	90.20%	9.24	<.0001
Isotomidae	605	78.80%	19.42	<.0001
Onychiuridae	567	68.60%	5.04	0.0002
Sminthuridae	124	53.20%	11.48	0.0024
Collembola	7759	55.00%	6.2	<.0001
Symphyla	407	73.00%	5.22	0.0001
Japygidae	219	63.00%	2.58	0.0263
Nematoda	344	89.00%	9.09	<.0001
Enchytraeidae	761	55.50%	4.28	0.0009
Coleoptera immature	356	49.70%	3.08	0.01
Coleoptera adult	94	60.60%	4.96	0.0002

Taxa exhibiting significant effects ($p < 0.05$) due to the interaction of time by date (time*date) in inundation experiment

Taxon	total	% freq in NT	F	P
<i>Protogamasellus spp.</i>	283	24.00%	8.64	<.0001
<i>Rhodacarus spp.</i>	390	82.30%	6.92	<.0001
Other Mesostigmata	1222	61.50%	9.79	<.0001
Brachychthoniidae	353	83.30%	4.57	0.0005
<i>Epilohmannia spp.</i>	278	57.90%	10.28	<.0001
<i>Eremobelba spp.</i>	120	60.80%	2.75	0.0191
<i>Rhysotritia spp.</i>	203	65.00%	9.73	<.0001
<i>Nothrus spp.</i>	394	96.20%	3.18	0.0082
<i>Zygoribatula spp.</i>	1867	93.00%	2.96	0.0128
<i>Scheloribates spp.</i>	2444	69.80%	22.65	<.0001
<i>Tectocepheus spp.</i>	5022	70.50%	36.97	<.0001
<i>Xylobates spp.</i>	1071	72.10%	19.24	<.0001
Other Oribatida	188	67.00%	9.71	<.0001
Oribatida immature	10161	68.80%	81.85	<.0001
Cunaxidae	356	53.90%	4.68	0.0004
<i>Eupodes spp.</i>	446	61.40%	5.62	<.0001
<i>Nanorchestes spp.</i>	785	48.00%	4.39	0.0007
<i>Speleorchestes spp.</i>	691	8.70%	7.48	<.0001
Scutacaridae	178	39.90%	3.61	0.0035
Tydeidae	224	87.10%	2.26	0.0487
Other Prostigmata	246	76.40%	12.38	<.0001
Acaridae	155	95.50%	3.05	0.0106
Other Astigmata	143	66.40%	2.72	0.0203
Hypopi	2092	82.20%	12.05	<.0001
Entomobryidae	344	57.00%	4.76	0.0003
Hypogastruridae	183	90.20%	17	<.0001
Isotomidae	605	78.80%	14.37	<.0001
Onychiuridae	567	68.60%	13.24	<.0001
Sminthuridae	124	53.20%	12.56	0.0017
Collembola	7759	55.00%	208.42	<.0001
Symphyla	407	73.00%	4.95	0.0002
Japygidae	219	63.00%	9.54	<.0001

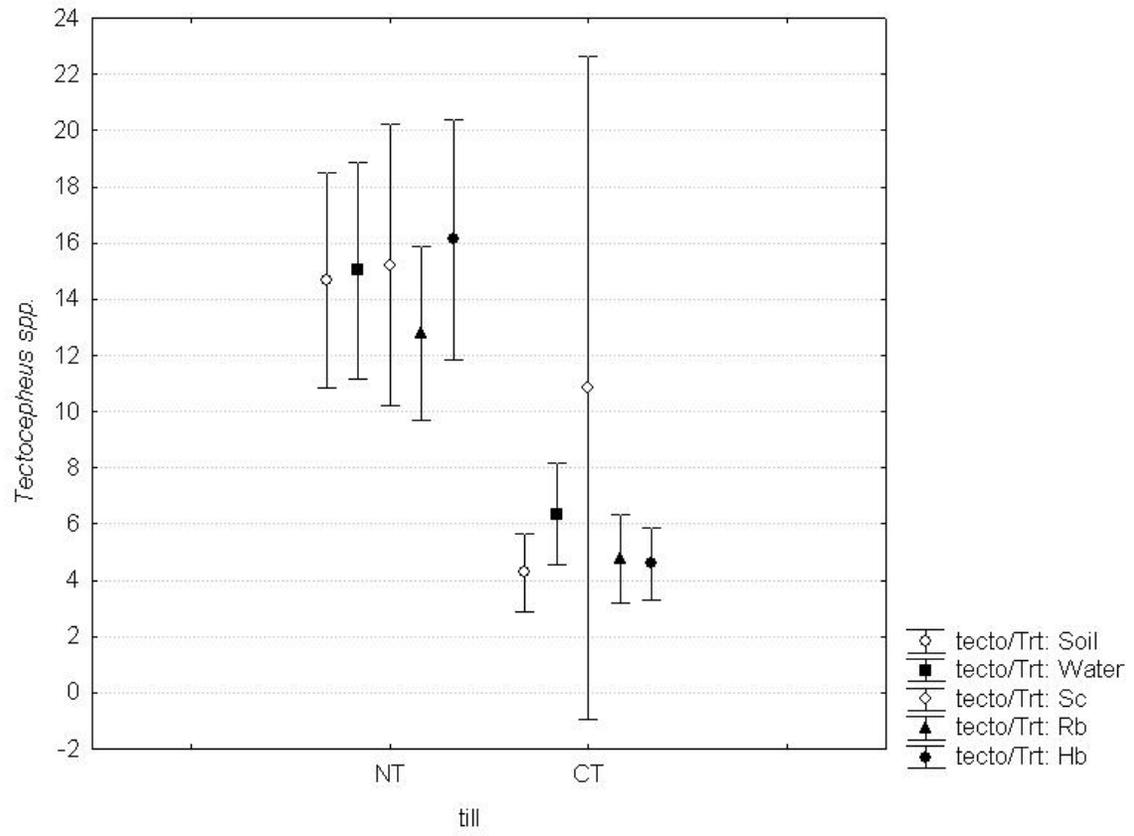
Thysanoptera	124	55.60%	5.9	<.0001
Nematoda	344	89.00%	3.08	0.0101
Coleoptera immature	356	49.70%	9.11	<.0001
Diptera immature	338	83.10%	5.16	0.0001
Other insects	123	56.90%	4.23	0.001

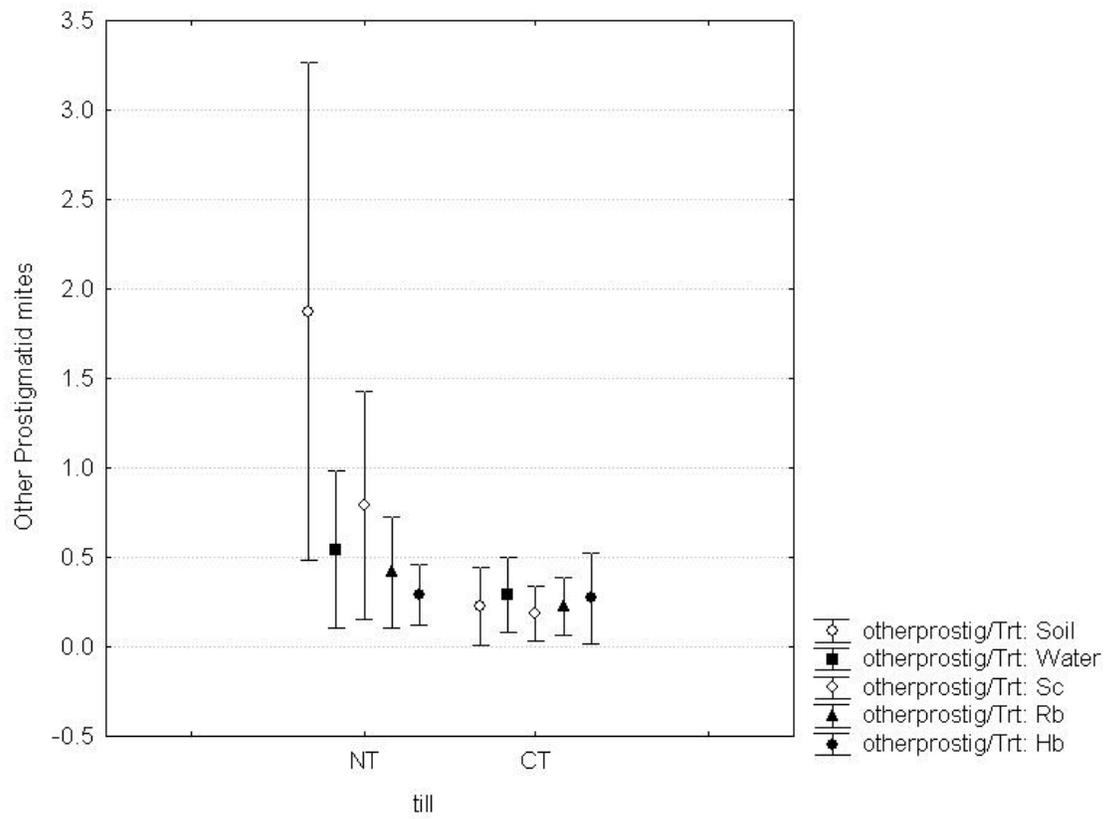
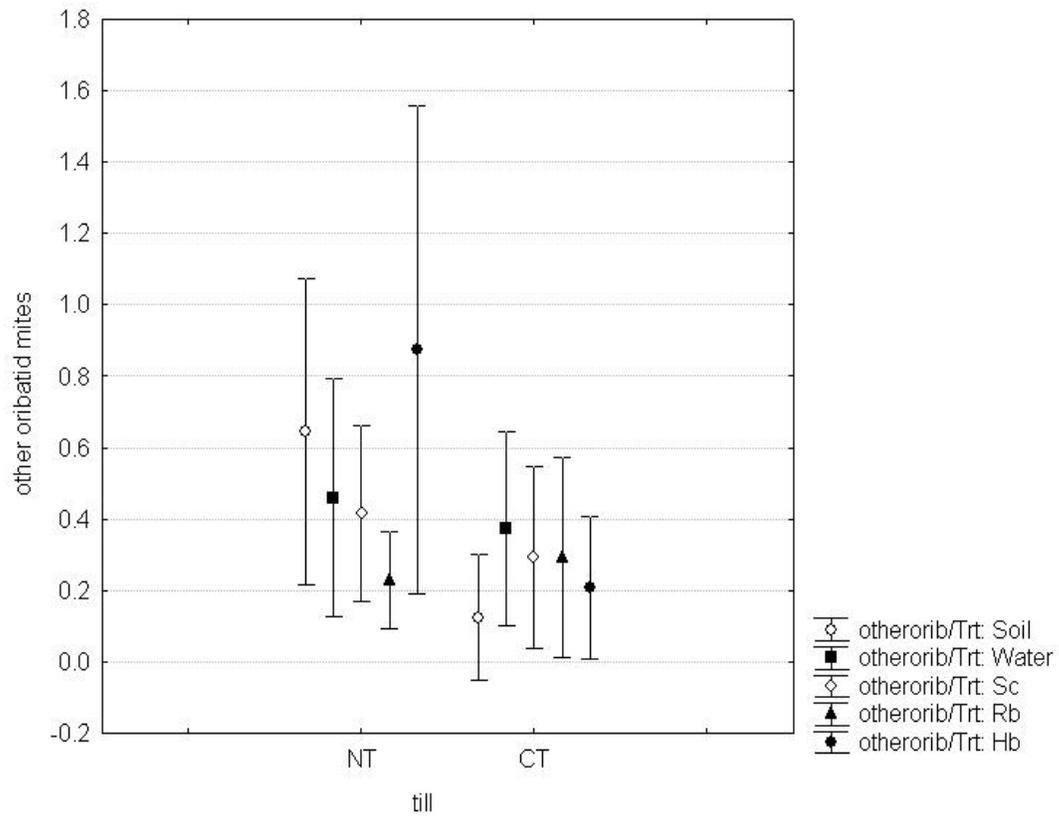
Taxa exhibiting significant effects ($p < 0.05$) due to the interaction of tillage type by time (till*time) in inundation experiment

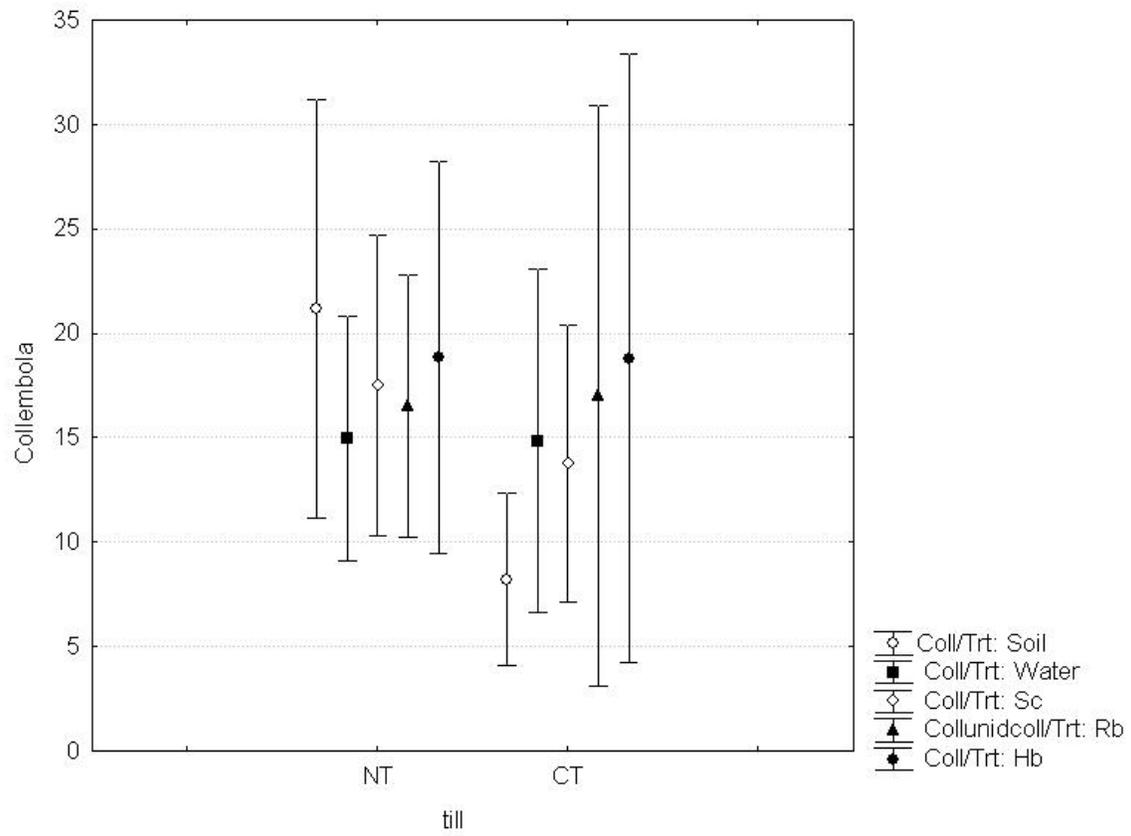
Taxon	total	% in NT	F	P
<i>Macrocheles spp.</i>	297	83.80%	9.95	0.0036
<i>Rhodacarus spp.</i>	390	82.30%	5.27	0.0288
<i>Nothrus spp.</i>	394	96.20%	4.91	0.0345
<i>Zygoribatula spp.</i>	1867	93.00%	6.24	0.0182
<i>Eupodes spp.</i>	446	61.40%	4.48	0.0426
Acaridae	155	95.50%	12.02	0.0016
Hypogastruridae	183	90.20%	8.41	0.0069
Thysanoptera	124	55.60%	5.66	0.024
Other insects	123	56.90%	6.66	0.015

Appendix I Taxa responsive to interaction of treatment by tillage type in inundation experiment

Mean abundance (in 150ml soil) of taxa (*Tectocepheus spp.*, other oribatid mites, other prostigmatid mites, Collembola) with significant response ($p < 0.05$) per treatment in No-till and Conventional-till soil in inundation experiment. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn. (N=48)

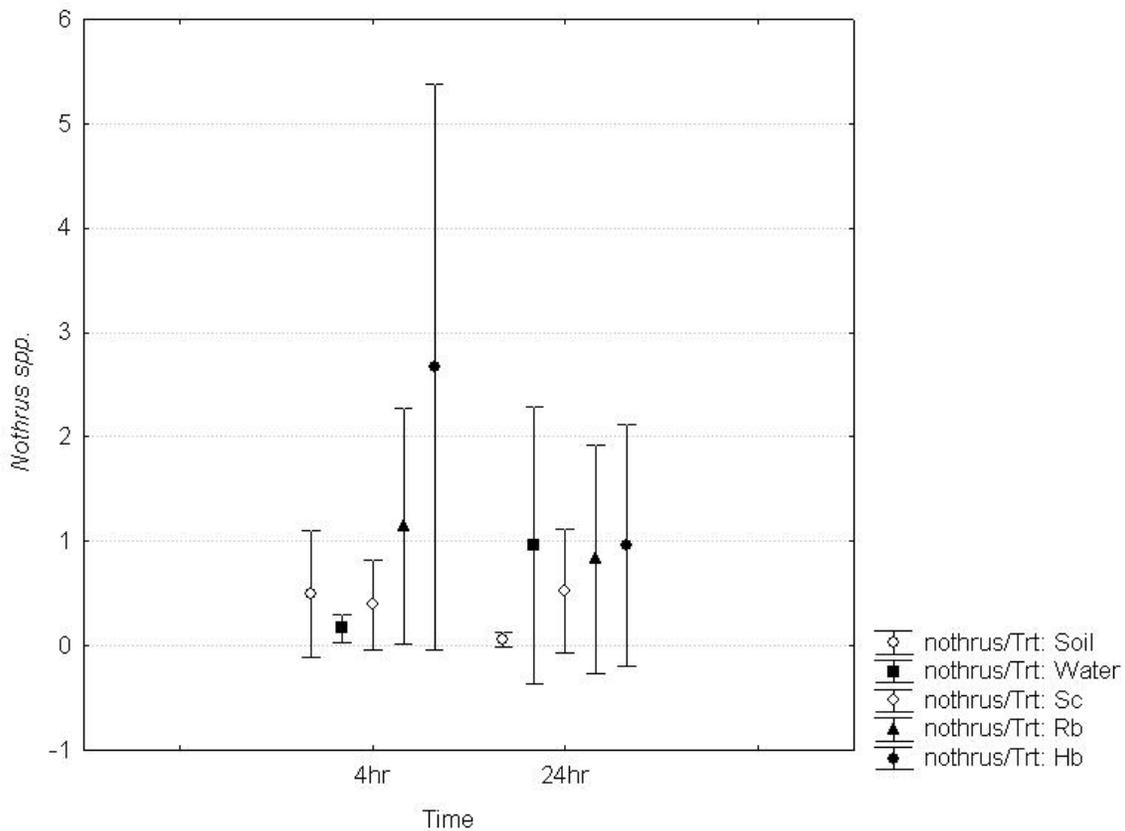


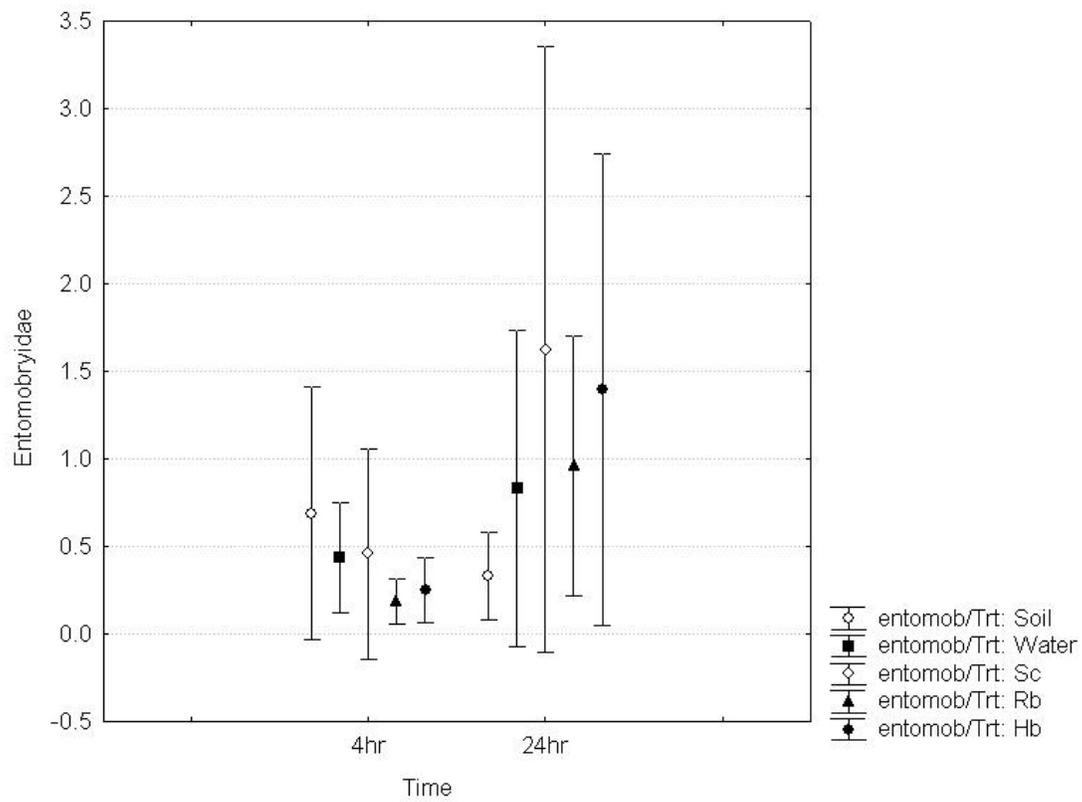
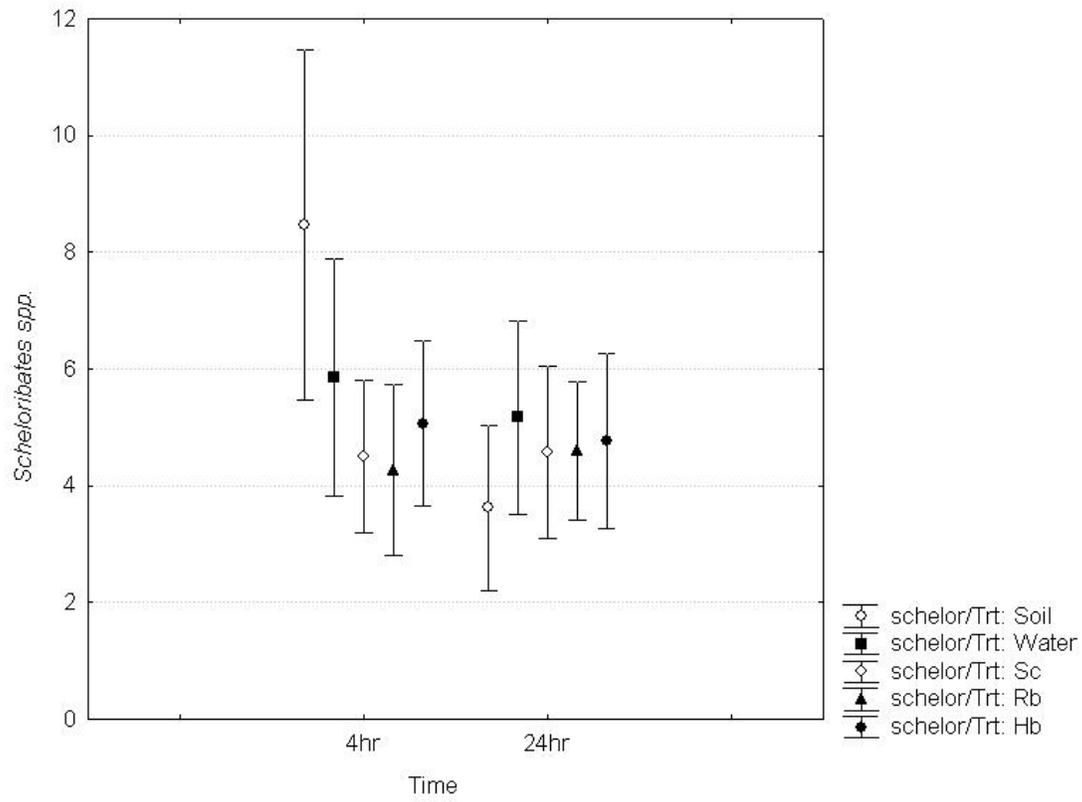


