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Entomopathogenic Nematodes as a Model System for Advancing the Frontiers of Ecology

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Abstract: Entomopathogenic nematodes (EPNs) in the families Heterorhabditidae and Steinernematidae have a mutualistic–symbiotic association with enteric γ-Proteobacteria (*Steinernema–Xenorhabdus* and *Heterorhabditis–Photorhabdus*), which confer high virulence against insects. EPNs have been studied intensively because of their role as a natural mortality factor for soil-dwelling arthropods and their potential as biological control agents for belowground insect pests. For many decades, research on EPNs focused on the taxonomy, phylogeny, biogeography, genetics, physiology, biochemistry and ecology, as well as commercial production and application technologies. More recently, EPNs and their bacterial symbionts are being viewed as a model system for advancing research in other disciplines such as soil ecology, symbiosis and evolutionary biology. Integration of existing information, particularly the accumulating information on their biology, into increasingly detailed population models is critical to improving our ability to exploit and manage EPNs as a biological control agent and to understand ecological processes in a changing world. Here, we summarize some recent advances in phylogeny, systematics, biogeography, community ecology and population dynamics models of EPNs, and describe how this research is advancing frontiers in ecology.

Key words: biodiversity, entomopathogenic nematodes, *Heterorhabditis,* multivariate analysis, *Photorhabdus*, soil ecology, soil food web, *Steinernema*, *Xenorhabdus*.

Although entomopathogenic nematodes (EPNs) have been exploited as biological control agents since the last half of the 20th century, much research remains to be done to understand how these organisms function in agricultural and other ecosystems. Specifically, it is critical to know when and how these nematodes will be effective and profitable biological controls. EPNs have been used with varying success to control soil insects. Parkman et al. (1996) documented the successful control of introduced mole crickets, *Scapteriscus* spp., in Florida pastures that was accomplished using an introduced species, *Steinernema scapterisci*, as a classical biological control agent. However, consistent efficacy of EPNs in augmentative applications against soil-dwelling insects in agricultural systems has not yet been achieved despite their predicted potential (Georgis et al., 2006). One of the reasons for this lack of success is insufficient understanding of the complexity of biotic and abiotic interactions that EPNs have in the soil environment in both managed and natural ecosystems.

Most research on EPNs has focused on their occurrence, efficacy and persistence (Gaugler, 2002; Grewal et al., 2005). Additionally, intensive research on naturally-occurring populations has revealed that EPNs can serve as an excellent model system for understanding biological, ecological and evolutionary processes involving other soil organisms (Burnell and Stock, 2000; Goodrich–Blair and Clarke, 2007; Denno et al., 2008; Stock and Goodrich–Blair, 2008). However, a focus on multidisciplinary approaches informed by biological, ecological, evolutionary and computational sciences is needed for advancing our knowledge of EPNs and their bacterial symbionts. In this respect, Thompson et al. (2001) defined four frontiers that should be taken into account when integrating studies in ecology: 1) The dynamics of coalescence in complex communities, 2) the evolutionary and historical determinants of ecological processes in the context of ecological memory, 3) the emergent properties of complex systems, and 4) the ecological topology (Table 1).

Thompson's ***first frontier*** relates to the study of physical and chemical factors (e.g., soil texture and structure, soil water status, gases, temperature, pH), numerous biotic factors (e.g., prey populations and communities, food-plants of herbivorous prey, intraguild predation) that influence predator-prey, host-parasite, and other food web interactions. The ***second frontier*** focuses on the role of 'ecological memory,' the consideration of disciplines such as biogeography, phylogeny and evolution as the background to understanding the interactions among organisms and their environment. The ***third frontier*** addresses the need for the integration of field-based ecological and laboratory-based biological information through mathematical models to reveal new associations between organisms, their emergent properties and patterns, and to predict the response of soil ecosystems to a changing world. The ***fourth frontier*** requires sufficient progress on each of the first three to span from short-term microcosm studies to long-term

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TABLE 1. Definitions of the main four concepts proposed in Thompson et al. (2001).

Frontier	Concept	Definition
N° 1: The dynamics of coalescence in complex communities	Dynamics of coalescence	The processes and interactions that promote and modulate the combination and integration of different elements in a community.
N° 2: The evolutionary and historical determinants of ecological processes	Ecological memory	The result of past environmental conditions and subsequent selection on populations that is encoded in the current structure of biological communities
N° 3: The appearance of complex systems and patterns that arise through relatively simple interactions.	Emergent property	A new quality, trait or effect that arises when components interact, providing a higher level of organization in the resulting pattern or system that cannot be reduced to the sum or difference of the components.
N° 4: The ecological topology	Ecological topology	The appropriate domains of causality in many ecological studies could extend beyond previously assumed spatial and temporal bounds.

and spatially extensive studies. Also required is the development of methodology that crosses or links spatial and temporal scales, synthesis of established knowledge to uncover consistent patterns, processes, and unifying principles, and the ability to share information. In this review, we illustrate the utility of EPNs as model systems considering Thompson's four frontiers (Thompson et al., 2001). We then discuss how this information is critical for the application and conservation of EPNs, and also for future research in other disciplines considering EPNs and their bacterial symbionts.