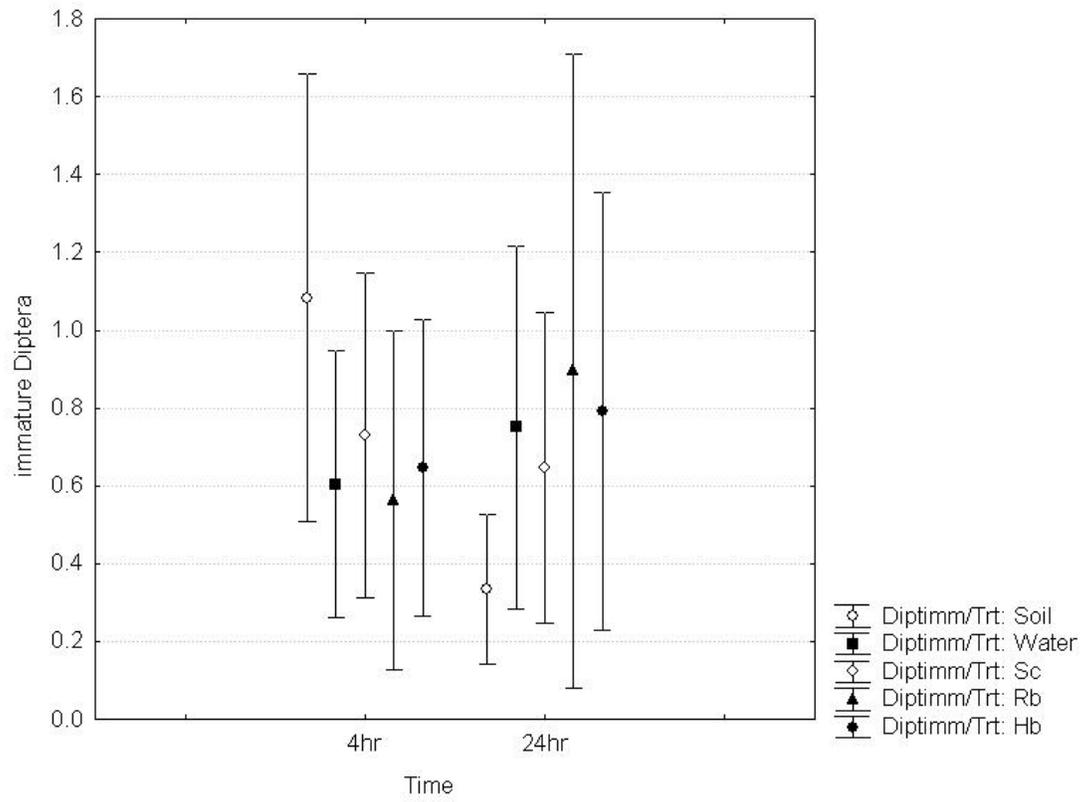


Appendix J Taxa responsive to interaction of sampling time by treatment in inundation experiment

Mean abundance of taxa (*Nothrus spp.*, *Scheloribates spp.*, Entomobryidae, Diptera (immature)) (in 150ml soil) at 4 hour and 24 hour sampling times per treatment in inundation experiment. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn. (N=48)







Appendix L SAS Code for contrasted ANOVA

All data were analyzed using the general linear model procedure (PROC GLM, SAS Institute 1996), and means were separated with the least significant difference (LSD SAS Institute 1996) SAS code for bait experiment

```
PROC IMPORT OUT= WORK.b
            DATAFILE= "F:\Copy of
PhD_data_masterSASversion_11feb04.XLS"
            DBMS=EXCEL2000 REPLACE,
            RANGE="Bait$",
            GETNAMES=YES,
RUN,
proc print , run,

data a, set b,
if year = . then delete,
date = trim(juliandate)||'_'||trim(year),
mites=astig+prostig+orib+mesos,
drop  soil_moisture water_potential soil_ph soil_texture
OM,
sqcoll=sqrt(coll), sqprost=sqrt(prostig),
lprost=log10(prostig+.5),
sqmesos=sqrt(mesos), lmesos=log10(mesos+.5),
sqmites=sqrt(mites), sqorib=sqrt(orib),
ltot=log10(total+.5), lmites=log10(mites+.5),
lother=log10(other+.5),
lastig=log10(astig+.5), lorib=log10(orib+.5),
lcoll=log10(coll+.5),
sqtecto=sqrt(tecto),
sqxylob=sqrt(xylobates),
sqprotog = sqrt(protogama),
sqhypoasp = sqrt(hypoaspis), sqrhodac=sqrt(rhoda),
sqcunax = sqrt(cunaxidae),
sqzygorib = sqrt(zygorib),
sqoppiidae = sqrt(oppiidae), sqcoleopimm =sqrt(coleopimm ),
sqsymph = sqrt(symph),
sqdiptimm = sqrt(diptimm),
sqEntomobryid = sqrt(Entomobryid), sqHypogas =sqrt(Hypogas
),
sqIso = sqrt(Iso),
sqOnych = sqrt(Onych),
```

```

options ls=78,
proc print data=a,
run,

proc glm data=a, class block till time trt date,
model lmesos lorib lastig lprost lcoll lother lmites ltot=
      block|till trt|time|till block*trt(till)
block*time(trt*till)
      date|till|time|trt date*block/ss3,
test h=till e=block*till,
test h=trt trt*till e=block*trt(till),
test h=time trt*time time*till trt*time*till
e=block*time(trt*till),
test h=date e=block*date,
contrast 'Soil vs dead' trt 1 0 0 0 -1 /e=block*trt(till),
contrast 'Soil vs nemas' trt 0 -1 -1 -1 3 /
e=block*trt(till),
contrast 'Dead vs nemas' trt 3 -1 -1 -1 0 /
e=block*trt(till),
contrast 'Hb vs Sc,Rb' trt 0 -1 .5 .5 0 /
e=block*trt(till),
contrast 'Hb,Rb vs Sc' trt 0 .5 .5 -1 0 /
e=block*trt(till),
contrast 'Hb,Sc vs Rb' trt 0 .5 -1 .5 0 /
e=block*trt(till),
means till*trt till*time*trt date date*till date*time,
means trt/lsd e=block*trt(till),
output out=p p= pmeso porib pastig pprost pcoll pother
pmites ptot
r=rmeso rorib rastig rprost rcoll rother rmites rtot,
run,

proc sort data=a, by till trt,
proc means data=a n mean stderr min max, by till trt,
var total coll mites,
run,

proc sort data=a, by till date,
proc means data=a n mean stderr min max, by till date,
var total coll mites,
run,

/* proc plot, plot rmeso*pmeso rorib*porib rastig*pastig
      rprost*pprost rcoll*pcoll rother*poother
      rmites*pmites rtot*ptot/vref=0,
run,*/

```

```

proc glm, class block time trt date, by till,
model lmesos lorib lastig sqprost lcoll lother ltot=
    block|trt trt|time block*time(trt)
    date|time|trt date*block/ss3,
test h=trt e=block*trt,
test h=time trt*time e=block*time(trt*till),
test h=date e=block*date,
contrast 'Soil vs dead' trt 1 0 0 0 -1 /e=block*trt(till),
contrast 'Soil vs nemas' trt 0 -1 -1 -1 3 /
e=block*trt(till),
contrast 'Dead vs nemas' trt 3 -1 -1 -1 0 /
e=block*trt(till),
contrast 'Hb vs Sc,Rb' trt 0 -1 .5 .5 0 /
e=block*trt(till),
contrast 'Hb,Rb vs Sc' trt 0 .5 .5 -1 0 /
e=block*trt(till),
contrast 'Hb,Sc vs Rb' trt 0 .5 -1 .5 0 /
e=block*trt(till),
means time*trt date date*time,
means trt/lsd e=block*trt,
run,

/*
proc glm data=a, class block till time trt date,
model sqtecto sqxylob sqprotog sqrhodac sqhypoasp=
    block|till time|till block*time(till) trt|time|till
block*trt(time*till)
    date|till|time|trt/ss3,
test h=till e=block*till,
test h=time time*till e=block*time(till),
test h=trt trt*time trt*till trt*time*till
e=block*trt(time*till),
contrast 'Soil vs dead' trt 1 0 0 0 -1
/e=block*trt(time*till),
contrast 'Hb vs Sc,Rb' trt 0 -1 .5 .5 0 /
e=block*trt(time*till),
means till*trt till*time*trt date,
output out=p2 p=ptect pxylo pprot prhod phypo
    r=rtect rxylo rprot rrhod rhypo,
proc plot data=p2, plot rtect*ptect rxylo*pxylo rprot*pprot
    rrhod*prhod rhypo*phypo/vref=0,
run,

proc glm data=a, class block till time trt date,
model sqcunax sqzygorib sqoppiidae sqcoleopimm sqsymph
sqdiptimm sqEntomobryid sqHypogas
sqIso sqOnych

```

```

= block|till time|till block*time(till) trt|time|till
block*trt(time*till)
      date|till|time|trt/ss3 ,
test h=till e=block*till,
test h=time time*till e=block*time(till),
test h=trt trt*time trt*till trt*time*till
e=block*trt(time*till),
manova H=trt e=block*trt(time*till),
contrast 'Soil vs dead' trt 1 0 0 0 -1
/e=block*trt(time*till),
contrast 'Hb vs Sc,Rb' trt 0 -1 .5 .5 0 /
e=block*trt(time*till),
means till*trt till*time*trt date,
means trt / lsd e=block*trt(time*till),
output out=p2 p=pcun pzygo poppi pcoleo psym
      r= rcun rzygo roppi rcoleo rsym,
run,
proc plot data=p2, plot rcun *pcun rzygo*pzygo roppi*poppi
      rcoleo*pcoleo rsym*psym/vref=0,
run, */

```

***** Other taxa

```

*****
data a, set a,
sqascid=sqrt(ascid), sqgamasell=sqrt(gamasell),
sqprotog=sqrt(protog),
sqhypoasp=sqrt(hypoasp), sqMacroch=sqrt(macroch),
      sqParasitid=sqrt(parasitid),
sqphytoseid=sqrt(phytoseid), sqRhoda=sqrt(rhoda),
squropod=sqrt(uropod), sqUnidmeso=sqrt(Unidmeso),
sqimm_meso=sqrt(imm-meso),
sqbrachychthoniidae=sqrt(brachychthoniidae),
sqepilohm=sqrt(epilohm), sqeremob=sqrt(eremob),
sqrhysotrit_pteroch=sqrt(rhysotrit_pteroch),
sqgalumna=sqrt(galumna), sqnothrus=sqrt(nothrus),
sqoppiid=sqrt(oppiid),
sqzygorib=sqrt(zygorib), sqschelor=sqrt(schelor),
sqtecto=sqrt(tecto), sqxylo=sqrt(xylo),
sqotherorib=sqrt(otherorib),
sqoribimm=sqrt(oribimm), sqcunax=sqrt(cunax),
sqcunaximm=sqrt(cunaximm), sqeupod=sqrt(eupod),
sqnanorch=sqrt(nanorch),
sqspeleo=sqrt(speleo), sqpygmep=sqrt(pygmep),
sqscutac=sqrt(scutac), sqstigmaeid=sqrt(stigmaeid),
sqtydeid=sqrt(tydeid),

```

```

sqotherprostig=sqrt(otherprostig), sqsancass=sqrt(sancass),
sqhistio=sqrt(histio), squnidastig=sqrt(unidastig),
sqhypopi=sqrt(hypopi), sqentomob=sqrt(entomob),
sqhypogas=sqrt(hypogas), sqiso=sqrt(iso),
sqonych=sqrt(onych),
sqsminth=sqrt(sminth), squnidcoll=sqrt(unidcoll),
sqchilop=sqrt(chilop), sqpaurop=sqrt(paurop),
sqsymph=sqrt(symph),
sqjapyg=sqrt(japyg), sqcoleopimm=sqrt(coleopimm),
sqcoleopad=sqrt(coleopad), sqdiptimm=sqrt(diptimm),
sqants=sqrt(ants),
sqnema=sqrt(nema), sqenchy=sqrt(enchy),
sqotherinsects=sqrt(otherinsects),
proc glm data=a, class block till time trt date,
model sqascid sqgamasell sqprotog sqhypoasp sqMacroch
      sqParasitid sqphytoseid
sqRhoda sqUropod sqUnidmeso
sqImm_Meso sqBrachychthoniidae sqEpilohm sqEremob
      sqRhysotrit_Pteroch sqGalumna sqNothrus
sqoppiid
sqZygorib sqSchelor sqTecto sqxylo sqOtherorib
      sqoribimm sqcunax sqCunaximm sqeupod sqNanorch
sqSpeleo sqPygmep sqscutac sqStigmaeid sqTydeid
      sqOtherprostig sqSancass sqHistio sqUnidastig
sqhypopi sqentomob sqHypogas sqIso sqOnych sqSminth
sqUnidcoll sqChilop sqPaurop sqsymph sqJapyg
sqColeopimm sqColeopad sqDiptimm sqants sqNema
      sqEnchy sqOtherinsects =
      block|till trt|time|till block*trt(till)
block*time(trt*till)
      date|till|time|trt date*block/ss3,
test h=till e=block*till,
test h=trt trt*till e=block*trt(till),
test h=time trt*time time*till trt*time*till
e=block*time(trt*till),
test h=date e=block*date,
contrast 'Soil vs dead' trt 1 0 0 0 -1 /e=block*trt(till),
contrast 'Soil vs nemas' trt 0 -1 -1 -1 3 /
e=block*trt(till),
contrast 'Dead vs nemas' trt 3 -1 -1 -1 0 /
e=block*trt(till),
contrast 'Hb vs Sc,Rb' trt 0 -1 .5 .5 0 /
e=block*trt(till),
contrast 'Hb,Rb vs Sc' trt 0 .5 .5 -1 0 /
e=block*trt(till),
contrast 'Hb,Sc vs Rb' trt 0 .5 -1 .5 0 /
e=block*trt(till),

```

```

means till*trt till*time*trt date date*till date*time,
means trt/lsd e=block*trt(till),
*output out=p p= pascid pgamasell pprotog pprost pcoll
pother pmites ptot
r=rascid rgamasell rprotog rprost rcoll rother rmites rtot,
run,
proc plot, plot rascid*pascid rgamasell*pgamasell
rprotog*pprotog
                rprost*pprost rcoll*pcoll rother*pother
                rmites*pmites rtot*ptot/vref=0,
run,

```

```

*** BY TILL

```

```

*****
proc glm data=a, class block till time trt date, by till,
model sqascid sqgamasell sqprotog sqhypoasp sqMacroch
sqParasitid sqphytoseid
sqRhoda sqUropod sqUnidmeso
sqImm_Meso sqBrachychthoniidae sqEpilohm sqEremob
sqRhysotrit_Pteroch sqGalumna sqNothrus
sqoppiid
sqZygorib sqSchelor sqTecto sqxylo sqOtherorib
sqoribimm sqcunax sqCunaximm sqeupod sqNanorch
sqSpeleo sqPygmep sqscutac sqStigmaeid sqTydeid
sqOtherprostig sqSancass sqHistio sqUnidastig
sqhypopi sqentomob sqHypogas sqIso sqOnych sqSminth
sqUnidcoll sqChilop sqPaurop sqsymph sqJapyg
sqColeopimm sqColeopad sqDiptimm sqants sqNema
sqEnchy sqOtherinsects =
    block|trt trt|time block*time(trt)
    date|time|trt date*block/ss3,
test h=trt e=block*trt,
test h=time trt*time e=block*time(trt*till),
test h=date e=block*date,
contrast 'Soil vs dead' trt 1 0 0 0 -1 /e=block*trt(till),
contrast 'Soil vs nemas' trt 0 -1 -1 -1 3 /
e=block*trt(till),
contrast 'Dead vs nemas' trt 3 -1 -1 -1 0 /
e=block*trt(till),
contrast 'Hb vs Sc,Rb' trt 0 -1 .5 .5 0 /
e=block*trt(till),
contrast 'Hb,Rb vs Sc' trt 0 .5 .5 -1 0 /
e=block*trt(till),
contrast 'Hb,Sc vs Rb' trt 0 .5 -1 .5 0 /
e=block*trt(till),
means time*trt date date*time,

```

```

means trt/lsd e=block*trt,
run,

*** untransformed *****,
proc glm data=a, class block till time trt date,
model ascid gamasell protog hypoasp Macroch
      Parasitid Phytoseid Rhoda Uropod Unidmeso
Imm_Meso Brachychthoniidae Epilohm Eremob
      Rhysotrit_Pteroch Galumna Nothrus oppiid
Zygorib Schelor Tecto xylo Otheroribs oribimm
      cunax Cunaximm eupod Nanorch
Speleo Pygmep scutac Stigmaeid Tydeidae
      Otherprostig Sancass Histio Unidastig
hypopi entomob Hypogas Iso Onych Sminth
      Unidcoll Chilop Paurop symph Japyg
Coleopimm Coleopad Diptimm ants Nema Enchy
      Otherinsects =
      block|till time|till block*time(till) trt|time|till
block*trt(time*till)
      date|till|time|trt /ss3,
test h=till e=block*till,
test h=time time*till e=block*time(till),
test h=trt trt*time trt*till trt*time*till
e=block*trt(time*till),
contrast 'Soil vs dead' trt 1 0 0 0 -1
/e=block*trt(time*till),
contrast 'Hb vs Sc,Rb' trt 0 -1 .5 .5 0 /
e=block*trt(time*till),
means till*trt till*time*trt date,
run,
proc princomp data=a out=pca ,* n=4,
var sqcunax sqzygorib sqoppiidae sqcoleopimm sqsymph
sqdiptimm sqEntomobryid sqHypogas
sqIso sqtecto sqxylob sqprotog sqrhodac,
run,
proc gplot data=pca, plot prin2*prin1=till,
run,
proc gplot data=pca, plot prin2*prin1=time,
run,
proc gplot data=pca, plot prin2*prin1=trt,
run,
symbol1 c=black v=dot,
symbol2 c=green v=circle,
symbol3 c=blue v=plus,
symbol4 c=red v=dot,
symbol5 c=red v=circle,
symbol6 c=red v=plus,

```

```
proc gplot data=pca, plot prin2*prin1=date,
run,

proc princomp data=a out=pca2 ,* n=4,
var lmesos lorib lastig lprost lcoll lother lmites,
run,
proc gplot data=pca2, plot prin2*prin1=till,
run,
proc gplot data=pca2, plot prin2*prin1=time,
run,
proc gplot data=pca2, plot prin2*prin1=trt,
run,
symbol1 c=black v=dot,
symbol2 c=green v=circle,
symbol3 c=blue v=plus,
symbol4 c=red v=dot,
symbol5 c=red v=circle,
symbol6 c=red v=plus,
proc gplot data=pca2, plot prin2*prin1=date,
run,
```