FRONTIER 1: EPNS AND COMMUNITY COALESCENCE

The soil sustains a high diversity of organisms that interact in complex food webs that are shaped by abiotic factors. The integration of habitat characteristics and limitations with spatial-temporal fluctuations in the numbers of their inhabitants, expand our understanding about complex ecological processes. Traditionally, the effects of abiotic factors on EPNs have been widely studied in laboratory experiments using soils or artificial substrates that have been treated to reduce interactions with other external factors (reviewed in Barbercheck, 1992; Glazer, 2002). Therefore, there is a need for a multidisciplinary approach to study such relationships in a wider context. Moreover, soil nematodes are currently recognized as key players in regulating soil food web composition, decomposition and mineralization, microbial transport, predation, and parasitism (Ferris et al., 2001). Even so, EPNs have rarely been incorporated into these studies. More recently, there has been a growing appreciation for complex interactions that are common in nature. This has been reflected by research on natural and managed systems that have focused on EPNs as a component of the broader food web and engaged in two–trophic and higher level trophic interactions (Denno et al., 2008; Ram et al. 2008; Stuart et al., 2008). This type of research demonstrates how EPNs can be used as a model for research that increases our knowledge about basic soil food-web structure and function, and belowground–aboveground interactions. In addition, this information potentially can be used to manipulate soil food webs to increase the efficacy of biological control in the soil.

In laboratory, greenhouse and field trials, many abiotic factors have been shown to be associated with the occurrence, movement, and persistence of EPNs. These include physical or chemical characteristics (e.g., soil moisture, temperature, pH, texture, structure and bulk density) and characteristics resulting from human activities (e.g., chemical or physical disturbance during ecosystem management such as fertilization, application of pesticides, etc.) (Stuart et al., 2006). In particular, soil moisture is a critical abiotic factor affecting EPN behavior, efficacy and survival because nematodes require water films of sufficient thickness and continuity to allow movement (reviewed in Kaya and Gaugler, 1993; Glazer, 2002; Shapiro–Ilan et al., 2002). Conversely, in very wet or saturated soils, oxygen may be limiting and nematode movement can be restricted due to lack of surface tension forces (Wallace, 1968). Soil texture and structure are also major factors affecting EPNs (Kaya and Gaugler, 1993; Shapiro–Ilan et al., 2002) and many studies on the effects of soil on EPNs have focused on soil texture. However, soil structure, geometry and porosity have rarely been studied, even though structural pore space affects the movement of water, air and organisms in soil. In managed systems, the observed effects of soil characteristics have been mixed. For example, suppression of the citrus root weevil, *Diaprepes abbreviatus,* by *Steinernema riobrave* is greater in coarse sandy soils than in fine textured soils (Shapiro et al., 2000; Duncan et al. 2001, 2003a). In contrast, the persistence of naturally occurring and inoculated populations of *Heterorhabditis bacteriophora* in turfgrass (Campbell et al., 1998), and *Steinernema carpocapsae* and *H. bacteriophora* in maize are not affected by soil texture (Millar and Barbercheck, 2002).

EPNs can serve as models for understanding the effects of disturbance on ecological interactions in soil. Similar to other soil fauna, the diversity of EPNs and their interactions with other organisms can be significantly altered by management practices such as irrigation, planting density, variety selection, tillage regime,