Appendix M Invertebrates collected in the bait experiment

All Invertebrates extracted in bait experiment, identified to the lowest taxonomic level, showing relative prevalence (% of total collected) in no-till (NT) and conventional-till (CT) soil. Pooled data derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, water (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Taxa	total #	# in NT	% in CT	#in NT	% in NT
Arachnida					
Acari					
Mesostigmata					
<i>Arctoseius spp.</i>	1	0	0.0%	1	100.0%
<i>Rhodacarellus spp.</i>	1	0	0.0%	1	100.0%
<i>Poecilochirus spp.</i>	4	0	0.0%	4	100.0%
Digamasellidae	2	0	0.0%	2	100.0%
Parasitidae	15	0	0.0%	15	100.0%
<i>Proprioseius spp.</i>	2	0	0.0%	2	100.0%
Polyaspididae	4	0	0.0%	4	100.0%
Veigaia	21	0	0.0%	21	100.0%
<i>Macrocheles spp.</i>	441	38	8.6%	403	91.4%
<i>Vulgarogamasus spp.</i>	28	3	10.7%	25	89.3%
<i>Cheiroseius spp.</i>	70	14	20.0%	56	80.0%
Ascidae	66	19	28.8%	47	71.2%
<i>Rhodacarus spp.</i>	394	121	30.7%	273	69.3%
Phytoseiidae	107	34	31.8%	73	68.2%
Uropodidae	90	30	33.3%	60	66.7%
Unidentified	332	128	38.6%	204	61.4%
<i>Lasioseius spp.</i>	22	9	40.9%	13	59.1%
<i>Gamasellodes spp.</i>	120	56	46.7%	64	53.3%
<i>Hypoaspis spp.</i>	609	301	49.4%	308	50.6%
Ologamasidae	2	1	50.0%	1	50.0%
Immature Mesostigmata	997	499	50.1%	498	49.9%

<i>Amblyseius spp.</i>	9	5	55.6%	4	44.4%
<i>Protogamasellus spp.</i>	683	633	92.7%	50	7.3%
Laelapidae	1	1	100.0%	0	0.0%
Zerconidae	1	1	100.0%	0	0.0%
Oribatida					
<i>Ceratozetes spp.</i>	1	0	0.0%	1	100.0%
<i>Haplochthonius spp.</i>	9	0	0.0%	9	100.0%
<i>Microzetes spp.</i>	2	0	0.0%	2	100.0%
<i>Mochlozetes spp.</i>	9	0	0.0%	9	100.0%
<i>Punctoribates spp.</i>	1	0	0.0%	1	100.0%
<i>Pterochthonius spp.</i>	48	0	0.0%	48	100.0%
Unidentified Oribatida	5	0	0.0%	5	100.0%
<i>Nothrus spp.</i>	270	4	1.5%	266	98.5%
<i>Zygoribatula spp.</i>	2226	65	2.9%	2161	97.1%
<i>Liochthonius spp.</i>	168	6	3.6%	162	96.4%
<i>Lamellobates spp.</i>	11	1	9.1%	10	90.9%
<i>Galumna spp.</i>	495	67	13.5%	428	86.5%
<i>Tectocepheus spp.</i>	4886	768	15.7%	4118	84.3%
<i>Eremobelba #2 spp.</i>	51	10	19.6%	41	80.4%
<i>Scheloribates spp.</i>	2856	689	24.1%	2167	75.9%
<i>Multioppia spp.</i>	32	9	28.1%	23	71.9%
Immature Oribatida	5640	1727	30.6%	3913	69.4%
<i>Poecilochthonius spp.</i>	93	29	31.2%	64	68.8%
<i>Oppiella spp.</i>	642	226	35.2%	416	64.8%
<i>Rhysotritria spp.</i>	439	157	35.8%	282	64.2%
<i>Berleszetes spp.</i>	37	15	40.5%	22	59.5%
<i>Xylobates spp.</i>	1456	676	46.4%	780	53.6%
<i>Brachychthonius spp.</i>	33	16	48.5%	17	51.5%
<i>Haplozetes spp.</i>	2	1	50.0%	1	50.0%
<i>Lohmannia spp.</i>	2	1	50.0%	1	50.0%
<i>Rostrozetes spp.</i>	183	97	53.0%	86	47.0%
<i>Eremobelba #1 spp.</i>	170	95	55.9%	75	44.1%
<i>Epilohmannia spp.</i>	599	424	70.8%	175	29.2%
<i>Ramusella spp.</i>	54	51	94.4%	3	5.6%
<i>Peloribates spp.</i>	3	3	100.0%	0	0.0%
<i>Oppia spp.</i>	1	1	100.0%	0	0.0%
Prostigmata					
<i>Raphignathus spp.</i>	1	0	0.0%	1	100.0%
Cheyletidae	10	1	10.0%	9	90.0%
Tydeidae	164	35	21.3%	129	78.7%
<i>Dactyloscirus spp.</i>	78	18	23.1%	60	76.9%
<i>Stigmaeus spp.</i>	107	26	24.3%	81	75.7%
<i>Puleaus spp.</i>	9	3	33.3%	6	66.7%
Tetranychidae	3	1	33.3%	2	66.7%
Tarsonemidae	41	14	34.1%	27	65.9%
Neocunaxidae	19	8	42.1%	11	57.9%
Immature Cunaxidae	243	108	44.4%	135	55.6%

Pygmephoridae	133	61	45.9%	72	54.1%
<i>Eupodes spp.</i>	951	445	46.8%	506	53.2%
Unidentified Prostigmata	6	3	50.0%	3	50.0%
<i>Nanorchestes spp.</i>	369	189	51.2%	180	48.8%
<i>Scutacarus spp.</i>	168	101	60.1%	67	39.9%
<i>Coleoscirus spp.</i>	185	119	64.3%	66	35.7%
<i>Rhagidia spp.</i>	12	8	66.7%	4	33.3%
Immature Prostigmata	37	26	70.3%	11	29.7%
<i>Speleorchestes spp.</i>	424	365	86.1%	59	13.9%
Cunaxidae	1	1	100.0%	0	0.0%
<i>Neoscirula spp.</i>	3	3	100.0%	0	0.0%
Lordallicidae	6	6	100.0%	0	0.0%
Astigmata					
Glycophagidae	2	0	0.0%	2	100.0%
Unidentified Astigmata	6	1	16.7%	5	83.3%
<i>Sancassania spp.</i>	487	86	17.7%	401	82.3%
Acaridae	94	21	22.3%	73	77.7%
Immature Astigmata	2137	486	22.7%	1651	77.3%
Histiostomatidae	285	157	55.1%	128	44.9%
Insecta					
Collembola					
Hypogastruridae	784	91	11.6%	693	88.4%
Onychiuridae	1945	500	25.7%	1445	74.3%
Unidentified Collembola	924	351	38.0%	573	62.0%
Isotomidae	2152	892	41.4%	1260	58.6%
Entomobryidae	1481	741	50.0%	740	50.0%
Sminthuridae	244	141	57.8%	103	42.2%
Other insects					
Dermeestidae larvae	1	0	0.0%	1	100.0%
Elateridae adult	2	0	0.0%	2	100.0%
Leiodidae larvae	3	0	0.0%	3	100.0%
Tipulidae larvae	9	1	11.1%	8	88.9%
Elateridae larvae	23	3	13.0%	20	87.0%
Eosentomidae	12	2	16.7%	10	83.3%
Cecidomyiidae larvae	6	1	16.7%	5	83.3%
Hemiptera	33	6	18.2%	27	81.8%
Staphylinidae larvae	37	9	24.3%	28	75.7%
Phoridae larvae	59	15	25.4%	44	74.6%
Phoridae adult	19	5	26.3%	14	73.7%
Enicocephalidae	10	3	30.0%	7	70.0%
Chrysomelidae adult	3	1	33.3%	2	66.7%
Carabidae larvae	36	12	33.3%	24	66.7%
Unidentified Diptera larvae	1249	465	37.2%	784	62.8%
Japygidae	377	141	37.4%	236	62.6%
Unidentified Coleoptera larvae	266	102	38.3%	164	61.7%
Staphylinidae adult	82	32	39.0%	50	61.0%
Chrysomelidae larvae	14	6	42.9%	8	57.1%

Unidentified Psocoptera	9	4	44.4%	5	55.6%
Scarabaeidae larvae	2	1	50.0%	1	50.0%
Scydmaenidae larvae	2	1	50.0%	1	50.0%
Cecidomyiidae adult	16	8	50.0%	8	50.0%
Mycetophilidae adult	2	1	50.0%	1	50.0%
Unidentified Hymenoptera	8	4	50.0%	4	50.0%
Thysanoptera	81	41	50.6%	40	49.4%
Unidentified Diptera adult	24	13	54.2%	11	45.8%
Unidentified Coleoptera adult	22	12	54.5%	10	45.5%
Homoptera	9	5	55.6%	4	44.4%
Liposcelis	68	38	55.9%	30	44.1%
Scydmaenidae adult	7	4	57.1%	3	42.9%
Chironomidae larvae	7	4	57.1%	3	42.9%
Pselaphidae adult	13	8	61.5%	5	38.5%
Ceratopogonidae larvae	11	8	72.7%	3	27.3%
Carabidae adult	34	25	73.5%	9	26.5%
Formicidae	1173	928	79.1%	245	20.9%
Chironomidae adult	1	1	100.0%	0	0.0%
Mycetophilidae larvae	2	2	100.0%	0	0.0%
Other invertebrates					
Unidentified Diplopoda	1	0	0.0%	1	100.0%
Nematoda	250	51	20.4%	199	79.6%
Unidentified Chilopoda	69	21	30.4%	48	69.6%
Unidentified Symphyla	518	166	32.0%	352	68.0%
Unidentified Pauropoda	81	32	39.5%	49	60.5%
Unidentified Annelida	5	2	40.0%	3	60.0%
Enchytraeidae	996	454	45.6%	542	54.4%

Appendix N Means tables for bait experiment

Mean (\pm std. error) abundance of 55 representative taxa (44,996 total individuals) collected in no-till soil in bait experiment. Pooled data derived from 6 sampling dates ((6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, water (controls),

Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Bait/No Till	NT									
Time	4hr	24hr								
Treatment	Hb	Hb	Rb	Rb	Sc	Sc	Soil	Soil	Dead	Dead
Arachnida										
Acari										
Mesostigmata										
Ascidae	0.375	0.292	0.625	0.708	0.375	0.792	0.417	0.375	0.500	0.625
	± 0.189	± 0.141	± 0.215	± 0.244	± 0.254	± 0.282	± 0.158	± 0.157	± 0.209	± 0.365
<i>Gamasellodes</i> spp.	0.208	0.500	0.417	0.500	0.042	0.250	0.167	0.333	0.125	0.125
	± 0.120	± 0.217	± 0.169	± 0.269	± 0.042	± 0.109	± 0.098	± 0.214	± 0.092	± 0.069
<i>Protogamasellus</i> spp.	0.167	0.000	0.208	0.250	0.250	0.292	0.083	0.625	0.125	0.083
	± 0.078	± 0.000	± 0.147	± 0.150	± 0.173	± 0.112	± 0.058	± 0.355	± 0.092	± 0.058
<i>Hypoaspis</i> spp.	1.750	1.958	0.833	1.042	0.750	1.750	0.958	1.167	1.208	1.417
	± 0.443	± 0.685	± 0.238	± 0.272	± 0.302	± 0.443	± 0.310	± 0.299	± 0.408	± 0.345
<i>Macrocheles</i> spp.	1.417	1.333	1.667	1.792	2.458	1.458	1.708	0.833	1.542	2.583
	± 0.648	± 0.411	± 0.517	± 0.514	± 0.893	± 0.318	± 0.658	± 0.267	± 0.466	± 1.175
Parasitidae	0.167	0.083	0.292	0.042	0.125	0.000	0.167	0.417	0.208	0.167
	± 0.115	± 0.083	± 0.175	± 0.042	± 0.092	± 0.000	± 0.098	± 0.248	± 0.104	± 0.167
Phytoseidae	0.250	0.583	0.417	0.500	0.167	0.333	0.250	0.167	0.042	0.583
	± 0.183	± 0.248	± 0.180	± 0.217	± 0.078	± 0.115	± 0.173	± 0.098	± 0.042	± 0.199
<i>Rhodacarus</i> spp.	1.167	0.958	0.708	1.417	1.042	1.750	1.167	1.000	0.958	1.208
	± 0.437	± 0.279	± 0.428	± 0.656	± 0.388	± 0.715	± 0.502	± 0.474	± 0.310	± 0.390
Uropodidae	0.208	0.167	0.750	0.458	0.083	0.083	0.167	0.125	0.167	0.292
	± 0.170	± 0.098	± 0.467	± 0.282	± 0.058	± 0.058	± 0.130	± 0.092	± 0.078	± 0.213
Other Mesostigmata	0.458	0.583	0.792	1.375	0.917	1.333	0.458	1.208	1.125	1.417
(male and	± 0.170	± 0.169	± 0.330	± 0.334	± 0.345	± 0.389	± 0.147	± 0.324	± 0.243	± 0.417
unidentified)										
immature	1.708	1.750	1.917	2.667	2.542	3.000	1.250	1.792	1.833	2.292
	± 0.419	± 0.342	± 0.356	± 0.527	± 0.645	± 0.574	± 0.347	± 0.307	± 0.384	± 0.672
Oribatida										
Brachychthoniidae	1.500	0.625	1.583	1.042	0.792	0.500	0.708	1.250	1.792	0.708
	± 0.454	± 0.281	± 0.524	± 0.359	± 0.324	± 0.200	± 0.304	± 0.713	± 0.858	± 0.237

<i>Epilohmannia spp.</i>	0.792	0.667	0.792	0.125	0.583	0.625	0.958	1.208	1.042	0.500
	±0.269	±0.223	±0.346	±0.069	±0.269	±0.215	±0.229	±0.330	±0.310	±0.200
<i>Eremobelba spp.</i>	0.292	0.500	0.583	0.708	0.458	0.417	0.417	0.667	0.250	0.542
	±0.252	±0.376	±0.232	±0.464	±0.180	±0.146	±0.158	±0.223	±0.150	±0.262
<i>Rhysotritia spp.</i>	0.833	0.875	2.792	1.208	2.458	1.375	0.375	1.708	1.083	1.042
	±0.398	±0.505	±2.492	±0.462	±1.292	±0.492	±0.157	±0.666	±0.466	±0.397
<i>Galumna spp.</i>	1.125	3.000	1.542	2.458	0.833	1.458	0.875	3.167	0.833	2.542
	±0.284	±1.009	±0.574	±0.883	±0.317	±0.408	±0.410	±1.604	±0.317	±0.752
<i>Nothrus spp.</i>	2.042	1.000	0.625	1.417	1.208	0.833	0.708	0.583	1.542	1.125
	±1.180	±0.599	±0.317	±0.541	±0.717	±0.402	±0.338	±0.255	±0.878	±0.588
Oppiidae	1.083	2.458	1.083	2.625	0.667	2.042	1.458	2.542	1.167	3.292
	±0.306	±0.545	±0.318	±0.836	±0.231	±0.498	±0.434	±0.532	±0.280	±0.703
<i>Zygoribatula spp.</i>	7.333	12.625	9.000	9.375	7.750	7.833	7.625	6.958	11.458	10.083
	±2.150	±3.813	±2.374	±3.356	±2.530	±2.055	±2.467	±1.417	±3.642	±2.767
<i>Scheloribates spp.</i>	4.125	9.250	8.250	12.542	9.000	10.167	5.958	11.292	6.458	13.250
	±0.743	±1.307	±1.304	±2.938	±1.972	±1.942	±1.168	±2.379	±1.175	±2.619
<i>Tectocepheus spp.</i>	16.833	17.375	18.250	19.250	14.333	19.208	15.125	16.958	17.917	16.333
	±2.817	±3.904	±2.802	±2.608	±1.951	±2.296	±2.050	±1.659	±2.812	±2.026
<i>Xylobates spp.</i>	2.958	2.917	3.000	3.292	3.417	2.958	4.000	3.500	3.208	3.250
	±0.813	±0.580	±0.764	±0.763	±0.551	±0.505	±0.799	±0.749	±0.602	±0.718
Other Oribatida	0.500	0.375	0.708	0.958	0.500	0.833	0.250	0.500	0.208	0.917
	±0.262	±0.132	±0.221	±0.343	±0.217	±0.349	±0.090	±0.209	±0.085	±0.380
Oribatida immature	14.208	12.667	18.125	21.542	14.875	16.333	16.542	15.625	16.583	16.542
	±2.887	±2.894	±3.493	±4.650	±2.722	±3.886	±4.719	±2.760	±3.361	±3.593
Prostigmata										
Cunaxidae	0.417	0.625	0.292	1.000	0.333	1.083	0.292	0.708	0.375	0.833
	±0.190	±0.239	±0.112	±0.319	±0.143	±0.288	±0.141	±0.213	±0.132	±0.305
Cunaxidae immature	0.417	0.417	0.375	0.792	0.333	0.958	0.250	0.917	0.667	0.500
	±0.208	±0.158	±0.132	±0.199	±0.115	±0.266	±0.109	±0.269	±0.223	±0.181
<i>Eupodes spp.</i>	0.417	2.167	1.042	3.208	1.042	3.000	0.708	3.542	1.167	4.792
	±0.133	±0.520	±0.272	±0.987	±0.332	±0.934	±0.272	±0.959	±0.280	±1.310
<i>Nanorchestes spp.</i>	0.583	0.583	0.792	0.792	0.500	0.583	1.167	0.625	1.167	0.708
	±0.275	±0.216	±0.434	±0.324	±0.248	±0.232	±0.477	±0.287	±0.636	±0.502
<i>Speleorchestes spp.</i>	0.083	0.167	0.125	0.083	0.333	0.333	0.250	0.333	0.458	0.292
	±0.058	±0.098	±0.069	±0.058	±0.223	±0.214	±0.109	±0.177	±0.170	±0.141
Pygmephoridae	0.042	0.042	0.083	0.167	0.042	0.083	0.083	2.292	0.167	0.000
	±0.042	±0.042	±0.058	±0.130	±0.042	±0.058	±0.058	±2.205	±0.078	±0.000
Scutacaridae	0.167	0.250	0.250	0.250	0.250	0.167	0.333	0.208	0.542	0.375
	±0.098	±0.138	±0.109	±0.250	±0.109	±0.098	±0.155	±0.085	±0.233	±0.118
Stigmaeidae	0.375	0.292	0.250	0.542	0.583	0.292	0.292	0.250	0.292	0.208
	±0.157	±0.175	±0.109	±0.190	±0.312	±0.127	±0.112	±0.109	±0.175	±0.085
Tydeidae	0.208	0.375	1.500	0.167	0.583	0.167	0.458	0.333	1.250	0.333
	±0.120	±0.207	±0.969	±0.078	±0.208	±0.098	±0.301	±0.223	±0.490	±0.155
Other Prostigmata	0.667	0.167	0.250	0.125	0.292	0.167	0.208	0.167	0.167	0.167
	±0.333	±0.078	±0.090	±0.125	±0.141	±0.098	±0.104	±0.098	±0.078	±0.098
Astigmata										
<i>Sancassania spp.</i>	0.625	3.083	0.250	4.042	0.125	1.375	1.500	0.750	1.167	3.792

	±0.385	±1.268	±0.109	±1.523	±0.069	±0.592	±1.205	±0.347	±0.838	±1.733
Histiostomatidae	0.292	0.375	0.792	1.250	0.292	0.458	0.750	0.292	0.417	0.417
	±0.127	±0.157	±0.248	±0.569	±0.141	±0.180	±0.308	±0.127	±0.169	±0.158
Other Astigmata	0.083	0.458	0.333	0.125	0.292	0.083	0.583	0.333	0.333	0.708
	±0.058	±0.233	±0.187	±0.092	±0.165	±0.058	±0.462	±0.167	±0.177	±0.327
Hypopi	12.917	5.375	14.500	4.083	8.958	3.167	6.875	2.792	5.917	4.208
	±6.845	±1.889	±7.693	±1.124	±3.101	±1.059	±2.301	±0.735	±1.502	±1.092
Insecta										
Japygidae	0.542	1.125	0.750	1.250	0.625	1.250	0.625	1.042	1.167	1.458
	±0.134	±0.363	±0.227	±0.250	±0.198	±0.277	±0.198	±0.237	±0.299	±0.318
Coleoptera immature	0.542	1.250	0.917	1.208	1.167	1.417	0.375	1.167	0.708	1.667
	±0.180	±0.264	±0.216	±0.217	±0.333	±0.430	±0.118	±0.293	±0.165	±0.317
Coleoptera adult	0.333	0.375	0.208	0.458	0.375	0.500	0.083	0.292	0.292	0.458
	±0.115	±0.157	±0.085	±0.170	±0.118	±0.190	±0.058	±0.112	±0.127	±0.134
Diptera immature	1.500	1.458	2.875	16.292	1.625	3.875	1.167	1.917	1.208	3.375
	±0.421	±0.584	±0.900	±6.266	±0.450	±1.182	±0.311	±0.474	±0.295	±1.098
Formicidae	0.125	0.042	0.167	2.083	0.542	1.208	0.167	0.125	1.583	4.167
	±0.092	±0.042	±0.130	±1.831	±0.335	±0.757	±0.098	±0.069	±0.715	±2.641
Other insects	0.542	0.375	0.417	0.458	0.417	0.833	0.667	0.708	0.750	1.542
	±0.159	±0.145	±0.180	±0.159	±0.103	±0.274	±0.214	±0.213	±0.257	±0.542
Collembola										
Entomobryidae	1.250	2.875	1.917	5.292	0.958	5.083	0.792	2.875	1.875	7.917
	±0.443	±0.731	±0.574	±1.726	±0.338	±1.118	±0.307	±0.765	±0.483	±2.013
Hypogastruridae	1.875	3.083	3.375	3.917	3.708	2.792	2.958	1.917	2.500	2.750
	±0.733	±0.955	±1.301	±1.755	±1.712	±0.808	±1.154	±0.681	±0.851	±0.813
Isotomidae	5.417	5.208	5.833	6.292	3.792	5.417	4.917	4.667	4.917	6.042
	±2.671	±1.111	±1.325	±1.738	±0.841	±1.199	±2.354	±1.014	±1.476	±1.505
Onychiuridae	4.250	3.167	6.833	8.792	7.208	5.750	8.292	5.083	4.083	6.750
	±1.218	±0.805	±1.837	±2.993	±2.284	±1.733	±2.808	±1.155	±1.068	±1.514
Sminthuridae	0.292	0.542	0.458	0.292	0.625	0.375	0.292	0.542	0.458	0.417
	±0.141	±0.233	±0.225	±0.141	±0.317	±0.179	±0.127	±0.241	±0.134	±0.133
Unidentified Collembola	3.917	1.458	1.792	1.417	2.458	1.833	2.792	2.167	2.750	3.292
	±2.696	±0.841	±0.921	±0.648	±1.316	±0.880	±1.320	±1.407	±1.060	±1.649
Other invertebrates										
Chilopoda	0.042	0.250	0.125	0.208	0.125	0.375	0.125	0.208	0.125	0.417
	±0.042	±0.173	±0.069	±0.085	±0.092	±0.157	±0.092	±0.104	±0.069	±0.133
Pauropoda	0.125	0.167	0.083	0.208	0.083	0.167	0.125	0.458	0.125	0.500
	±0.092	±0.098	±0.058	±0.104	±0.058	±0.078	±0.069	±0.170	±0.069	±0.225
Symphyla	0.875	2.458	1.292	1.917	1.042	2.167	0.542	1.083	1.125	2.167
	±0.236	±0.558	±0.272	±0.403	±0.252	±0.949	±0.180	±0.262	±0.309	±0.630
Nematoda	1.000	0.583	1.292	0.917	0.792	1.042	0.708	0.625	0.333	1.000
	±0.434	±0.180	±0.606	±0.356	±0.269	±0.369	±0.285	±0.281	±0.143	±0.371
Enchytraeidae	1.708	1.542	1.917	3.042	3.292	1.917	2.958	2.042	2.083	2.083
	±0.436	±0.518	±0.474	±0.955	±0.902	±0.807	±0.733	±0.693	±0.699	±0.722
Total	103.125	112.875	126.042	157.958	108.417	123.542	103.125	114.458	111.542	144.250
	±15.969	±13.242	±18.394	±14.535	±14.530	±11.467	±18.906	±10.028	±11.506	±13.523

Mean (\pm std. error) abundance of 55 representative taxa (44,996 total individuals) collected in conventional till soil in bait experiment. Pooled data derived from 6 sampling dates ((6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 4 blocks, 2 sampling times (4, 24 hrs) and 5 treatments (soil, water (controls), Sc=*Steinernema carpocapsae*, Rb=*Steinernema riobrave*, Hb=*Heterorhabditis bacteriophora* (nematode strains))

Bait/Conv Till	CT									
Time	4hr	24hr								
Treatment	Hb	Hb	Rb	Rb	Sc	Sc	Soil	Soil	Dead	Dead
Arachnida										
Acari										
Mesostigmata										
Ascidae	0.083	0.000	0.333	0.292	0.167	0.167	0.125	0.375	0.042	0.250
	± 0.058	± 0.000	± 0.155	± 0.153	± 0.130	± 0.098	± 0.092	± 0.145	± 0.042	± 0.124
<i>Gamasellodes</i> spp.	0.083	0.542	0.083	0.208	0.167	0.417	0.083	0.417	0.083	1.000
	± 0.058	± 0.233	± 0.058	± 0.104	± 0.098	± 0.240	± 0.083	± 0.262	± 0.058	± 0.371
<i>Protogamasellus</i> spp.	1.167	3.958	0.875	6.667	1.333	5.708	0.792	3.292	1.000	5.000
	± 0.344	± 0.892	± 0.629	± 2.027	± 0.672	± 1.947	± 0.248	± 1.533	± 0.366	± 1.232
<i>Hypoaspis</i> spp.	0.833	1.583	1.125	2.083	1.167	1.542	1.042	1.542	1.417	1.792
	± 0.317	± 0.351	± 0.320	± 0.524	± 0.311	± 0.361	± 0.244	± 0.462	± 0.294	± 0.462
<i>Macrocheles</i> spp.	0.125	0.167	0.042	0.042	0.208	0.167	0.208	0.292	0.083	0.250
	± 0.069	± 0.098	± 0.042	± 0.042	± 0.134	± 0.098	± 0.104	± 0.127	± 0.058	± 0.173
Parasitidae	0.000	0.000	0.000	0.042	0.042	0.000	0.042	0.000	0.000	0.000
	± 0.000	± 0.000	± 0.000	± 0.042	± 0.042	± 0.000	± 0.042	± 0.000	± 0.000	± 0.000
Phytoseiidae	0.167	0.167	0.083	0.250	0.167	0.083	0.208	0.292	0.208	0.083
	± 0.078	± 0.115	± 0.058	± 0.150	± 0.130	± 0.058	± 0.085	± 0.153	± 0.134	± 0.058
<i>Rhodacarus</i> spp.	0.458	0.750	0.333	0.417	0.542	0.750	0.625	0.625	0.292	0.958
	± 0.199	± 0.409	± 0.223	± 0.232	± 0.269	± 0.471	± 0.375	± 0.247	± 0.141	± 0.666
Uropodidae	0.042	0.125	0.000	0.417	0.125	0.250	0.000	0.208	0.000	0.333
	± 0.042	± 0.125	± 0.000	± 0.232	± 0.125	± 0.173	± 0.000	± 0.134	± 0.000	± 0.253
Other Mesostigmata	0.208	0.458	0.583	0.417	0.958	0.708	0.667	0.542	0.792	0.625
(male and	± 0.104	± 0.225	± 0.169	± 0.190	± 0.316	± 0.204	± 0.223	± 0.170	± 0.233	± 0.168
unidentified)										
immature										
Mesostigmata	1.667	2.875	1.375	3.167	2.375	2.542	1.417	2.917	1.500	3.792
	± 0.344	± 0.512	± 0.446	± 0.898	± 0.561	± 0.561	± 0.380	± 0.583	± 0.335	± 0.754
Oribatida										
Brachychthoniidae	0.458	0.042	0.458	0.167	0.125	0.333	0.083	0.292	0.250	0.125
	± 0.190	± 0.042	± 0.295	± 0.130	± 0.092	± 0.155	± 0.058	± 0.213	± 0.150	± 0.069
<i>Epilohmannia</i> spp.	1.250	1.542	1.250	2.125	1.625	1.625	2.083	1.833	2.667	1.917
	± 0.455	± 0.413	± 0.372	± 0.700	± 0.551	± 0.481	± 0.707	± 0.914	± 0.756	± 0.819
<i>Eremobelba</i> spp.	0.458	0.292	0.500	0.458	0.792	0.458	0.208	0.875	0.292	0.542
	± 0.225	± 0.185	± 0.200	± 0.217	± 0.404	± 0.262	± 0.134	± 0.444	± 0.127	± 0.289

<i>Rhysotritia</i> spp.	0.292	0.875	0.792	0.458	0.333	0.542	0.917	0.708	0.958	0.750
	±0.112	±0.363	±0.208	±0.147	±0.115	±0.233	±0.288	±0.316	±0.292	±0.250
<i>Galumna</i> spp.	0.042	0.417	0.208	0.500	0.292	0.167	0.250	0.625	0.458	0.208
	±0.042	±0.294	±0.208	±0.351	±0.252	±0.098	±0.173	±0.389	±0.295	±0.120
<i>Nothrus</i> spp.	0.000	0.000	0.000	0.042	0.083	0.000	0.042	0.000	0.000	0.000
	±0.000	±0.000	±0.000	±0.042	±0.083	±0.000	±0.042	±0.000	±0.000	±0.000
Oppiidae	1.500	1.292	1.083	2.083	0.917	2.292	0.875	3.167	0.750	2.042
	±0.608	±0.383	±0.593	±0.727	±0.300	±0.615	±0.423	±0.957	±0.314	±0.579
<i>Zygoribatula</i> spp.	0.167	0.583	0.125	0.458	0.250	0.333	0.292	0.542	0.417	0.417
	±0.098	±0.208	±0.092	±0.199	±0.124	±0.130	±0.127	±0.217	±0.158	±0.180
<i>Scheloribates</i> spp.	1.958	4.833	2.625	4.833	3.625	3.792	2.083	4.292	3.750	4.375
	±0.428	±0.820	±0.678	±1.268	±0.732	±0.717	±0.737	±0.748	±0.808	±0.782
<i>Tectocepheus</i> spp.	2.958	3.958	2.875	3.333	3.375	3.833	3.042	4.833	3.875	4.708
	±0.711	±0.738	±0.795	±0.784	±0.651	±0.816	±0.674	±1.093	±0.710	±1.104
<i>Xylobates</i> spp.	2.375	3.250	2.667	2.583	3.417	2.500	2.042	3.958	2.708	4.500
	±0.642	±0.781	±0.870	±0.709	±1.478	±0.692	±0.672	±1.691	±0.741	±1.506
Other Oribatida	0.458	0.292	0.583	0.500	0.542	0.500	0.208	0.667	0.458	0.708
	±0.340	±0.127	±0.275	±0.376	±0.241	±0.241	±0.104	±0.433	±0.225	±0.279
Oribatida immature	6.750	8.000	9.250	8.500	8.667	8.000	8.750	7.792	8.917	8.583
	±1.050	±1.428	±1.997	±1.476	±1.881	±1.866	±1.974	±1.426	±1.417	±1.573
Prostigmata										
Cunaxidae	0.250	0.958	0.250	1.458	0.458	1.375	0.167	1.333	0.208	1.500
	±0.124	±0.266	±0.124	±0.340	±0.180	±0.306	±0.098	±0.293	±0.085	±0.399
Cunaxidae immature	0.500	1.250	0.458	0.708	0.292	0.458	0.375	0.750	0.583	1.167
	±0.376	±0.387	±0.225	±0.237	±0.153	±0.170	±0.157	±0.302	±0.190	±0.311
<i>Eupodes</i> spp.	0.667	1.792	1.333	4.042	1.167	5.833	0.750	2.667	0.500	3.167
	±0.238	±0.385	±0.305	±1.074	±0.402	±2.318	±0.271	±0.616	±0.159	±0.573
<i>Nanorchestes</i> spp.	1.167	0.500	1.083	1.125	1.625	0.875	1.000	0.583	1.125	0.625
	±0.576	±0.217	±0.390	±0.757	±0.766	±0.265	±0.470	±0.376	±0.392	±0.215
<i>Speleorchestes</i> spp.	2.833	1.583	2.667	1.750	1.250	2.625	0.958	1.792	2.167	2.292
	±1.028	±0.561	±1.306	±0.455	±0.400	±0.938	±0.388	±0.643	±1.130	±1.218
Pygmephoridae	0.375	0.292	0.083	0.292	0.333	0.417	0.333	0.250	0.625	0.500
	±0.334	±0.175	±0.083	±0.127	±0.206	±0.262	±0.214	±0.109	±0.403	±0.295
Scutacaridae	0.417	0.333	0.792	1.208	0.583	0.500	0.375	1.083	0.333	0.542
	±0.208	±0.115	±0.376	±0.590	±0.199	±0.269	±0.239	±0.470	±0.130	±0.241
Stigmaeidae	0.083	0.125	0.042	0.083	0.250	0.292	0.125	0.083	0.000	0.042
	±0.083	±0.125	±0.042	±0.083	±0.250	±0.292	±0.125	±0.083	±0.000	±0.042
Tydeidae	0.083	0.250	0.292	0.292	0.083	0.083	0.125	0.042	0.250	0.125
	±0.058	±0.150	±0.127	±0.175	±0.058	±0.083	±0.069	±0.042	±0.109	±0.069
Other Prostigmata	0.292	0.083	0.083	0.250	0.417	0.208	0.292	0.500	0.042	0.375
	±0.095	±0.058	±0.083	±0.173	±0.225	±0.147	±0.112	±0.225	±0.042	±0.254
Astigmata										
<i>Sancassania</i> spp.	0.167	0.792	0.208	0.792	0.250	0.375	0.292	0.542	0.083	1.000
	±0.115	±0.324	±0.134	±0.301	±0.138	±0.224	±0.175	±0.295	±0.058	±0.417
Histiostomatidae	0.208	0.708	0.583	1.042	0.250	0.833	0.542	0.625	0.333	1.500
	±0.104	±0.378	±0.208	±0.383	±0.109	±0.253	±0.233	±0.350	±0.130	±0.408
Other Astigmata	0.000	0.083	0.083	0.208	0.000	0.208	0.083	0.167	0.042	0.042

	±0.000	±0.058	±0.058	±0.104	±0.000	±0.134	±0.083	±0.130	±0.042	±0.042
Hypopi	2.083	2.958	1.292	1.542	1.667	2.167	2.417	2.708	2.417	2.000
	±0.545	±0.939	±0.285	±0.454	±0.664	±0.573	±0.771	±0.588	±0.759	±0.538
Insecta										
Japygidae	0.250	1.000	0.542	0.792	0.625	0.958	0.292	0.458	0.667	0.583
	±0.109	±0.282	±0.248	±0.241	±0.232	±0.343	±0.112	±0.180	±0.253	±0.199
Coleoptera immature	0.208	0.875	0.292	1.417	0.458	1.042	0.417	0.917	0.333	0.750
	±0.085	±0.250	±0.141	±0.300	±0.147	±0.259	±0.119	±0.275	±0.143	±0.173
Coleoptera adult	0.250	0.167	0.292	0.500	0.375	0.583	0.208	0.500	0.208	0.458
	±0.109	±0.078	±0.175	±0.135	±0.215	±0.199	±0.104	±0.147	±0.104	±0.208
Diptera immature	0.250	7.167	2.417	5.500	0.875	1.875	0.750	0.417	1.417	0.500
	±0.109	±6.561	±1.205	±2.663	±0.435	±0.781	±0.505	±0.158	±0.754	±0.209
Formicidae	5.667	0.458	0.792	0.792	2.417	16.250	0.958	0.000	7.000	10.333
	±5.010	±0.199	±0.631	±0.749	±2.417	±11.704	±0.958	±0.000	±5.304	±5.739
Other insects	0.250	0.458	0.333	1.167	0.333	0.667	0.333	0.750	0.833	0.917
	±0.090	±0.170	±0.115	±0.305	±0.130	±0.143	±0.115	±0.202	±0.187	±0.366
Collembola										
Entomobryidae	0.542	5.000	1.292	6.958	0.708	5.625	0.875	2.833	1.458	9.417
	±0.255	±1.563	±0.844	±1.572	±0.221	±1.502	±0.410	±0.914	±0.485	±3.037
Hypogastruridae	0.292	0.333	0.375	0.542	0.250	0.292	0.500	0.667	0.792	0.292
	±0.141	±0.155	±0.179	±0.217	±0.109	±0.112	±0.301	±0.246	±0.330	±0.112
Isotomidae	3.000	4.333	3.250	6.208	3.417	6.375	2.750	3.500	2.875	4.500
	±0.805	±1.202	±1.185	±1.651	±1.066	±1.910	±0.975	±1.023	±0.912	±1.343
Onychiuridae	1.250	3.167	1.292	2.333	1.667	3.167	1.917	3.042	1.875	3.625
	±0.326	±1.033	±0.423	±0.734	±0.630	±1.265	±0.541	±0.956	±0.718	±1.199
Sminthuridae	0.667	1.125	0.625	0.667	0.542	0.542	0.500	0.708	0.667	0.625
	±0.322	±0.373	±0.287	±0.214	±0.199	±0.159	±0.170	±0.304	±0.206	±0.340
Unidentified Collembola	1.167	1.792	1.083	2.667	0.875	1.625	1.417	1.208	1.292	1.500
	±0.488	±0.942	±0.492	±1.508	±0.410	±1.213	±0.545	±0.742	±0.606	±0.834
Other invertebrates										
Chilopoda	0.000	0.167	0.083	0.125	0.000	0.125	0.000	0.250	0.083	0.292
	±0.000	±0.098	±0.058	±0.069	±0.000	±0.069	±0.000	±0.124	±0.058	±0.112
Pauropoda	0.083	0.042	0.083	0.125	0.125	0.292	0.167	0.125	0.250	0.375
	±0.058	±0.042	±0.058	±0.092	±0.069	±0.127	±0.098	±0.069	±0.183	±0.157
Symphyla	0.292	1.083	0.583	0.917	0.500	0.917	0.458	0.958	0.333	1.375
	±0.141	±0.458	±0.232	±0.225	±0.269	±0.240	±0.190	±0.327	±0.155	±0.473
Nematoda	0.208	0.250	0.208	0.125	0.375	0.417	0.583	0.208	0.250	0.250
	±0.104	±0.124	±0.085	±0.092	±0.189	±0.376	±0.208	±0.085	±0.109	±0.124
Enchytraeidae	1.833	2.042	1.292	1.542	2.417	1.833	2.708	1.167	3.875	1.833
	±0.589	±0.767	±0.560	±0.462	±0.991	±0.613	±0.918	±0.311	±1.690	±0.619
Total	48.833	77.167	51.333	87.208	55.875	95.542	48.750	70.917	63.833	95.458
	±7.644	±7.843	±6.520	±7.820	±6.315	±11.074	±6.024	±8.227	±8.002	±10.903

Appendix O Taxa from bait experiment that exhibit significant effects due to experimental factors

Taxa from bait experiment that exhibit significant effects ($p < 0.05$) due to experimental factors (date, block, time and tillage type) in . Pooled data is derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 2 sampling times (4 or 24 h time), 2 tillage regimes (conventional tillage and no-tillage till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied to a corn field

Taxa with significant effects ($p < 0.05$) due to sampling date				
Taxon	total	% in NT	F	P
<i>Gamasellodes spp.</i>	138	46.40%	3.29	0.0332
<i>Hypoaspis spp.</i>	647	47.60%	5.54	0.0044
Phytoseidae	120	65.80%	6.66	0.0019
Brachychthoniidae	308	81.80%	3.06	0.0422
<i>Epilohmannia spp.</i>	605	28.90%	5.24	0.0055
Oppiidae	826	53.50%	5.99	0.0031
<i>Zygoribatula spp.</i>	2247	96.20%	3.64	0.0235
<i>Scheloribates spp.</i>	3035	71.40%	36.13	<.0001
Oribatida immature	5910	66.20%	16.21	<.0001
Cunaxidae	334	42.80%	4.23	0.0134
Cunaxidae immature	292	46.20%	6.72	0.0018
<i>Eupodes spp.</i>	1032	49.00%	12.73	<.0001
<i>Nanorchestes spp.</i>	413	43.60%	9.9	0.0002
Scutacaridae	215	31.20%	4.14	0.0146
Stigmaeidae	108	75.00%	3.48	0.0276
Entomobryidae	1573	47.00%	15.8	<.0001
Hypogastruridae	797	87.00%	13.89	<.0001
Isotomidae	2225	56.60%	25.41	<.0001
Onychiuridae	2005	72.10%	8.32	0.0006
Sminthuridae	263	39.20%	9.33	0.0003
Collembola	924	62.00%	35.28	<.0001
Paupoda	89	55.10%	7.24	0.0012
Japygidae	384	61.50%	5.22	0.0057
Coleoptera immature	411	60.80%	10.68	0.0002

Coleoptera adult	166	48.80%	13.81	<.0001
Diptera immature	1355	62.50%	7.53	0.001
Nematoda	268	74.30%	4.15	0.0144

Taxa with significant effects ($p < 0.05$) due to block

Taxon	total	% in NT	F	P
Ascidae	166	73.50%	4.45	0.0045
<i>Gamasellodes</i> spp.	138	46.40%	8.57	<.0001
<i>Protogamasellus</i> spp.	765	6.50%	12.25	<.0001
<i>Hypoaspis</i> spp.	647	47.60%	5.32	0.0014
<i>Macrocheles</i> spp.	441	91.40%	32.62	<.0001
<i>Rhodacarus</i> spp.	411	66.40%	46.75	<.0001
Uropodidae	96	62.50%	21.52	<.0001
Other Mesostigmata	375	61.90%	5.04	0.002
Brachychthoniidae	308	81.80%	7.58	<.0001
<i>Epilohmannia</i> spp.	605	28.90%	13.67	<.0001
<i>Eremobelba</i> spp.	233	49.80%	4.9	0.0024
<i>Galumna</i> spp.	504	84.90%	60.41	<.0001
Opiidae	826	53.50%	9.7	<.0001
<i>Zygoribatula</i> spp.	2247	96.20%	25.22	<.0001
<i>Scheloribates</i> spp.	3035	71.40%	4.65	0.0034
<i>Tectocepheus</i> spp.	5001	82.30%	7.86	<.0001
<i>Xylobates</i> spp.	1500	52.00%	13.99	<.0001
Oribatida immature	5910	66.20%	20.57	<.0001
Cunaxidae	334	42.80%	5.58	0.001
Cunaxidae immature	292	46.20%	4.9	0.0025
<i>Eupodes</i> spp.	1032	49.00%	5.3	0.0014
<i>Nanorchestes</i> spp.	413	43.60%	9.87	<.0001
<i>Speleorchestes</i> spp.	537	11.00%	35.44	<.0001
Scutacaridae	215	31.20%	6.63	0.0002
Stigmaeidae	108	75.00%	9.39	<.0001
<i>Sancassania</i> spp.	509	78.80%	16.5	<.0001
Histiostomatidae	287	44.60%	3.36	0.0192
Other Astigmata	102	78.40%	5.43	0.0012
Hypopi	2161	76.40%	20.29	<.0001
Hypogastruridae	797	87.00%	16.32	<.0001
Isotomidae	2225	56.60%	9.92	<.0001
Onychiuridae	2005	72.10%	21.13	<.0001
Sminthuridae	263	39.20%	4.24	0.006
Collembola	924	62.00%	9.98	<.0001
Chilopoda	75	64.00%	4.01	0.0081
Symphyla	530	66.40%	7.27	0.0001
Japygidae	384	61.50%	11.88	<.0001
Diptera immature	1355	62.50%	4.18	0.0064
Formicidae	1317	18.60%	9.56	<.0001
Nematoda	268	74.30%	3.86	0.0099
Enchytraeidae	1035	52.40%	14.82	<.0001

Taxa with significant effects (p<0.05) due to tillage regime (NT=no-till vs. CT=conventional-till)

Taxon	total	% in NT	F	P
Ascidae	166	73.50%	10.47	0.048
<i>Protogamasellus spp.</i>	765	6.50%	21.77	0.0186
Brachychthoniidae	308	81.80%	19.58	0.0214
<i>Galumna spp.</i>	504	84.90%	9.51	0.054
<i>Zygoribatula spp.</i>	2247	96.20%	15.53	0.0291
<i>Scheloribates spp.</i>	3035	71.40%	11.55	0.0425
<i>Tectocepheus spp.</i>	5001	82.30%	23.59	0.0167
Oribatida immature	5910	66.20%	23.43	0.0168
Stigmaeidae	108	75.00%	63.24	0.0041
Hypopi	2161	76.40%	18.26	0.0235
Hypogastruridae	797	87.00%	62.69	0.0042
Onychiuridae	2005	72.10%	34.34	0.0099
Chilopoda	75	64.00%	68.71	0.0037
Coleoptera immature	411	60.80%	18.35	0.0234