fertility inputs, pesticide use and various other factors (reviewed in Shapiro–Ilan et al., 2002; Barbercheck and Hoy, 2005; Stuart et al., 2006). Mechanical disturbances such as tillage can have profound effects on the biological and functional properties of the soil. For example, soil faunal biomass often drops with increased agricultural usage, especially where conventional tillage is practiced (Stinner and House, 1990). In managed systems, lack of physical disturbance (stability) and favorable soil conditions (adequate moisture, aeration, structure) have favored successful use of inundative application of EPNs (Shapiro–Ilan et al., 2002). Under a conventional tillage regime, the soil surface also tends to have greater fluctuations in temperature and moisture than under conservation tillage management. Consequently, EPNs are more frequently detected in reduced tillage regimes than in conventional tillage (Brust, 1991; Shapiro et al., 1999; Hummel et al., 2002; Millar and Barbercheck, 2002; Campos-Herrera et al., 2008). Compaction and removal of surface residue resulting from tillage also contribute to reduction in soil moisture and pore space for soil organisms (Stinner and House, 1990; Millar and Barbercheck, 2002). The greater complexity of the soil environment associated with relatively high levels of crop residue in conservation tillage regimes might influence the abundance of EPNs through provision of a greater number and diversity of hosts (Brust, 1991). Surface residues could benefit nematode persistence through protection from desiccation or ultraviolet light, and increase insect pest suppression by EPNs (Shapiro et al., 1999) or enhance nematode movement (Jabbour and Barbercheck, 2008). However, the effects of tillage on EPNs are variable and depend on the EPN species present and their associated foraging strategies (Campbell and Gaugler, 1997; Hummel et al., 2002; Millar and Barbercheck, 2002).

The effects of biotic factors on EPNs have received less attention, probably due to methodological limitations. Knowledge of the interactions of soil organisms with their environments is critical for the development of models for soil management that are focused on system stability and resilience. Numerous biotic factors influence predator–prey, host–parasite, and other food web interactions (Rosenheim et al., 1995). In relation to this, a broad range of host and non–host arthropods, competitors, predators, parasites and pathogens (reviewed by Kaya, 2002; Stuart et al., 2006) can influence EPN survival and reproduction. Additionally, omnivory is common in detrital food webs, adding to the list of organisms that might interact with EPNs and impact their population levels (Walter et al., 1987; Walter and Ikonen, 1989). Recent ecological studies have illustrated the utility of EPNs as regulators of soil food webs, and the effects of soil food webs on aboveBelowground interactions. (De Deyn and Van der Putten, 2005; Hooper et al. 2005; Stuart et al., 2006; Denno et al., 2008). Some of these studies will be reviewed here to illustrate the utility of EPNs for understanding biotic interactions across a range of trophic interaction complexity.

Research on EPNs can provide insights into parasite–prey interactions, as these nematodes act both parasites and prey in soil. The primary biotic factor influencing the occurrence and persistence of EPNs at a particular location is probably the presence of suitable insect hosts (Peters, 1996; Mráček et al., 1999). Regulation of soil biota through predation is widespread in soil food webs and there are many examples of regulation of densities of soil animals and microbes by their consumers (reviewed by Wardle et al., 2004). Predation on EPNs has not been studied extensively, but a wide range of soil organisms could play an important role in regulating EPN populations. For example, the ubiquity and abundance of nematophagous fungi (NF), bacteria, nematodes, mites, collembolans and other microarthropods in soil suggest that these organisms might have considerable impact on EPNs in the natural environment (reviewed in Kaya, 2002). Under laboratory conditions, omnivorous and nematophagous predators can be voracious feeders (Gilmore and Raffensperger, 1970). The capacity of a predator to exert a regulatory effect on a population of nematodes is determined partly by its ability to increase their population level and/or predation rate as prey density increases. Many nematophagous organisms have rapid development times and high reproductive capacities, many species (e.g., predatory mesostigmatid mites) exhibit at least some degree of specificity towards nematodes, and many are capable of reproducing rapidly by parthenogenesis (Walter et al., 1987; Walter and Ikonen, 1989). The potential impact of natural enemies of EPNs has generally been assessed in observation chambers or in pots of sterilized soil (Gilmore and Raffensperger, 1970; Epsky et al., 1988; Gilmore and Potter, 1993) and, although these artificial systems do not reproduce more complex field conditions, there is some evidence that supports the role that predation by soil fauna might play in the lack of persistence of applied EPNs (Rosenheim et al., 1995; Kaya, 2002; Wilson and Gaugler, 2004; Duncan et al., 2007; El–Borai et al., 2007; Karagoz et al., 2007).

Additionally, EPN–infected insect cadavers represent a resource with which soil organisms can interact. The cadavers of at least some EPN species have been shown to be repellent to certain ant species, and thereby provide some measure of protection for the developing nematodes (Baur et al., 1998; Zhou et al., 2002). This effect has been demonstrated for a limited number of arthropod and EPN species (Baur et al., 1998; Kaya, 2002; Greenwood et al., 2011; Jabbour and Barbercheck, 2011; Gulçu et al., 2012). Baur et al. (1998) hypothesized the existence of an "ant–repellent factor" associated with *Heterorhabditis–Photorhabdus* infections because