Taxa with significant effects (p<0.05) due to sampling time (4hrs vs 24hrs)

Taxon	total	% in NT	F	P
<i>Gamasellodes spp.</i>	138	46.40%	15.84	0.0004
<i>Protogamasellus spp.</i>	765	6.50%	46.81	<.0001
<i>Hypoaspis spp.</i>	647	47.60%	9.49	0.0044
<i>Rhodacarus spp.</i>	411	66.40%	4.58	0.0405
Brachychthoniidae	308	81.80%	6.87	0.0136
<i>Galumna spp.</i>	504	84.90%	11.98	0.0016
Oppiidae	826	53.50%	45.78	<.0001
<i>Scheloribates spp.</i>	3035	71.40%	43.76	<.0001
Cunaxidae	334	42.80%	89.45	<.0001
Cunaxidae immature	292	46.20%	25.38	<.0001
<i>Eupodes spp.</i>	1032	49.00%	78	<.0001
<i>Nanorchestes spp.</i>	413	43.60%	6.05	0.0199
<i>Sancassania spp.</i>	509	78.80%	39.83	<.0001
Hypopi	2161	76.40%	8.6	0.0064
Entomobryidae	1573	47.00%	177.74	<.0001
Isotomidae	2225	56.60%	17.5	0.0002
Chilopoda	75	64.00%	24.43	<.0001
Paupoda	89	55.10%	7.1	0.0123
Symphyla	530	66.40%	32.03	<.0001
Japygidae	384	61.50%	20.82	<.0001
Coleoptera immature	411	60.80%	80.99	<.0001
Coleoptera adult	166	48.80%	7.54	0.0101
Diptera immature	1355	62.50%	23.86	<.0001
Enchytraeidae	1035	52.40%	5.04	0.0323
Other insects	306	52.60%	12.02	0.0016

Appendix P Taxa that exhibit significant effects due to interactions of experimental factors in bait experiment

Taxa that exhibit significant effects ($p < 0.05$) due to interactions of major factors in bait experiment. Pooled data is derived from 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 2 sampling times (4 or 24 h time), 2 tillage regimes (conventional tillage and no-tillage till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied to a corn field

Taxa with significant response ($p < 0.05$) to the interaction of tillage type by date sampled (till*date)				
Taxon	total	% in NT	F	P
Ascidae	166	73.50%	4.67	0.0004
<i>Gamasellodes spp.</i>	138	46.40%	3.47	0.0046
<i>Protogamasellus spp.</i>	765	6.50%	7.76	<.0001
<i>Macrocheles spp.</i>	441	91.40%	7.79	<.0001
<i>Rhodacarus spp.</i>	411	66.40%	5.08	0.0002
Uropodidae	96	62.50%	2.47	0.033
Other Mesostigmata	375	61.90%	4.56	0.0005
Brachychthoniidae	308	81.80%	5.56	<.0001
<i>Epilohmannia spp.</i>	605	28.90%	16.59	<.0001
<i>Zygoribatula spp.</i>	2247	96.20%	6.38	<.0001
<i>Schelorbates spp.</i>	3035	71.40%	14.25	<.0001
<i>Xylobates spp.</i>	1500	52.00%	8.11	<.0001
Oribatida immature	5910	66.20%	19.07	<.0001
Cunaxidae	334	42.80%	2.47	0.0325
Cunaxidae immature	292	46.20%	10	<.0001
<i>Eupodes spp.</i>	1032	49.00%	10.33	<.0001
<i>Speleorchestes spp.</i>	537	11.00%	5.61	<.0001
Pygmephoridae	156	46.20%	2.94	0.0133
Scutacaridae	215	31.20%	7.68	<.0001
Stigmaeidae	108	75.00%	3.26	0.007
<i>Sancassania spp.</i>	509	78.80%	3.08	0.0101
Histiostomatidae	287	44.60%	3.75	0.0026
Hypopi	2161	76.40%	13.41	<.0001

Hypogastruridae	797	87.00%	17.05	<.0001
Isotomidae	2225	56.60%	15.41	<.0001
Onychiuridae	2005	72.10%	8.63	<.0001
Sminthuridae	263	39.20%	4.46	0.0006
Collembola	924	62.00%	4.64	0.0004
Chilopoda	75	64.00%	2.28	0.0465
Paupoda	89	55.10%	4.54	0.0005
Symphyla	530	66.40%	7.28	<.0001
Japygidae	384	61.50%	5.05	0.0002
Nematoda	268	74.30%	4.64	0.0004
Enchytraeidae	1035	52.40%	11.73	<.0001

Taxa with significant response ($p<0.05$) to the interaction of time sampled by date sampled (time*date)

Taxon	total	% in NT	F	P
<i>Protogamasellus spp.</i>	765	6.50%	5.89	<.0001
Other Mesostigmata	375	61.90%	2.74	0.0197
Brachychthoniidae	308	81.80%	2.3	0.0448
<i>Eremobelba spp.</i>	233	49.80%	2.56	0.0278
Oppiidae	826	53.50%	4.59	0.0005
<i>Zygoribatula spp.</i>	2247	96.20%	2.28	0.0469
<i>Eupodes spp.</i>	1032	49.00%	8.05	<.0001
<i>Speleorchestes spp.</i>	537	11.00%	3.02	0.0112
Pygmephoridae	156	46.20%	2.89	0.0145
Scutacaridae	215	31.20%	6.56	<.0001
<i>Sancassania spp.</i>	509	78.80%	15.12	<.0001
Histiostomatidae	287	44.60%	3.83	0.0023
Other Astigmata	102	78.40%	10.11	<.0001
Hypopi	2161	76.40%	15.22	<.0001
Entomobryidae	1573	47.00%	10.96	<.0001
Isotomidae	2225	56.60%	3.22	0.0077
Onychiuridae	2005	72.10%	6.05	<.0001
Sminthuridae	263	39.20%	3.02	0.0113
Collembola	924	62.00%	15.41	<.0001
Chilopoda	75	64.00%	2.51	0.0305
Coleoptera adult	166	48.80%	2.78	0.0179
Diptera immature	1355	62.50%	4.39	0.0007
Formicidae	1317	18.60%	2.39	0.0381

Taxa with significant response ($p<0.05$) to the interaction of treatment by date sampled (trt*date)

Taxon	total	% in NT	F	P
Ascidae	166	73.50%	1.71	0.0312
<i>Schelorbates spp.</i>	3035	71.40%	2.04	0.0061
<i>Tectocephus spp.</i>	5001	82.30%	1.85	0.0161

Stigmaeidae	108	75.00%	1.98	0.0084
<i>Sancassania spp.</i>	509	78.80%	1.79	0.0215
Diptera immature	1355	62.50%	3.02	<.0001

Taxa with significant response ($p < 0.05$) to the interaction of tillage type by time sampled (till*time)

Taxon	total	% in NT	F	P
Phytoseidae	120	65.80%	5.36	0.0276
Other Mesostigmata	375	61.90%	4.98	0.0332
<i>Galumna spp.</i>	504	84.90%	5.87	0.0216
Cunaxidae	334	42.80%	11.93	0.0017
Hypopi	2161	76.40%	16.19	0.0004
Entomobryidae	1573	47.00%	4.85	0.0355
Onychiuridae	2005	72.10%	5.01	0.0328

Taxa with significant response ($p < 0.05$) to the interaction of tillage type by treatment (till*trt)

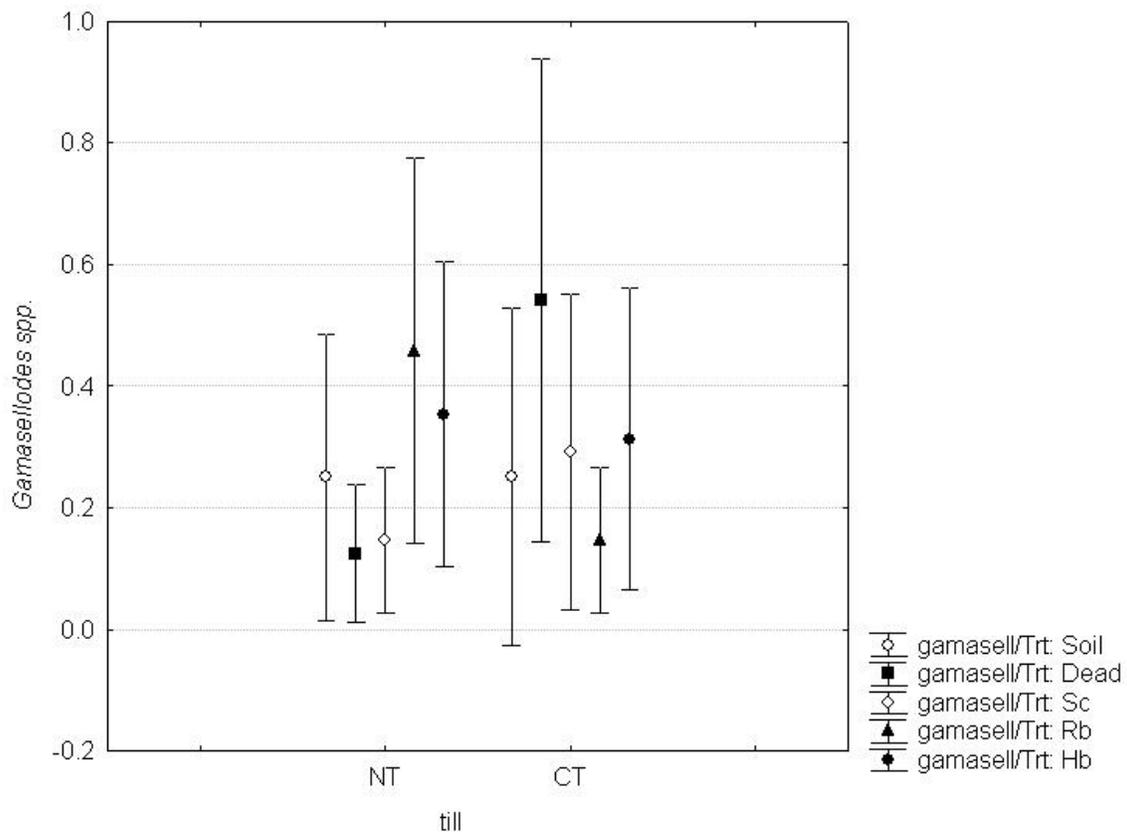
Taxon	total	% in NT	F	P
<i>Gamasellodes spp.</i>	138	46.40%	4.75	0.0058
<i>Macrocheles spp.</i>	441	91.40%	3.1	0.0344
Phytoseidae	120	65.80%	2.85	0.046
<i>Galumna spp.</i>	504	84.90%	3.89	0.0142
<i>Eupodes spp.</i>	1032	49.00%	3.02	0.0375
<i>Nanorchestes spp.</i>	413	43.60%	3.89	0.0142

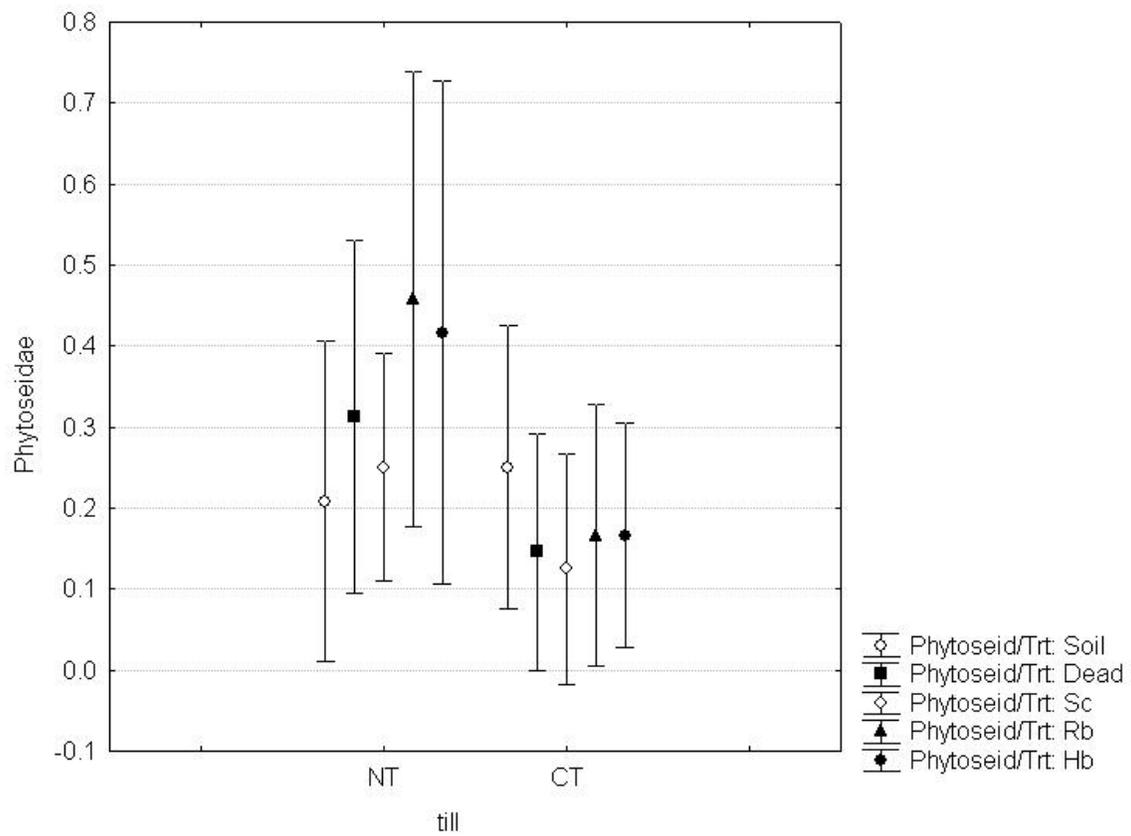
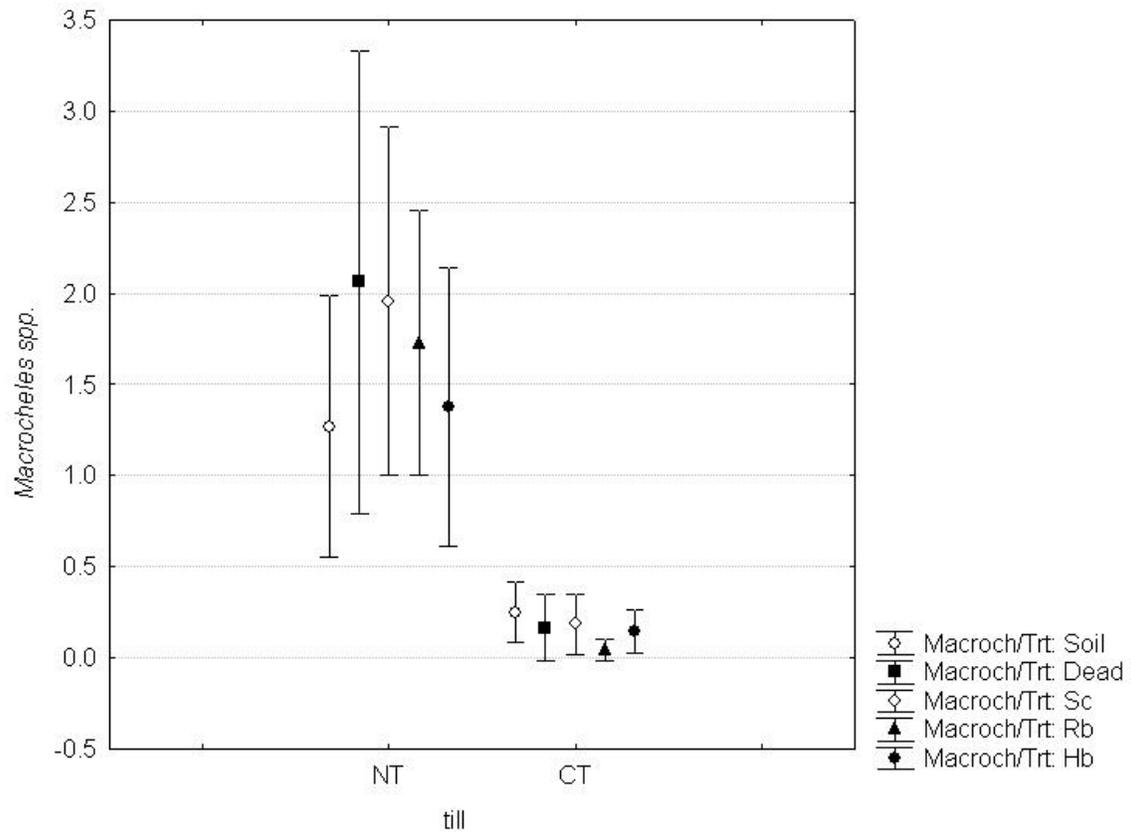
Taxa with significant response ($p < 0.05$) to the interaction of time sampled by treatment (time*trt)

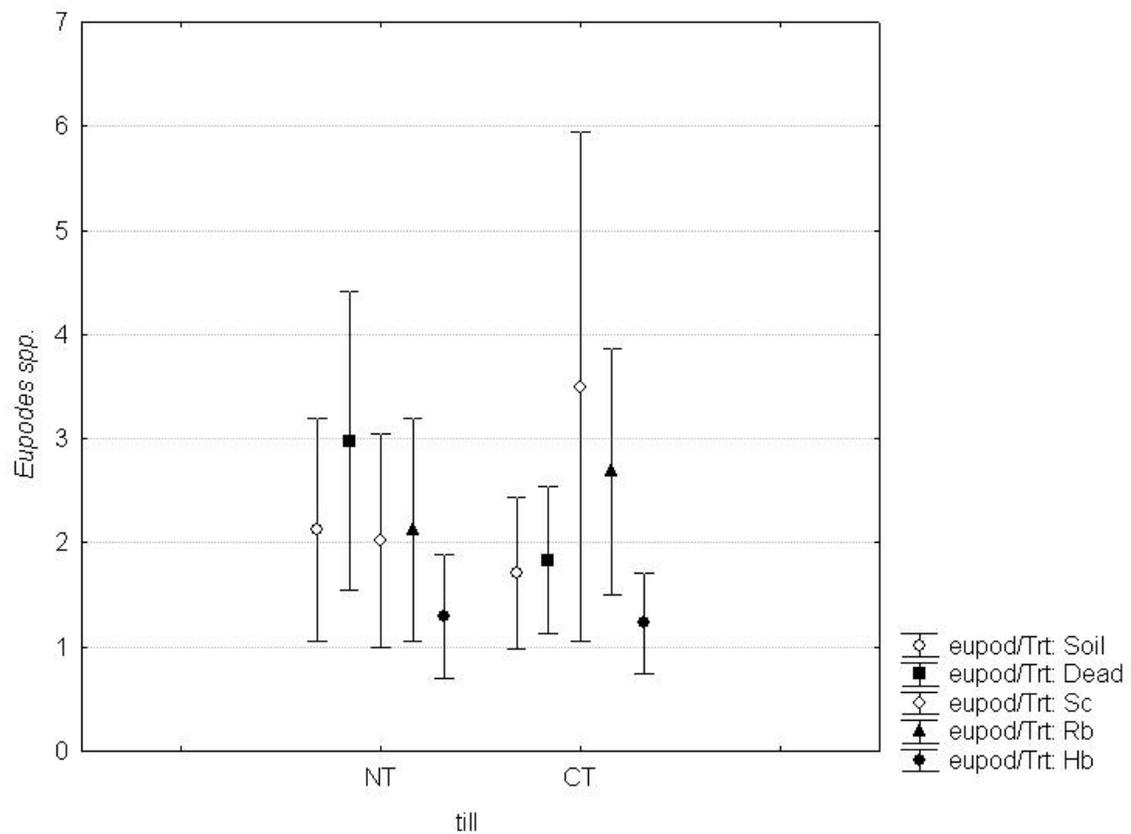
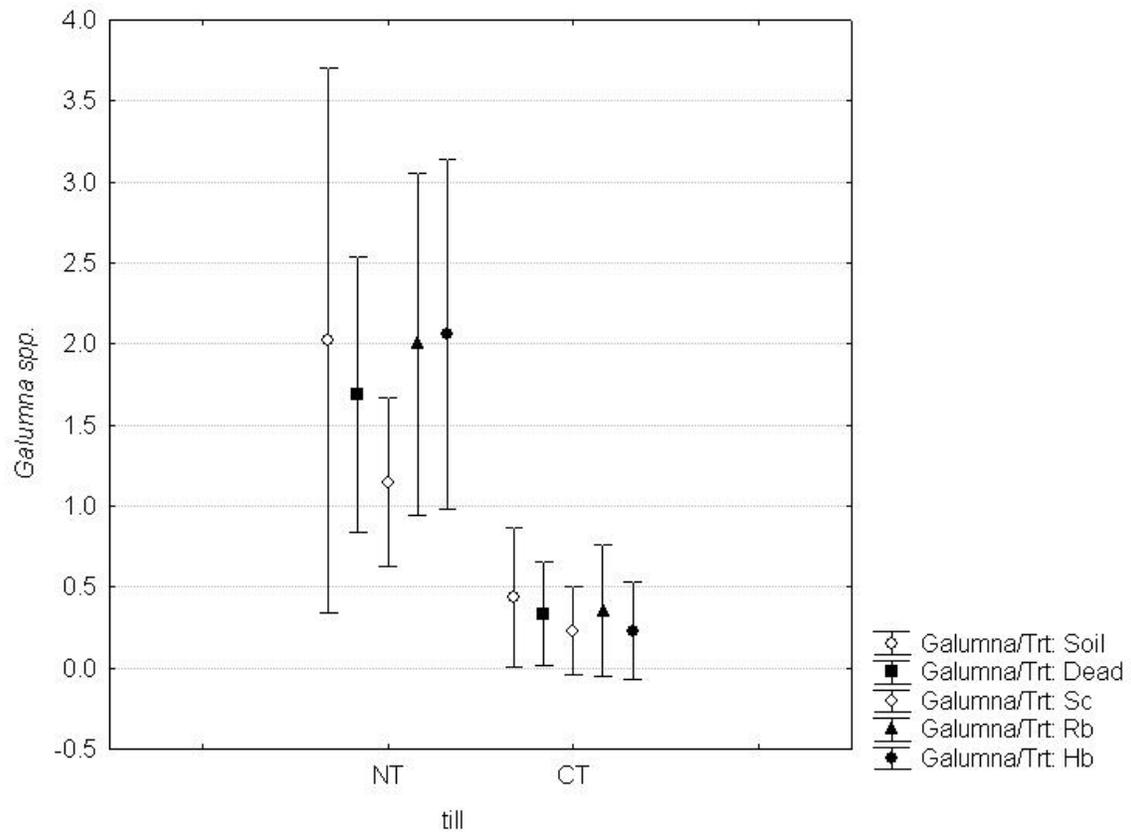
Taxon	total	% in NT	F	P
Brachychthoniidae	308	81.80%	3.95	0.0108
Diptera immature	1355	62.50%	4.17	0.0084