ants scavenged significantly more steinernematid–killed (60–85%) than heterorhabditid–killed (10–20%) insects. When these authors tested the effect of the bacteria–infected cadavers in the field, none of the insects killed by *P. luminescens* were scavanged compared with 70% of those killed by *X. nematophila*. These results and later studies by Zhou et al. (2002) suggested that *P. luminescens* is responsible for preventing ants from foraging on heterorhabditid–killed hosts. More recently, Gulçu et al. (2012) showed that the predator repellant–activity of the EPN–bacteria complex extends to crickets, wasps and calliphorid flies. The authors proposed the new terminology "scavenger deterrent factor" to describe this phenomenon. Fewer arthropods were associated with non-augmented soil controls and soil treated with *Heterorhabditis*–infected cadavers, than soil treated with *Steinernema*-infected cadavers (Greenwood et al., 2011). Karagoz et al. (2007) suggested that the observed pattern is due to arthropod repellency associated with heterorhabditid nematodes. Soil microarthropod abundance and community composition differed between treatments that provided resources (*S. carpocapsae*–killed) compared with those that did not (sham burial control) (Jabbour and Barbercheck, 2011). Similar to the results of Greenwood et al. (2011), soil surrounding *S. carpocapsae*–killed insect larvae contained more dipterans, acarid mites, staphylinid beetles, onychiurid and entomobryid collembolans, and immature and male mesostigmatid mites than soil at sham burial sites. Even though most of these arthropods are capable of nematophagy, the relative abundance of EPNs was not associated with arthropod community composition. Perhaps the great reproductive potential of EPNs dampens the potential negative effects of their natural enemies.

Frontier 2: Evolutionary Understanding of Epns and Their Symbiotic Bacteria: Phylogeny, Systematics and Ecological Memory

EPNs currently comprise two families: Steinernematidae and Heterorhabditidae (Dillman et al., 2012). The most current taxonomic account for the Steinernematidae recognizes the genus *Neosteinernema*, which contains only one species, *N. longicurvicauda*, and the genus *Steinernema* (type genus) with more than 60 recognized species (Table 2). The second family, Heterorhabditidae, contains a single genus, *Heterorhabditis*, with more than 20 currently recognized species (Table 2). These nematodes have a mutualistic association with Gram–negative γ–Proteobacteria in the genera *Xenorhabdus* (for steinernematids) and *Photorhabdus* (for heterorhabditids) (Table 2). Each individual nematode harbors one bacterial species; moreover, a nematode species is associated with only one bacterial species, with the exception of *H. bacteriophora*. Some bacterial species are able to share different nematode hosts (Lee and Stock, 2010a). Recent studies have described 21 species of *Xenorhabdus* and three species of *Photorhabdus,* containing 12 subspecies (Tailliez et al., 2006, 2010).

The increasing number of described species and the dearth of expertise on traditional morphological diagnostic methods have necessitated supplementary approaches such as molecular methods to properly characterize and diagnose EPN taxa. In this respect, nucleotide sequence analysis has proven to be a useful tool not only for diagnostics at different taxonomic levels, but also for providing valuable data for phylogenetic inference about EPNs (Nguyen et al., 2001; Stock et al., 2001; Spiridonov et al., 2004; Adams et al., 2007). A limitation of these molecular hypotheses is that they were inferred using data from a single genetic locus (nuclear ribosomal DNA). To address the potential limitations of single–locus molecular hypotheses, multilocus approaches have been proposed to assess phylogenetic relationships among *Steinernema* taxa (Nadler et al. 2006; Lee and Stock, 2010a).

The diagnosis and identification of bacterial symbiont species and strains has undergone changes in methodology, similar to that used for EPN's, ranging from phenotypic traits, biochemical and biophysical techniques to molecular methods. For example, molecular methods such as restriction analysis of PCR amplified gene products and riboprinting have been employed to determine diversity among entomopathogenic bacterial species. These methods have also been used for rapid identification of bacteria and to avoid tedious phenotypic characterization techniques (Szállás et al., 2001). More recently, sequence data of single and multigene datasets has been used to identify *Xenorhabdus* and *Photorhabdus* species and/or strains and to develop hypotheses about their evolutionary relationships (Liu et al., 2001; Tailliez et al 2006, 2010; Lee and Stock 2010b). In addition, sequence data has been used to develop coevolutionary hypotheses between these bacteria and their nematode hosts. With respect to the *Steinernema–Xenorhabdus* complex, Lee and Stock (2010b) developed the first comprehensive hypothesis for host–symbiont evolutionary trajectories. In this study, 30 *Steinernema–Xenorhabdus* pairs were considered. Reconstruction of the associations showed two scenarios that maximized cospeciation to 12 events, each of the scenarios contained 17 host switches (i.e. a bacterium switched to a different nematode host) and 7 occurrences of sorting (i.e. absence of a symbiont lineage from that of the host). In a similar study, Maneesakorn et al. (2011) examined the coevolutionary history between *Heterorhabditis* and their *Photorhabdus* symbionts and although limited to a single gene approach, the authors concluded that this mutualistic partnership evolved in concert.

We now have access to nearly complete genomes of several EPN and bacterial symbiont species, which

TABLE 2. List of described species of entomopathogenic nematodes and their bacterial symbionts

Entomopathogenic nematode species	Symbiont species
Family Steinernematidae	
Genus *Neosteinernema*	
N. longicurvicauda	undescribed
Genus *Steinernema*	**Genus *Xenorhabus***
S. abbasi	*H. indica*
S. aciari	undescribed
S. affine	*X. bovienii*
S. akhursti	undescribed
S. amazonense	undescribed
S. anatoliense	*X. nematophila*
S. apuliae	*X. kozodoii*
S. arenarium	*X. kozodoii*
S. ashiuense	undescribed
S. asiaticum	undescribed
S. backanense	undescribed
S. beddingi	undescribed
S. bicornutum	*X. budapestensis*
S. boemarei	*X. kozodoii*
S. brasiliense	undescribed
S. carpocapsae	*X. nematophila*
S. ceratophorum	*X. budapestensis*
S. cholashanense	undescribed
S. costaricense	undescribed
S. cubanum	*X. poinarii*
S. cumgarense	undescribed
S. diaprepesi	*X. doucetiae*
S. eapokense	undescribed
S. feltiae	*X. bovienii*
S. glaseri	*X. poinarii*
S. *guangdongense*	undescribed
S. hebeiense	undescribed
S. hermaphroditum	*X. griffiniae*
S. intermedium	*X. bovienii*
S. jollieti	*X. bovienii*
S. karii	*X. hominickii*
S. khoisanae	undescribed
S. kraussei	*X. bovienii*
S. kushidai	*X. japonica*
S. leizhouense	undescribed
S. litorale	undescribed
S. loci	undescribed
S. longicaudum	*X. beddingii*
S. monticolum	*X. hominickii*
S. neocurtillae	undescribed
S. oregonense	*X. bovienii*
S. pakistanense	undescribed
S. puertoricense	*X. romanii*
S. puntauvense	*X. bovienii*
S. rarum	*X. szentirmaii*
S. riobrave	*X. cabanillasii*
S. ritteri	undescribed
S. robustispiculum	undescribed
S. sangi	*X. vietnamese*
S. sasonense- undescribed	undescribed
S. scapterisci	*X. innexi*
S. scarabaei	*X. koppenhoeferi*
S. siamkayai	*X. stockiae*
S. sichuanense	*X. bovienii*
S. silvaticum	undescribed
S. tami	undescribed
S. texanum	undescribed
S. thanhi	undescribed
S. tielingense	undescribed
S. websteri	*X. nematophila*
S. weiseri	*X. bovienii*
S. xechuanense	undescribed
S. yirgalemense	undescribed
Family Heterorhabditidae	
Genus *Heterorhabditis*	**Genus *Photorhabdus***
H. amazonensis	undescribed
H. atacamensis	undescribed
H. bacteriophora	*P. luminescens* *P. temperata*
H. baujardi	undescribed
H. downesi	*P. temperata*
H. floridensis	undescribed
H. georgiana	*P. luminescens*
H. gerrardi	*P. asymbiotica*
H. indica	*P. luminiscens*
H. marelatus	undescribed
H. megidis	*P. temperata*
H. mexicana	undescribed
H. safricana	undescribed
H. sonorensis	*P. luminescens*
H. taysarae	undescribed
H. zealandica	*P. temperata*

(*continued*)

TABLE 2. Continued.

allows for large–scale comparative analysis (Schwartz et al., 2011). New genome sequences of these mutualistic partners together with novel analytical methods will help improve our understanding of their phylogenies, will generate a better understanding of genome evolution in these organisms and will contribute to the advancement of the evolutionary history of EPNs, their obligate symbionts, their insect hosts, and their ecological roles.

Although molecular techniques have provided a tremendous amount of unbiased data for systematic studies of EPNs, it would be a mistake to replace classical morphological approaches with molecular methods. Together, morphological and molecular data will continue to provide a more comprehensive view of EPN evolution, and more robust taxonomic statements (Stock and Reid, 2004; Adams et al., 2006; Stock, 2009).