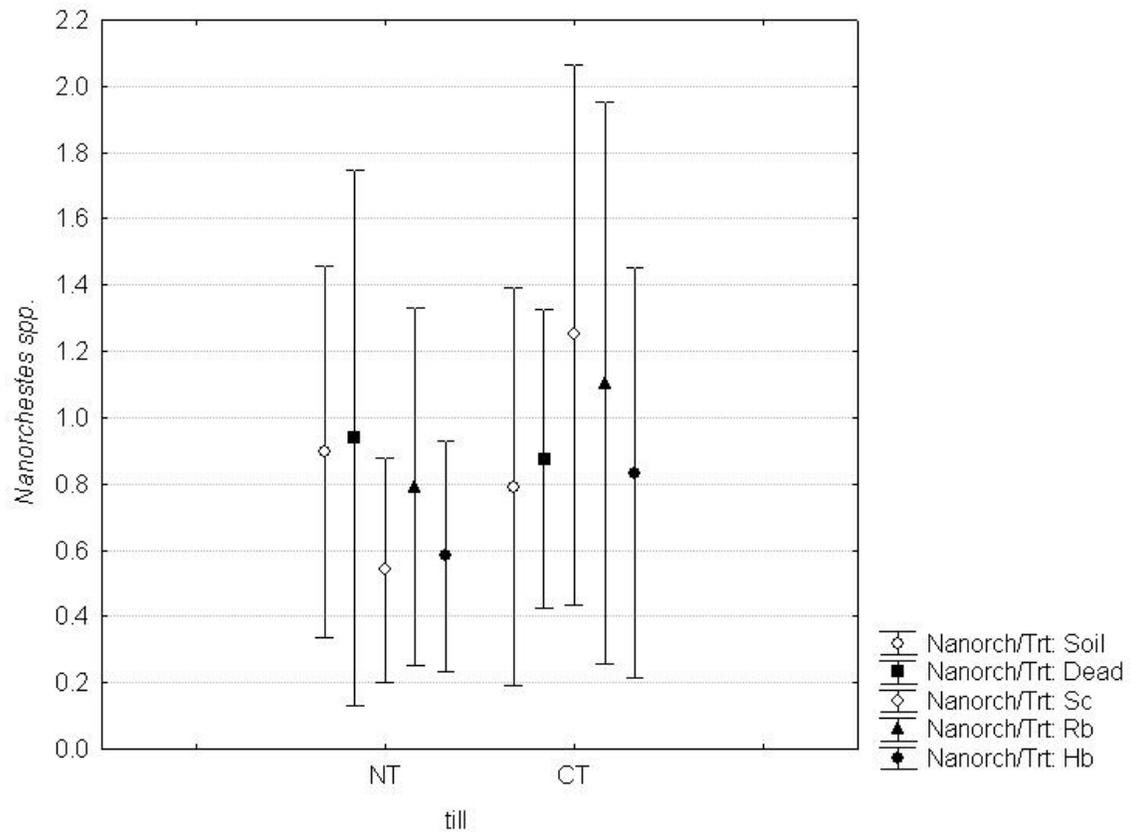
Appendix Q Taxa responsive to interaction of treatment by tillage type in bait experiment

Mean abundance (in 150ml soil) of (*Gamasellodes spp.*, *Macrocheles spp.*, *Phytoseidae*, *Galumna spp.*, *Eupodes spp.*, *Nanorchestes spp.*) per treatment in No-till and Conventional-till soil in bait experiment. Data is summed over 6 sampling dates (6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 2 sampling times (4 or 24 h), and 5 treatments (2 controls= soil, dead, 3 nematode treatments= *Steinernema carpocapsae* CEFS strain (Sc), *Steinernema riobrave* (Rb), and *Heterorhabditis bacteriophora* CEFS strain (Hb) applied in corn. (N=48)



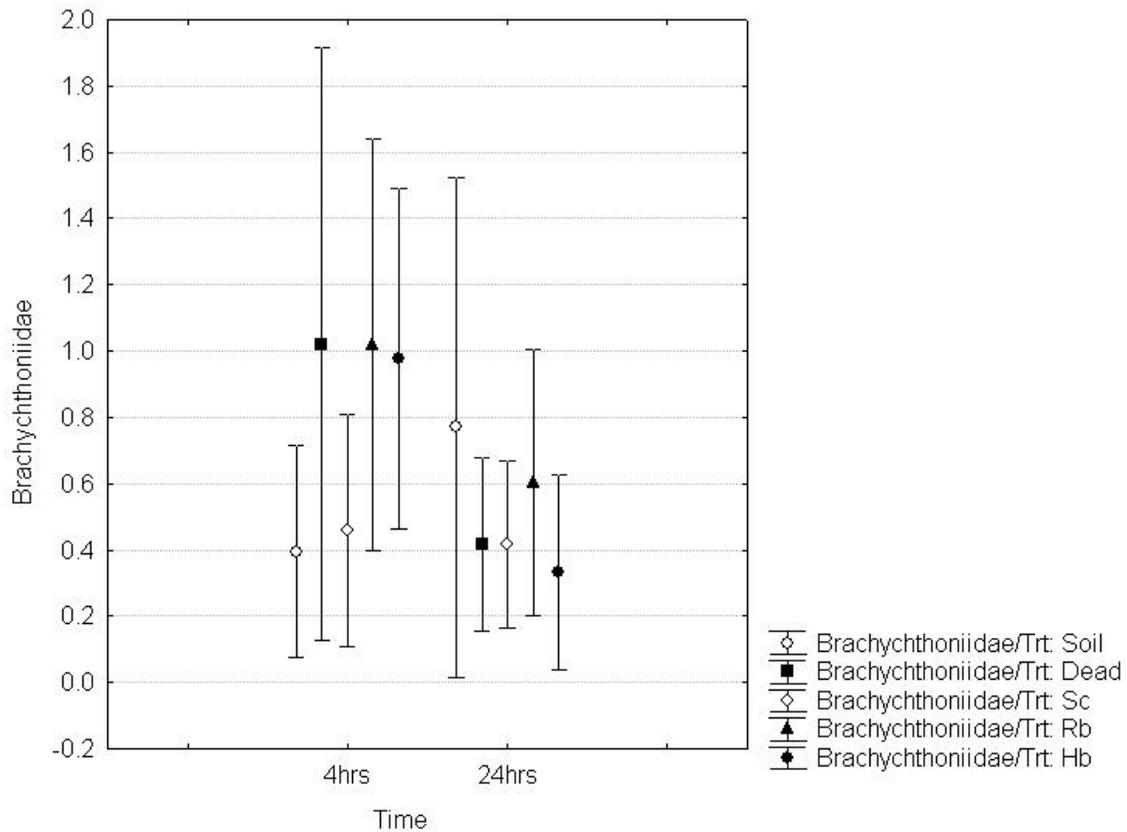


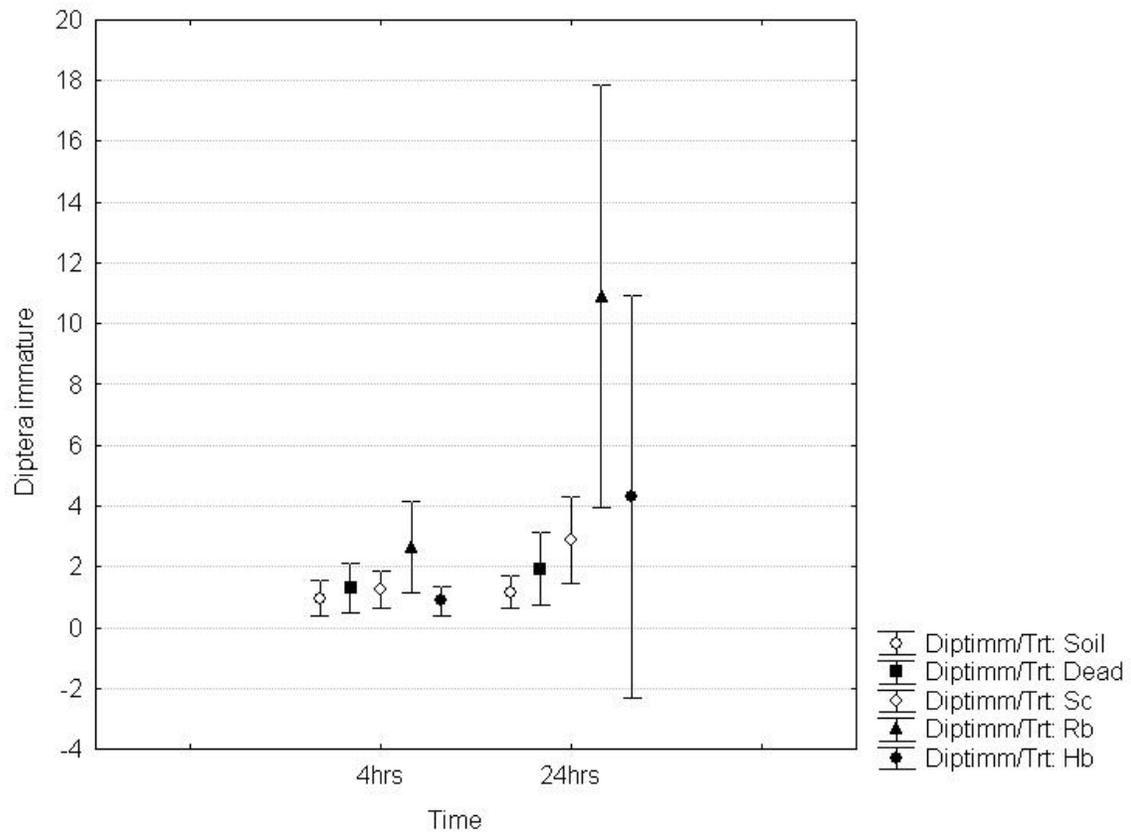




Appendix R Taxa responsive to interaction of sampling time by treatment in bait experiment

Mean abundance of (Brachychthoniidae, Diptera (immature)) (in 150ml soil) per treatment at 4 hour and 24 hour sampling times in bait experiment. Data is summed over 6 sampling dates ((6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn. (N=48)





Appendix S General Linear Model ANOVA (LSD SAS procedure)

The GLM Procedure

Dependent Variable: sqhypoasp

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	194				
Error	285				
Corrected Total	479				

R-Square	Coeff Var	Root MSE	sqhypoasp Mean
0.599418	88.42713	0.698700	0.790142

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Block ¹⁷	3				
till	1				
block*till	3				
Trt	4				
Time	1				
Time*Trt ¹⁵	4				
till*Trt	4				
till*Time	1				
till*Time*Trt	4				
block*Trt(till)	24				
block*Time(till*Trt)	30				
date	5				
till*date ⁴	5				
Time*date ⁵	5				
till*Time*date	5				
Trt*date ⁷	20				
till*Trt*date	20				
Time*Trt*date	20				
till*Time*Trt*date	20				
block*date	15				

Tests of Hypotheses Using the Type III MS for block*till as an Error Term

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Till ²	1				

Tests of Hypotheses Using the Type III MS for block*Trt(till) as an Error Term

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Trt ⁸	4				
till*Trt	4				

Tests of Hypotheses Using the Type III MS for block*Time(till*Trt) as an Error Term

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Time ³	1				
Time*Trt	4				
till*Time ⁶	1				
till*Time*Trt	4				

Tests of Hypotheses Using the Type III MS for block*date as an Error Term

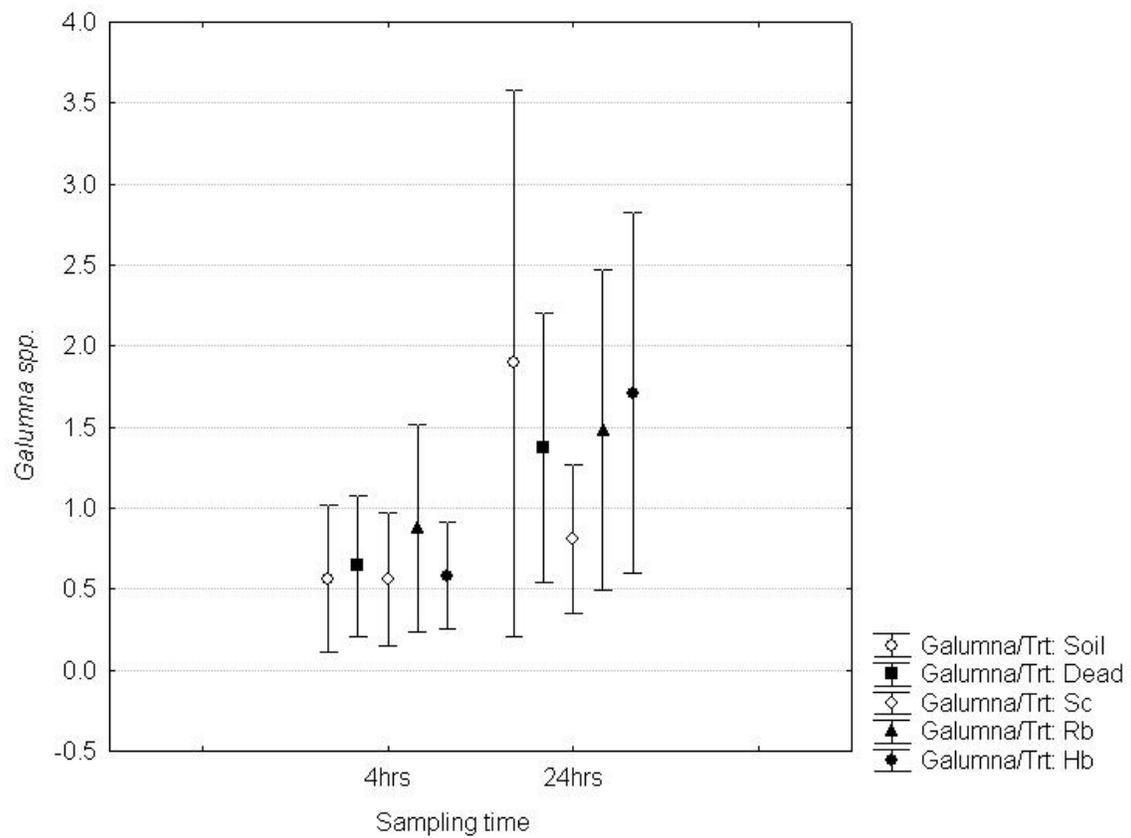
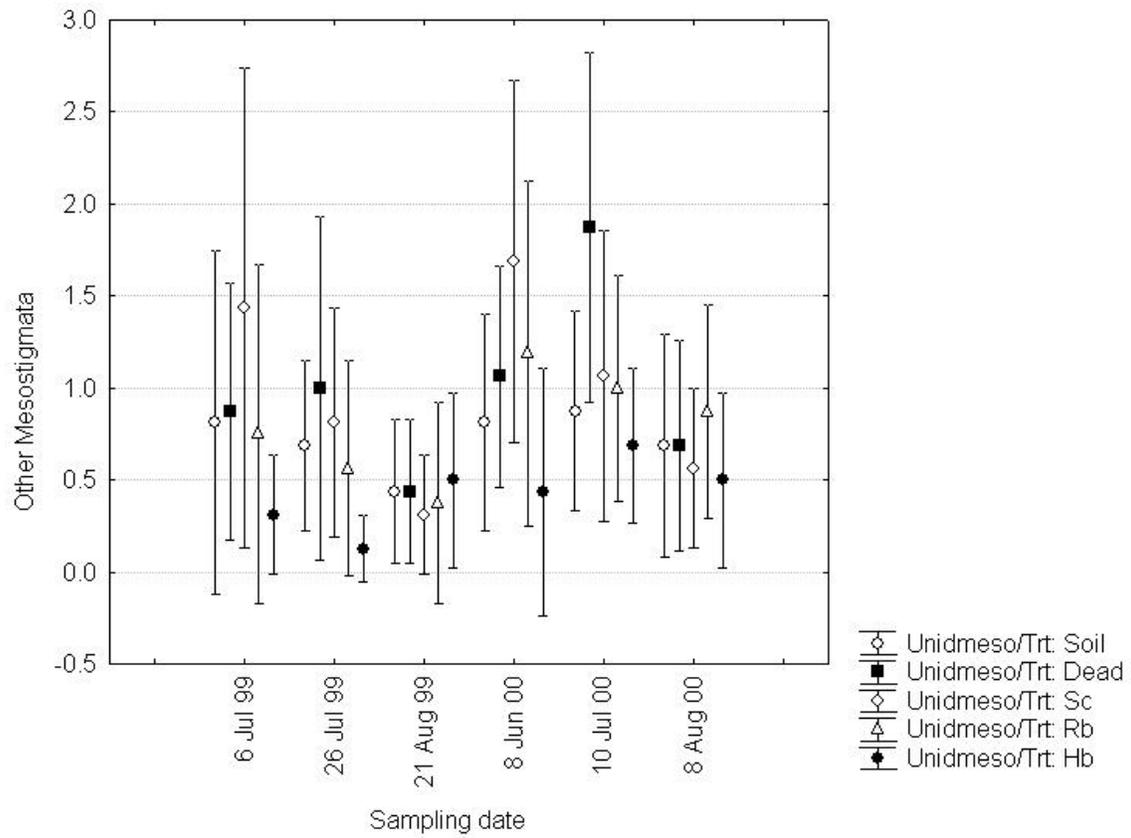
Source	DF	Type III SS	Mean Square	F Value	Pr > F
Date1	5				

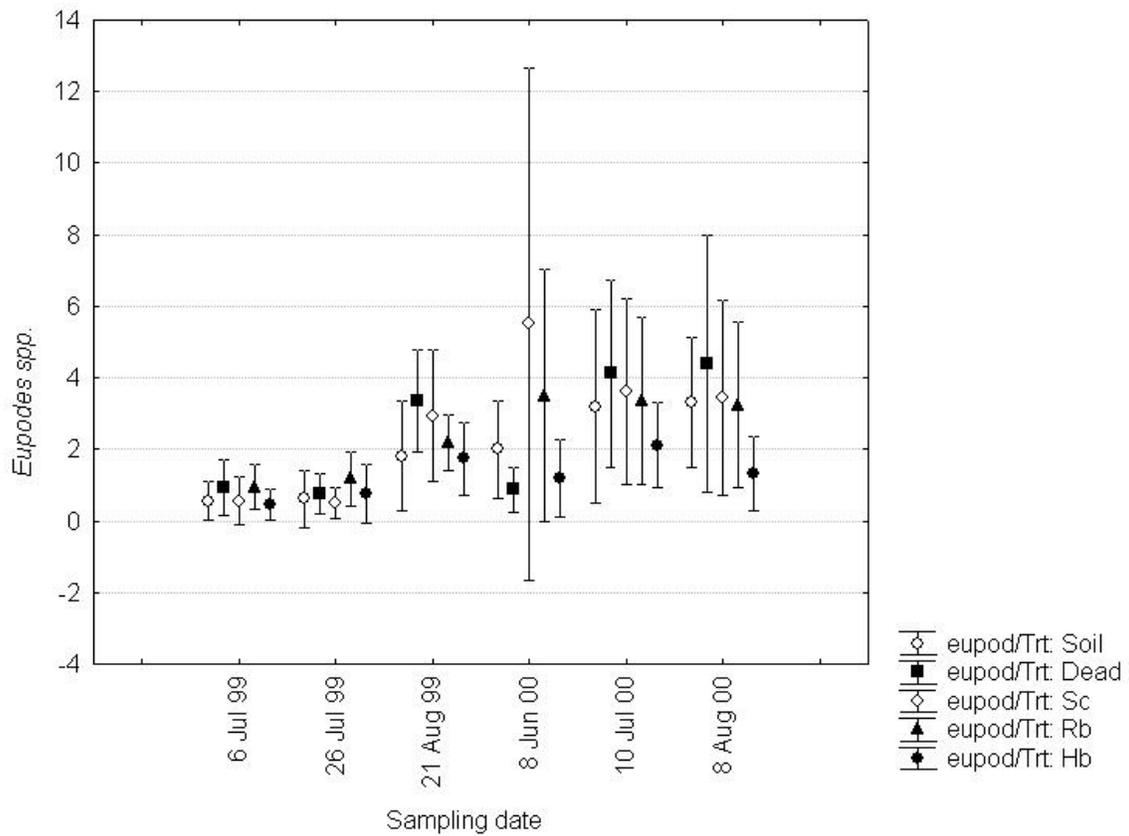
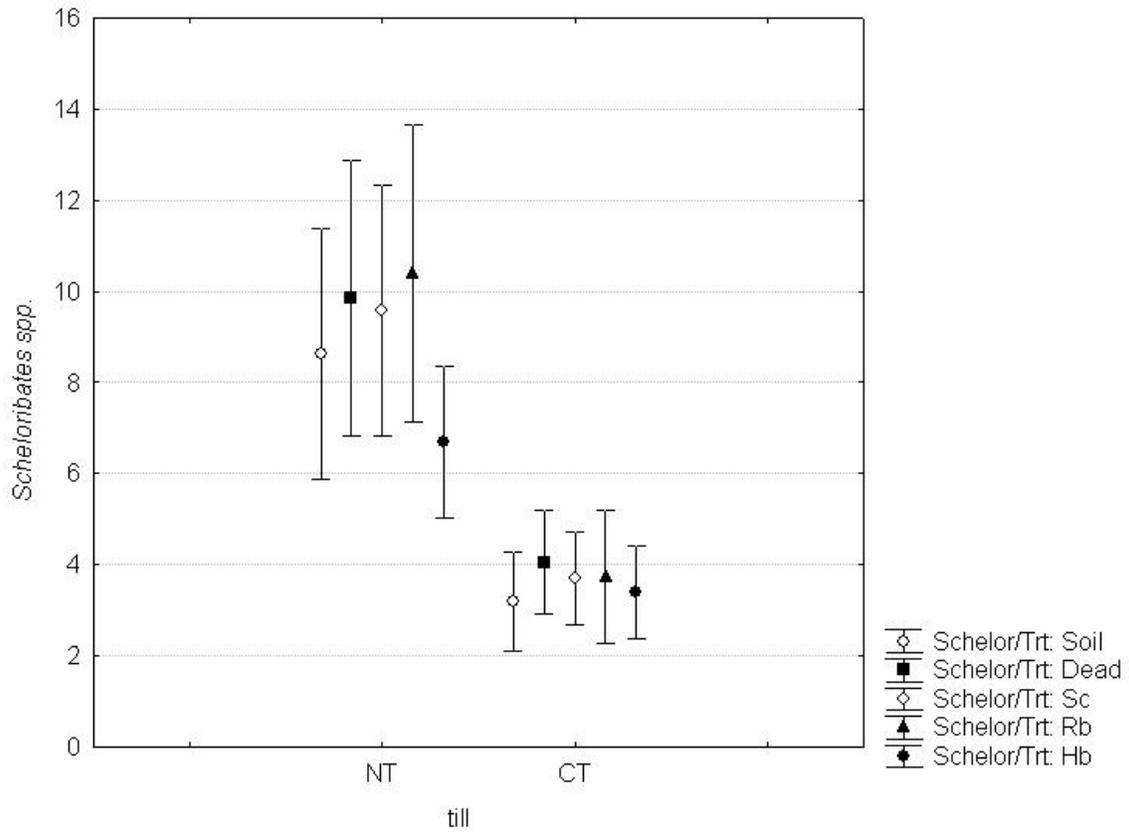
Tests of Hypotheses Using the Type III MS for block*Trt(till) as an Error Term