Correct identification of species is critical to understanding observations made in ecological studies. Description and identification of new isolates and species has been the focus of surveys worldwide for decades. The main goal has been the discovery of strains adapted to local conditions and insect pests. At a global scale, EPNs are ubiquitous (with the exception of Antartica where they have not been detected) and EPNs have a patchy or local aggregative distribution. Although current knowledge of EPN geographic distribution is in part an artifact of sampling efforts, species such as *Steinernema feltiae* and *S. carpocapsae* have been found to have a cosmopolitan distribution (Hominick, 2002). Four EPN species, *S. feltiae*, *S. carpocapsae*, *Heterorhabditis indica* and *H. bacteriophora* are pervasive: these steinernematids have been found in all continents except Africa,

whereas *H. bacteriophora* has not been detected in Asia, and *H. indica* has not been detected in South America, Europe or Africa (Hominick, 2002; Adams et al., 2006). This distribution pattern suggests that dispersal mechanisms can be highly effective and probably occur by a combination of active and passive dissemination mechanisms (Adams et al., 2006).

At present, North America and Asia account for more than 40 nominal *Steinernema* species (~ 70 % of all described species) (Figure 1). *Steinernema feltiae* and *S. carpocapase* remain the most omnipresent species. Within the Heterorhabditidae, more than 15 *Heterorhabditis* spp. have been recovered, with *H. bacteriophora* as the most widely distributed species, followed by *H. indica* and *Heterorhabditis baujardi*. South and North America take the lead in diversity of *Heterorhabdtitis* species encountered (Figure 1). Europe has been the most extensively and intensively sampled continent. In Europe, nine named *Steinernema* spp. have been recorded, with *S. feltiae* and *Steinernema affine* the most widespread species, whereas three named *Heterorhabditis* species have been reported, with *Heterorhabditis megidis* as the species most widely distributed. Based on the latest account (Adams et al., 2006), the number of EPN species in the Australian continent includes three *Steinernema* and three *Heterorhabditis* species. In Africa, sampling efforts have recently increased dramatically, and many new and already–known species have been discovered and are being identified (Hattings et al., 2008; Abu–Shadi et al., 2011; Malan et al., 2011; Kanga et al., 2012). For example, in South Africa, novel species such as *Steinernema khoisanae* and *Heterorhabditis safricana* were discovered, and at least three novel species of *Steinernema* are currently being described (Hattings et al., 2008).

As more surveys with diverse sampling strategies are undertaken, the complexity of habitat preferences of EPNs have become more apparent. Factors such as soil type, distribution of suitable hosts, physiological and behavioral adaptations are key factors affecting the distribution of EPN species (Adams et al., 2006; Stuart et al., 2006). In general, heterorhabditids prefer sandy coastal soils. Some taxa prefer more calcareous soils or more acidic soils (*H. bacteriophora* and *Heterorhabditis marelata*, respectively), while others range beyond coastal regions (*H. bacteriophora*) and are broadly distributed in turf and weedy habitats (*H. megidis*) (Stuart and Gaugler, 1994; Stock et al., 1996; Constant et al., 1998). Prevalence of steinernematids is highest in woodlands (Hominick et al., 1996). Recent extensive and intensive surveys conducted in Europe and the USA revealed habitat preference for several steinernematids (Hominick et al, 1995; Stock et al., 1999; Sturhan and Linskova, 1999; Sturhan, 1999). *S. feltiae* prevails in grasslands and woodlands (Hominick, 2002). This species and *S. affine* are virtually the only steinernematids found in arable soils in Germany (Sturhan, 1999). *Steinernema kraussei* and *S. intermedium* are mainly forest/woodland species. *S. kraussei* has been found in coniferous forests in Europe and North America (USA and Canada) on both the east and west coasts (Sturhan, 1999; Sturhan and Linskova, 1999) and was recently isolated in high altitude woodland in Spain (Campos–Herrera et al., 2007). Along with the increasing complexity of habitat relationships described above, new techniques are being introduced to study these relationships.

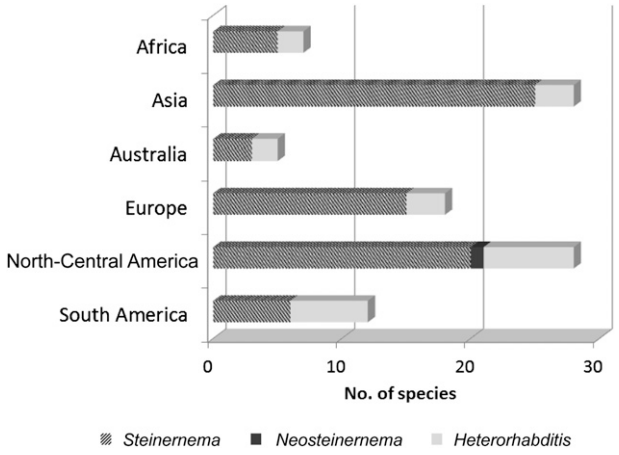

Fig. 1. World distribution of *Steinernema* spp. and *Heterorhabditis* spp.