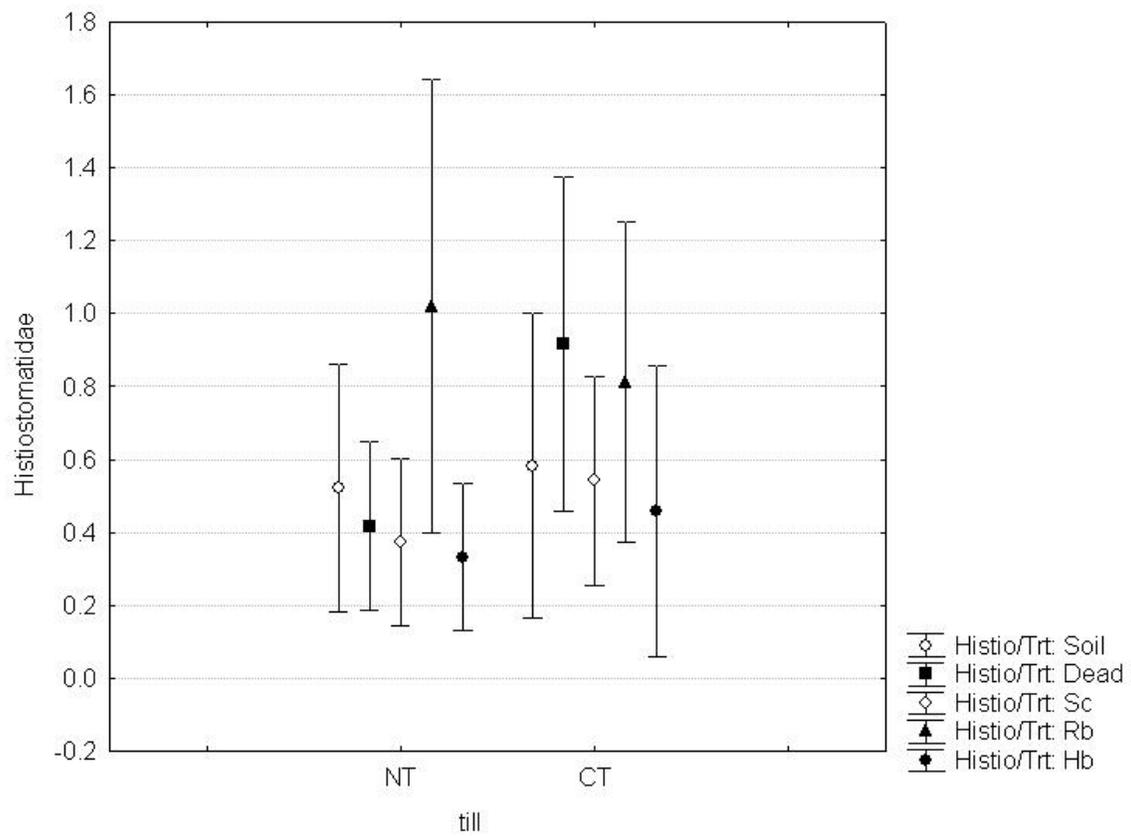
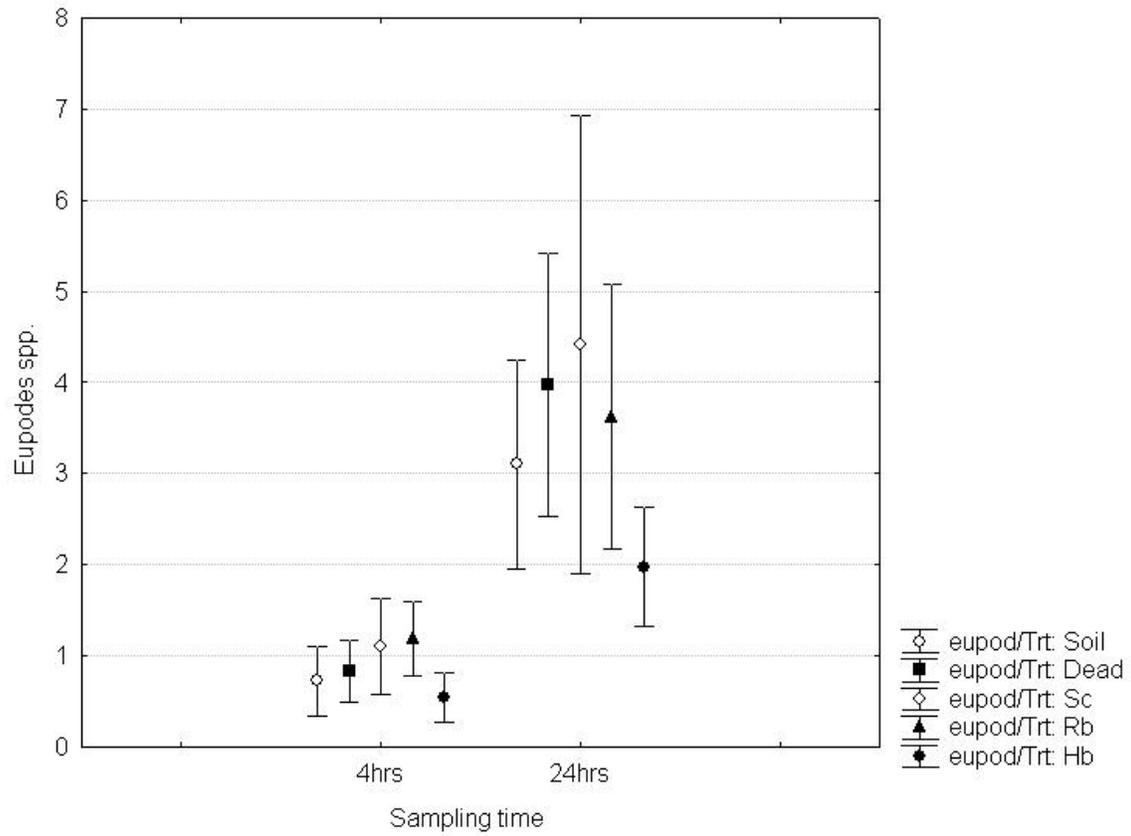
Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
Soil vs dead ⁹	1				
Soil vs nemas ¹⁰	1				
Dead vs nemas ¹¹	1				
Hb vs Sc, Rb ¹²	1				
Hb, Rb vs Sc ¹³	1				
Hb, Sc vs Rb ¹⁴	1				

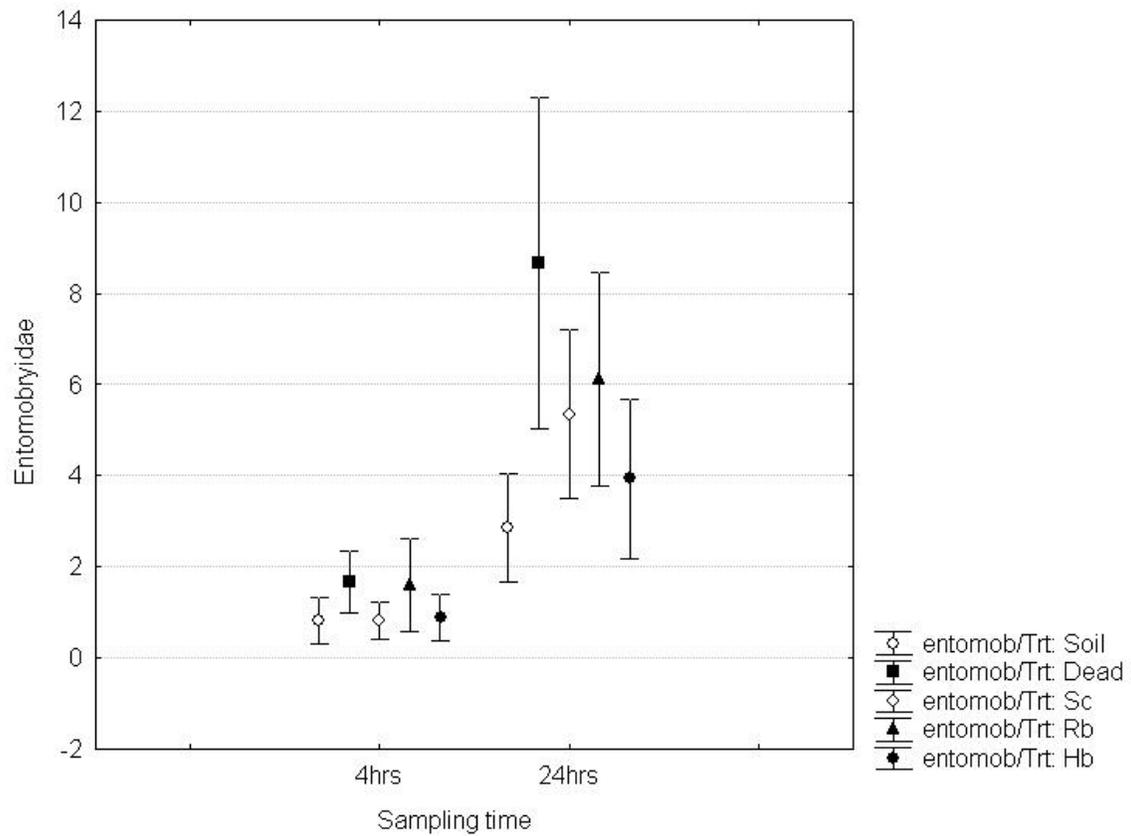
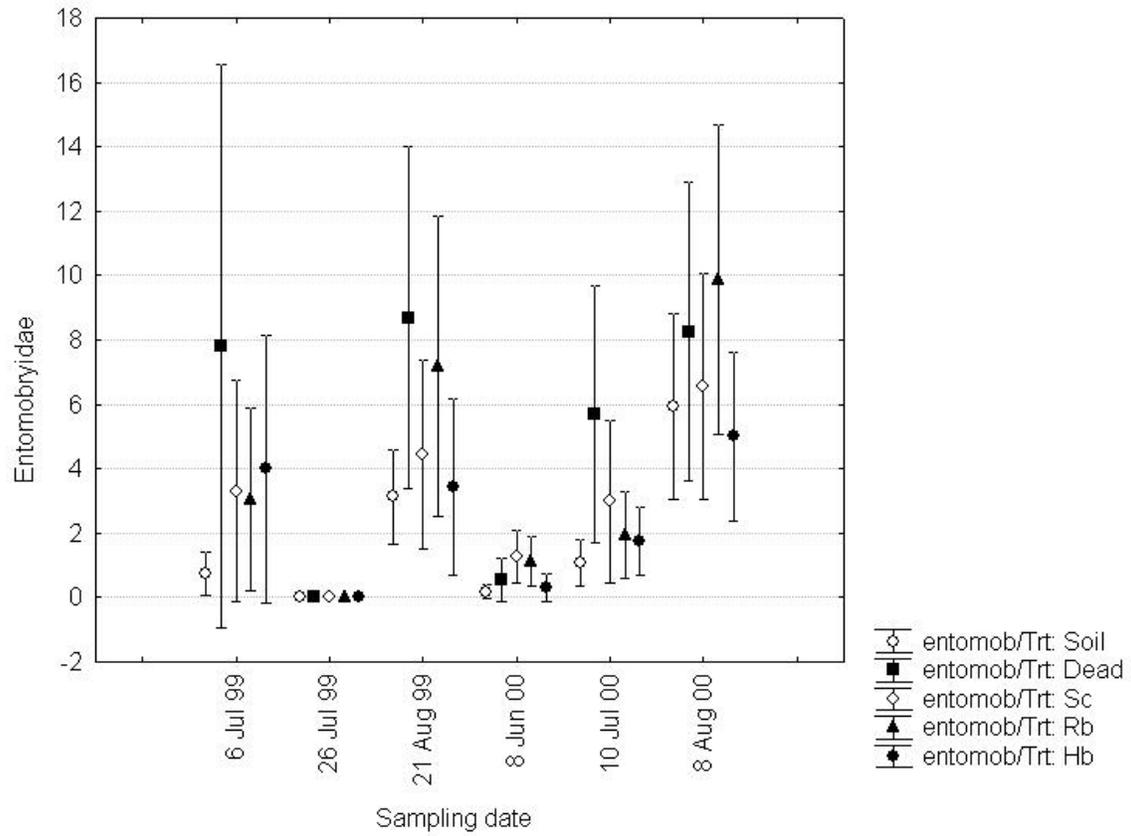
Appendix T Taxa responsive to treatment in bait experiment

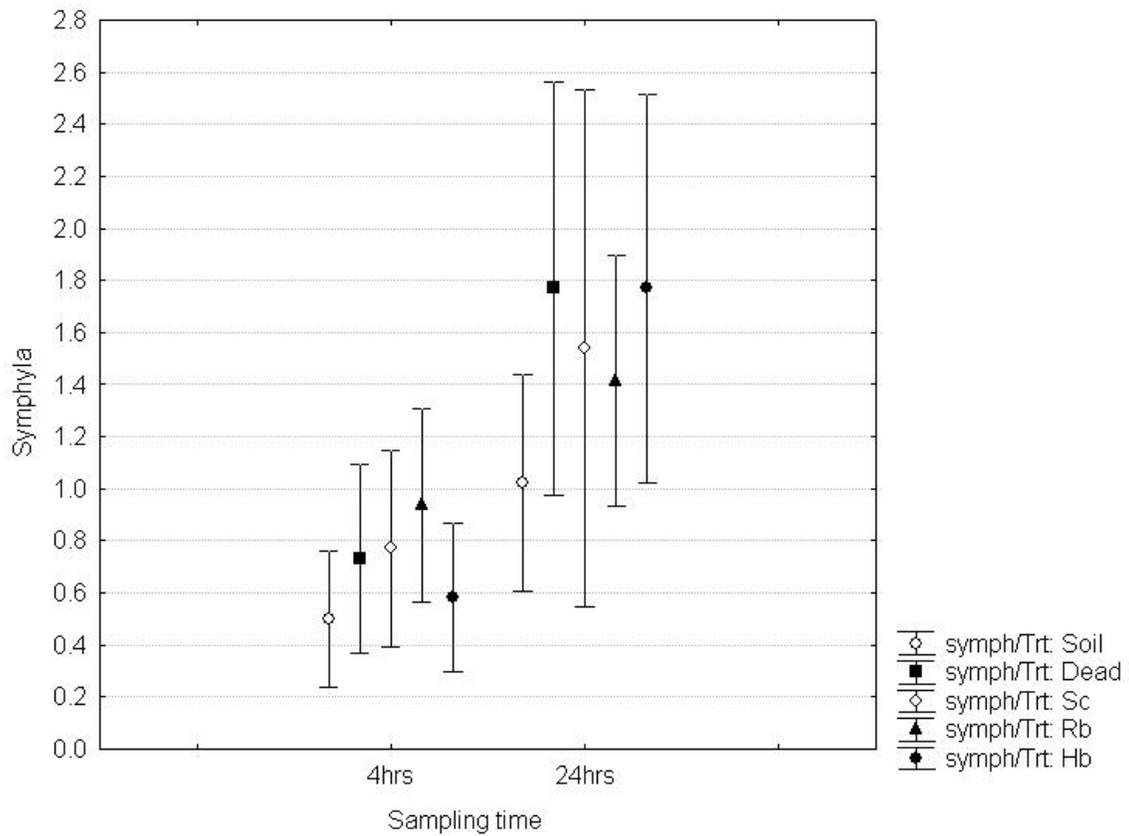
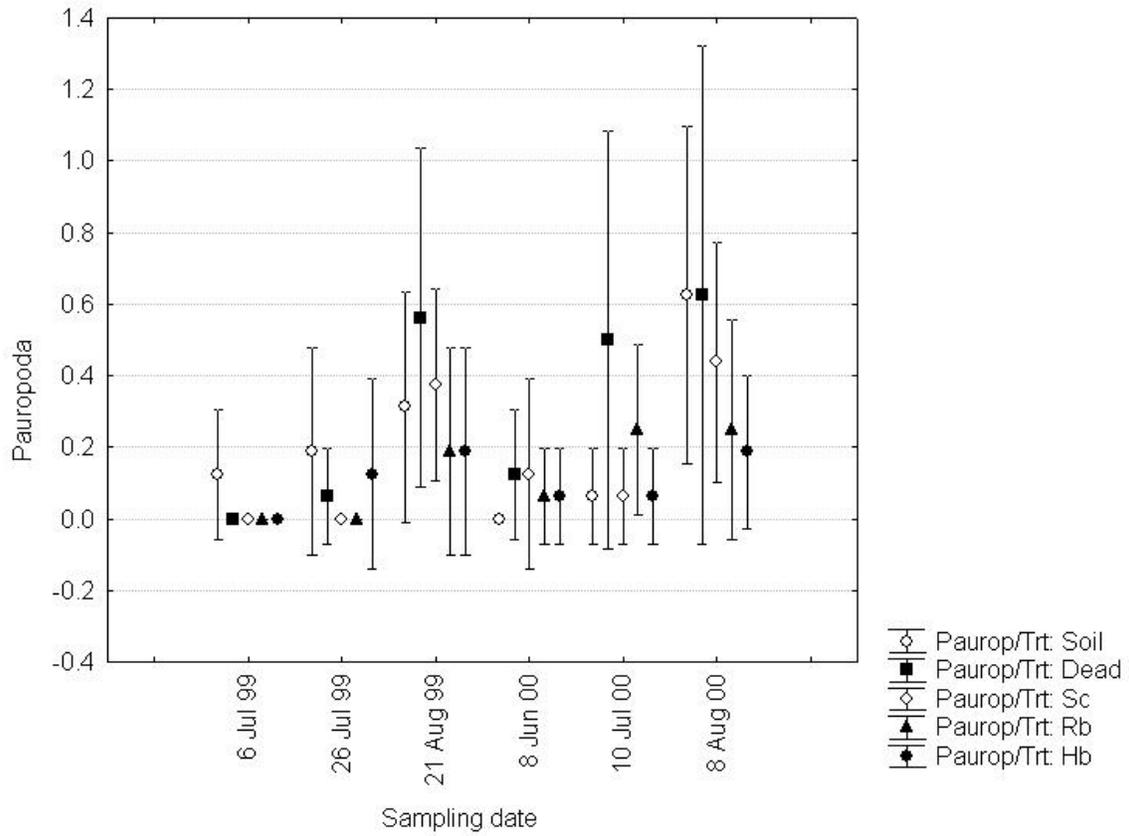
Graphs of mean abundance of taxa (Other Mesostigmata (by sampling date), *Galumna* spp. (by sampling time), *Scheloribates* spp. (by tillage type), *Eupodes* spp. (by sampling date), *Eupodes* spp. (by sampling time) Histiostomatidae (by tillage type), Entomobryidae (by sampling date), Entomobryidae (by sampling time), Pauropoda (by sampling date), Symphyla (by sampling time), Formicidae (by tillage type), exhibiting significant response ($p < 0.05$) to treatment effects in bait experiment. Data is summed over 6 sampling dates ((6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn. (N=48)

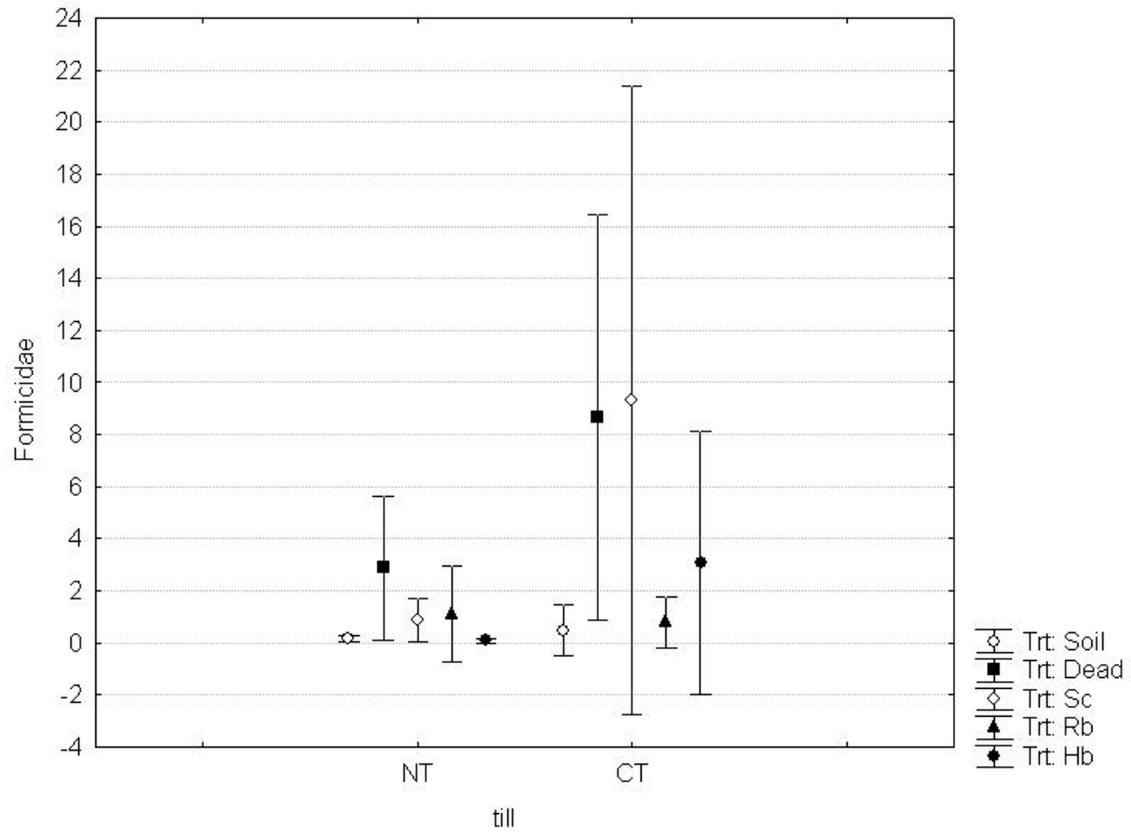






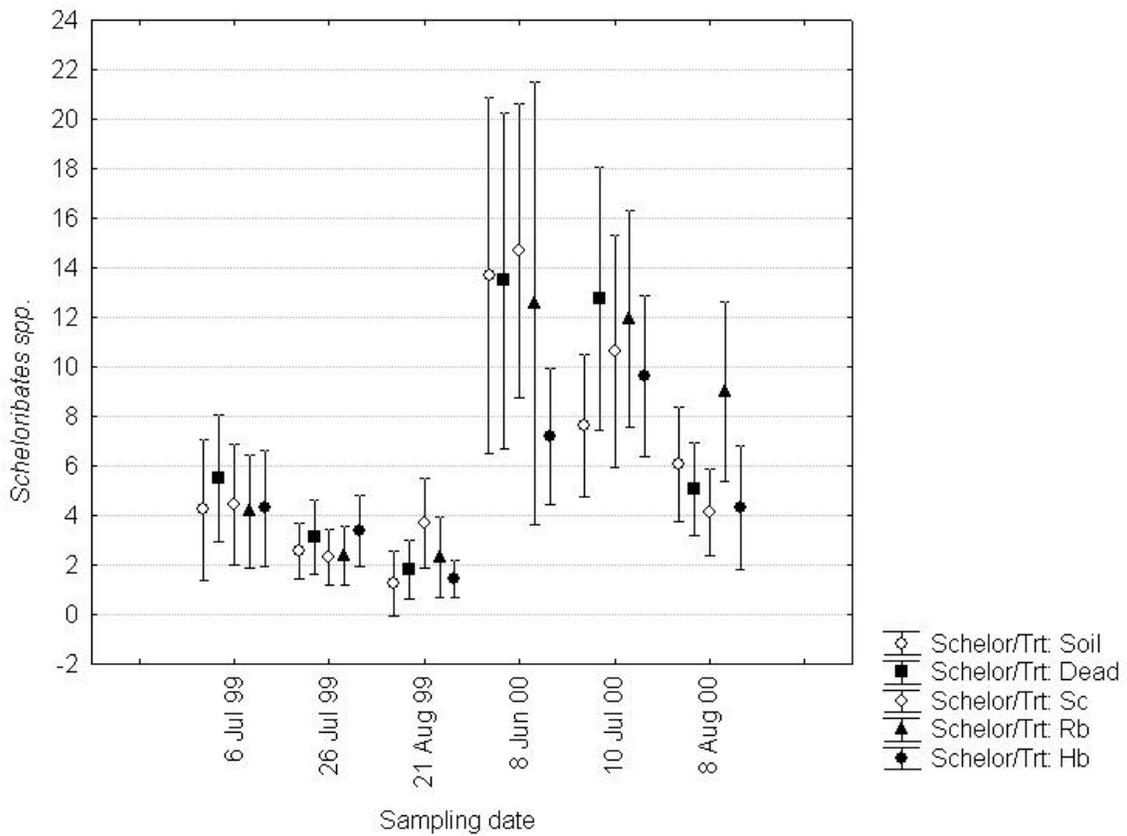
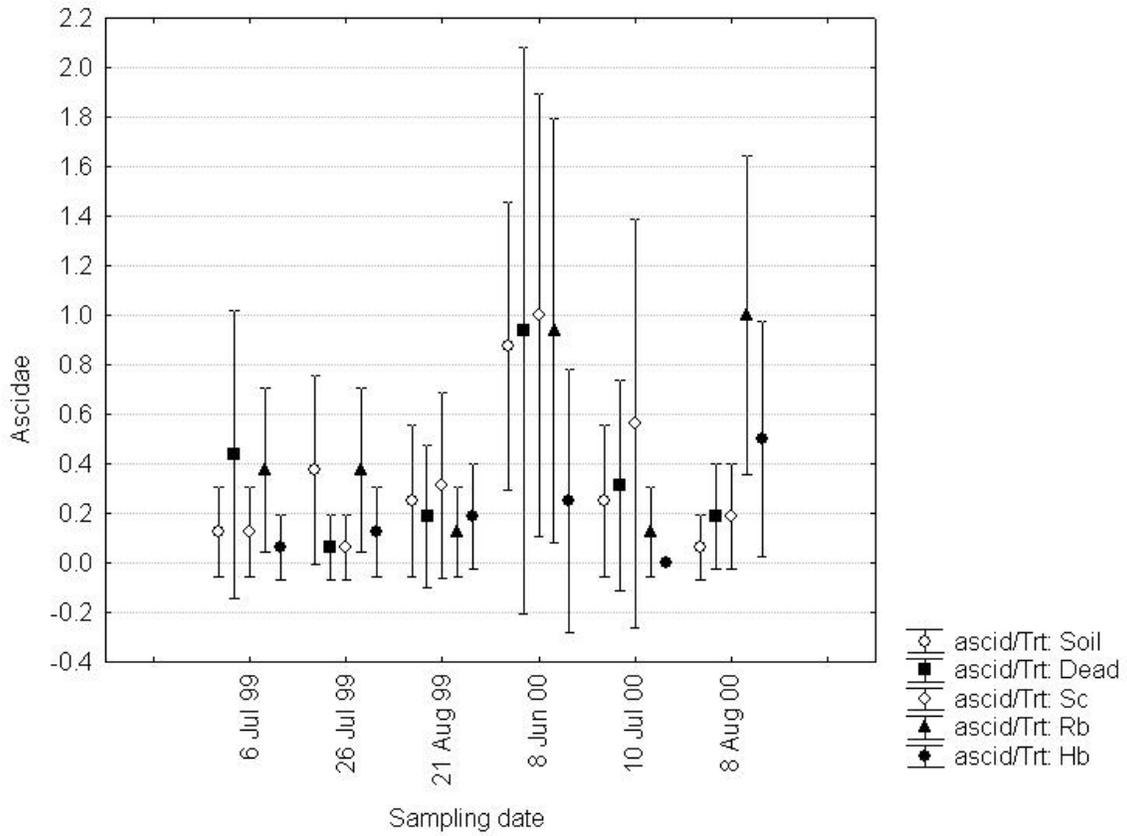


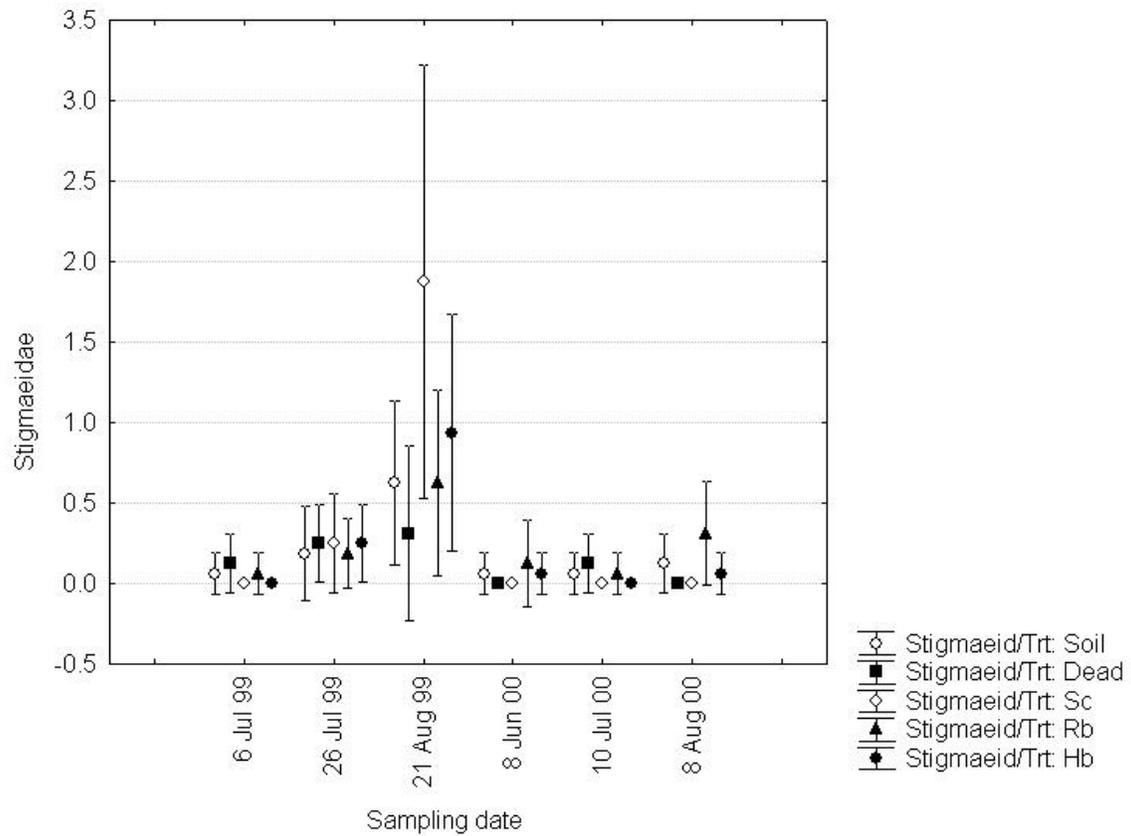
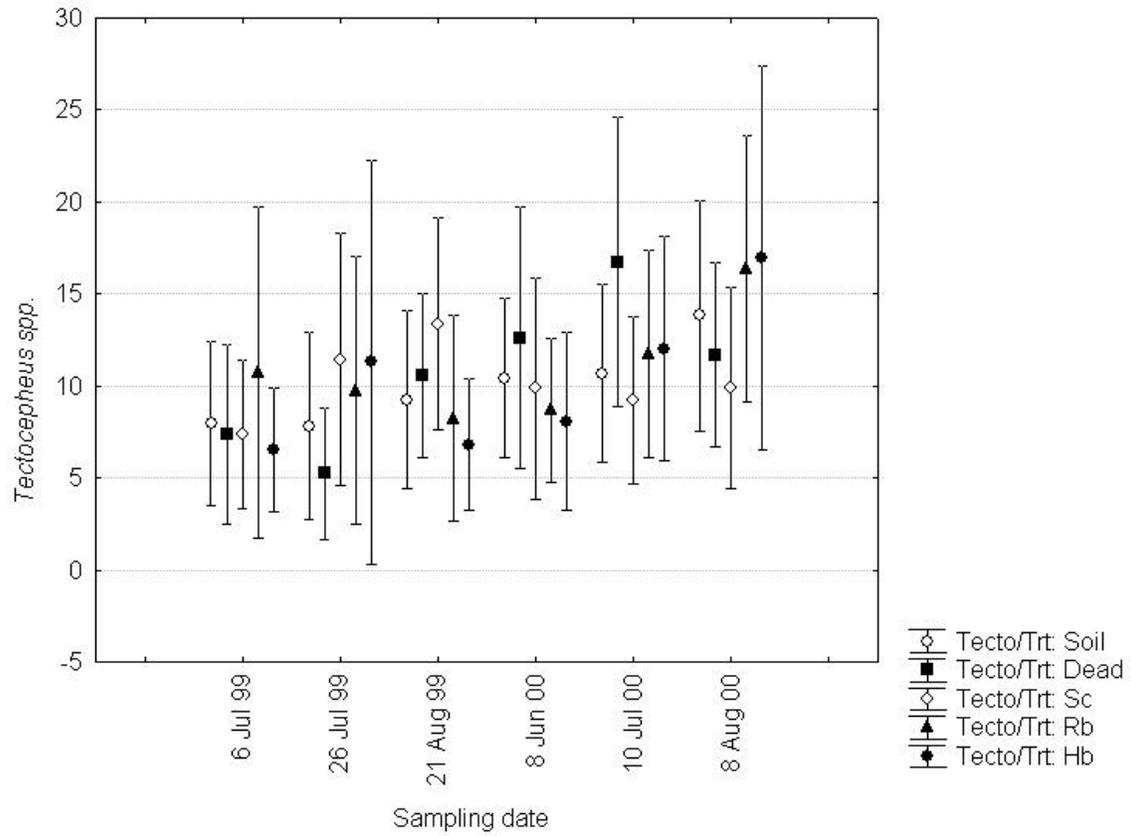


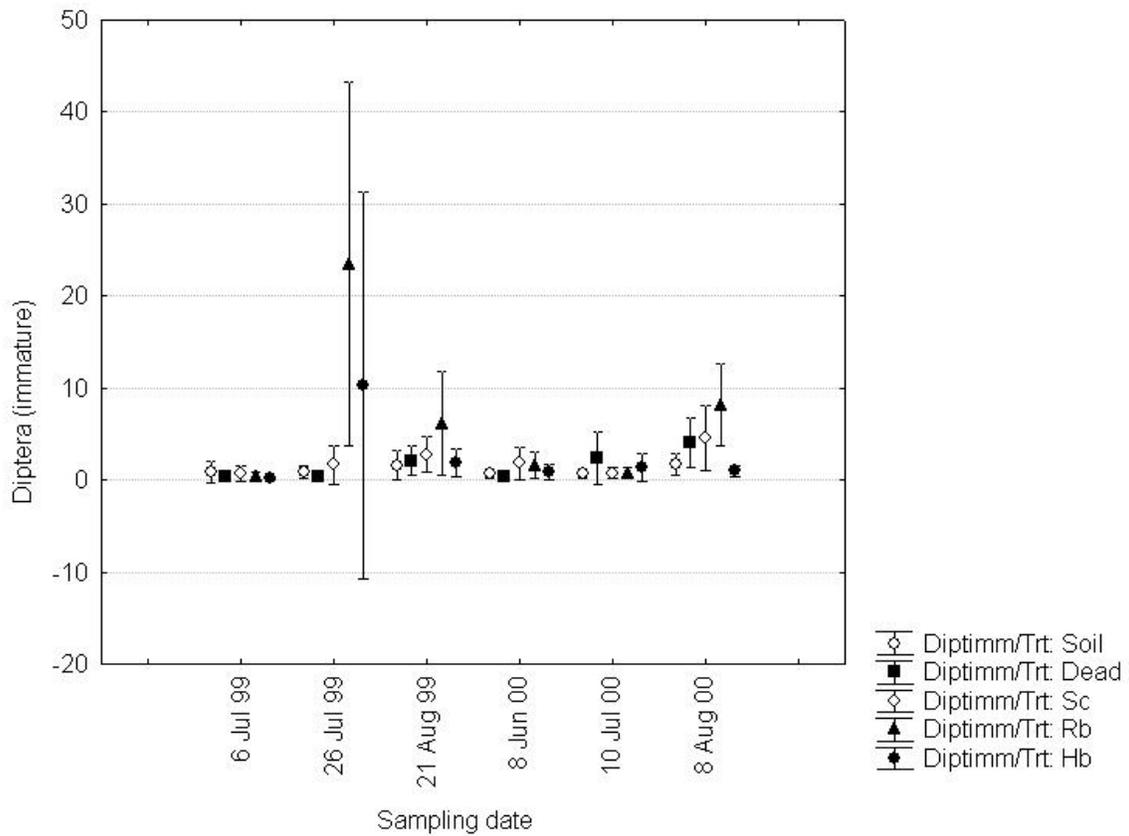
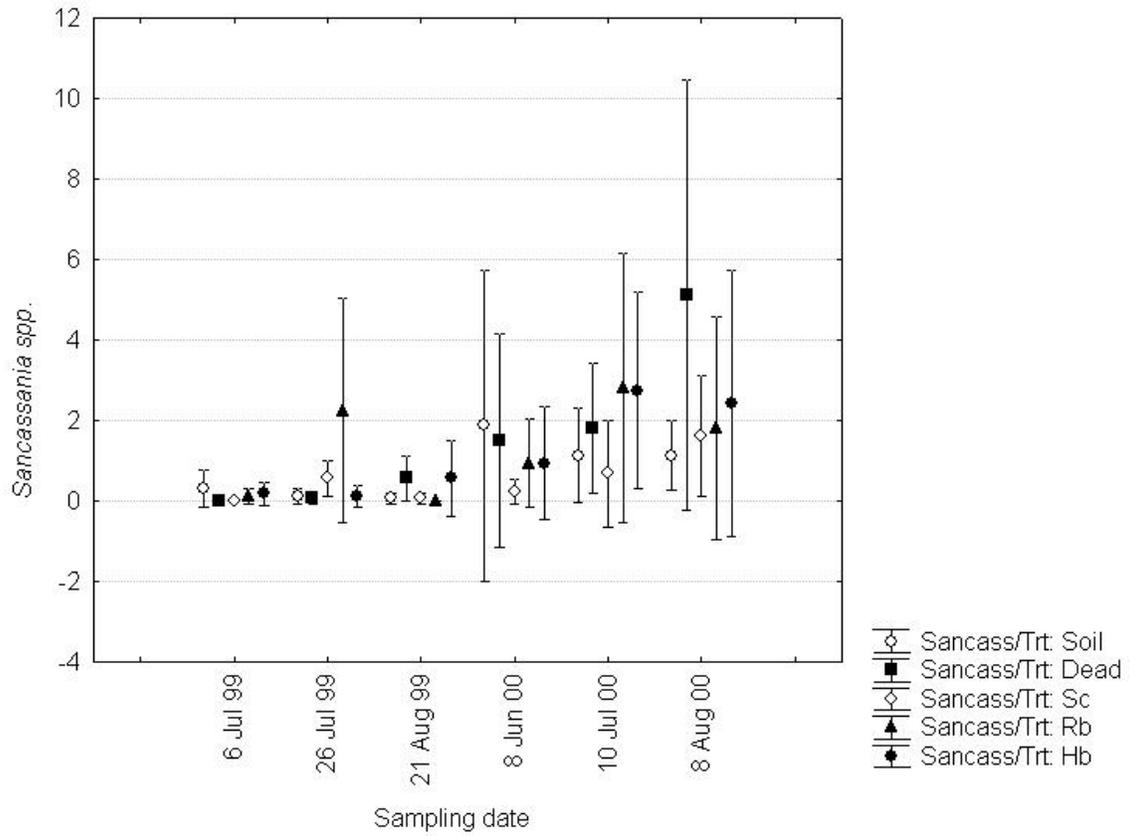


Appendix U Taxa responsive to interaction of sampling date by treatment in bait experiment

Graphs of mean abundance of taxa (*Ascidae*, *Scheloribates spp.*, *Tectocephus spp.*, *Stigmaeidae*, *Sancassania spp.*, Diptera (immature)), exhibiting significant response ($p < 0.05$) to effects due to the interaction of sampling date by treatment in bait experiment. Data is summed over 6 sampling dates ((6Jul99, 26Jul99, 21Aug99, 8Jun00, 10Jul00, 8Aug00), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn. (N=48)







Appendix V Taxa responsive to interaction of treatment by sampling date in inundation experiment

Graphs of Total abundance (per treatment) of taxa (*Tectocepheus spp*, immature Oribatida (in no-till), immature Oribatida (in conventional-till), Hypopi (Acaridae) (in no-till), Hypopi (Acaridae) (in conventional-till), Sminthuridae, adult Coleoptera (in no-till), adult Coleoptera (in conventional-till)) exhibiting significant response ($p < 0.05$) to effects due to the interaction of treatment by sampling date in inundation experiment. Data is summed over 6 sampling dates (3Aug99, 23May00, 21Jun00, 1Aug00, 4Jun01, 2Jul01), 2 sampling times (4 or 24 h), 2 tillage regimes (no-till and conventional till), and 5 treatments (2 controls: Soil, Water, 3 nematode treatments: *Steinernema carpocapsae* CEFS (Sc), *Steinernema riobrave* (Rb) and *Heterorhabditis bacteriophora* CEFS (Hb) applied in corn.