Frontier 3: Emergent Properties of Population Dynamics and Trophic Interations

There is a growing interest in studying the linkage between biodiversity and ecosystem function and the integration of aboveground – belowground feedback (Wardle et al., 2004; De Deyn and van der Putten, 2005; Hooper et al., 2005). EPNs are ideally suited for serving as model systems in this type of study, specifically to examine higher level trophic interactions in soil and above–belowground feedbacks (Denno et al., 2008). For example, in an agronomic context, the reduction in root damage mediated by augmented EPNs is reflected aboveground by a decrease in the number of adults emerging from the soil and an increase of plant biomass and yield (Duncan et al., in press). Plants play a key role in EPN interactions because they directly affect the soil abiotic-biotic environment. For example, plant root density can affect the ability of EPNs to find a host insect (Choo and Kaya, 1991). Furthermore, Ennis et al. (2010) observed that when artificially damaging the roots of a plant to emulate insect feeding, *S. carpocapsae*'s ability to find an insect host increased.

The efficacy of natural enemies of herbivorous insects can be directly related to the plant's secondary chemistry. This phenomenon has been demonstrated for several insect pathogens, including EPNs (Barbercheck, 1993; Barbercheck et al., 1995; Grewal et al., 1995;

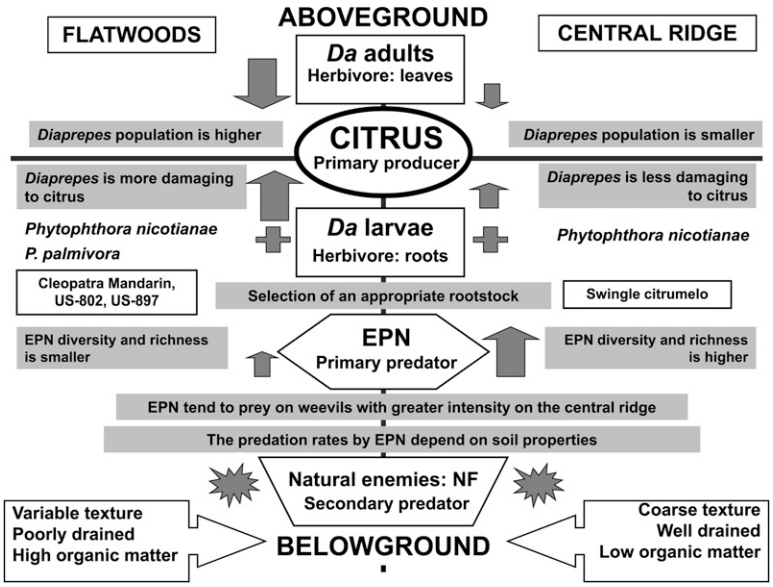

FIG. 2. EPNs in trophic cascades in an agricultural system, citrus groves in Florida (USA). Da = *Diaprepes abbreviatus* (citrus root weevil); NF= nematophagous fungi. For detailed description, see the corresponding text.

Rasmann et al., 2005; Gassmann et al., 2010). The attack of a plant by herbivorous arthropods can result in considerable changes in the plant's chemical phenotype. The emission of herbivore–induced plant volatiles (HIPV) results in the attraction of predators and parasites of the herbivores that induced these changes (Dicke et al., 2009). The suppressive effect of EPNs on root–feeding insects mediated through the production of HIPVs has been studied. For example, the sesquiterpene (*E*)–β–caryophyllene is a volatile compound emitted by maize in response to aboveground herbivory by lepidopteran larvae (Turlings et al., 1998) and in roots wounded by western corn rootworm (Kolner et al. 2008). Rasmann et al. (2005) demonstrated the activity of this volatile as an attractant for EPNs that parasitize rootworms. In relation to this finding, Ali et al. (2010) found that citrus roots recruited significantly more nematodes (*Steinernema diaprepesi*) when infested with *Diaprepes abbreviatus* larvae than non–infested roots, and identified the HIPVs released mainly pregeijerene. When applied in field experiments, this chemical attracted several native EPNs and significantly increased weevil mortality, which demonstrated the potential for using this chemical to improve biocontrol (Ali et al., 2012).

Studies of trophic cascades, in which EPNs benefit plants by reducing herbivore pressure, have produced significant insights for biological control of soil–dwelling insect pests. In coastal California, native *H. marelatus* populations are dynamically linked with populations of the ghost caterpillar, *Hepialus californicus*, and the bush lupine, *Lupinus arboreus* (reviewed in Strong, 2002; Ram et al. 2008). Ghost moth larvae inflict severe root damage and can kill bush lupines. *H. marelatus* causes high mortality of these caterpillars, and the spatial distribution of this EPN is positively correlated with fluctuations in the caterpillar population and local distribution of lupine bushes. Indeed, in the absence of *H. marelatus*, lupine mortality increased as a function of *H. californicus* density. Mature bush lupines possess a dense canopy and thick detrital layer that reduces desiccation and helps maintain a zone of relatively moist soil around their taproots. Abiotic factors, such as soil moisture, affected the nematodes' survival and played a critical role in the trophic cascade (Preisser and Strong, 2004). The survival of infective juveniles (IJs) increased in the lupine rhizospheres during dry summer conditions (Dugaw et al., 2005).

The role of EPNs in a trophic cascade has also been documented in citrus groves in Florida (reviewed in Stuart et al., 2008) (Figure 2). These groves are widely affected by a pest–disease complex involving the weevil *D. abbreviatus* and plant–pathogenic fungi in the genus *Phytophthora*. This pathogen complex represents one of the foremost biotic threats to citrus. *Diaprepes* weevils are typically less abundant in Central Ridge groves than in Flatwoods groves (McCoy et al., 2003; Futch et al., 2005). Similarly, native communities of EPNs are generally more diverse and more prevalent in citrus groves on the well–drained, coarse sandy soils of the Central Ridge than in those on the poorly–drained, finer textured soils of the Flatwoods (Duncan et al., 2003a). The difference in weevil abundance appears to be directly related to EPN prevalence in groves with different soil types, and soil type appears to influence prevalence of EPNs either directly (restricting nematode movement and host searching ability) or indirectly (soil food web interactions). These foodweb interactions also vary

when considering different habitats and include: i) competition with the free–living bactivorous nematodes (FLBN) *Pellioditis* sp. in the weevil cadavers (Duncan et al., 2003b), ii) antagonism by nematophagous fungi (NF) and iii) parasitism by *Paenibacillus* species that reproduce in *D. abbreviatus* and impair EPN motility in soil (El–Borai et al., 2005; Duncan et al., 2007). The presence of the nematode *S. riobrave* increased the number of *Pellioditis* sp., which developed in *Diaprepes* cadavers (Duncan et al., 2003b). Also, EPN augmentation consistently increased the prevalence of trapping NF (Duncan et al., 2007). Integration of these results on post-application biology of EPNs is fundamental to providing growers with environmentally-friendly IPM alternatives. Research approaches such as these provide an excellent opportunity for expanding our understanding of the dynamics of soil food web interactions and contribute to advancing the frontier of emergent properties of complex systems.

Frontier 4: Spatial and Temporal Modeling of Epn Population Dynamics and Ecosystem Processes

Research on the quantitative ecology of EPNs has contributed substantially to this frontier in ecology. Understanding EPN population change requires an understanding of their reproduction, dispersal and survival. EPN reproduction takes place entirely within an insect host, whereas IJ survival and dispersal take place mostly in the soil. Once inside a host, reproduction can be limited by host size, suitability and host defensive mechanisms. A number of intrinsic mechanisms contribute to EPN IJ survival in the soil, including dispersal (active and passive) to avoid harsh environments or seek more suitable environments and insect hosts, and physiological mechanisms to withstand desiccation, high or low temperature extremes, and other harsh environmental conditions. Many studies have contributed to our understanding of EPN population dynamics and their interactions with other organisms. In this section we review some of the key studies on modeling EPN population dynamics, habitat characteristics and spatial-temporal ecological community relationships.

Population models: Temporal population dynamics can be modeled as a flow through a series of states, starting at an arbitrary point in the life cycle: active IJ outside of a host ⇒ juvenile inside host ⇒ adults ⇒ juveniles (⇒ repeat over multiple generations) ⇒ active IJs outside of hosts (which may also periodically enter an inactive stage, facultative quiescence or anhydrobiosis under adverse conditions). The rates of flow between each state are where mechanistic and quantitative understanding of EPN biology is needed to develop mathematical equations that represent those rates. If spatial as well as temporal dynamics are to be considered, then states can be referenced by location, and additional rates representing movement of IJs or infected hosts to and from each location are needed. Mortality results in loss of EPNs from any of the states described above, and requires additional rate equations. The many rate equations described above are the focus of the following review of some selected literature useful in developing mathematical models of EPN population dynamics across temporal and spatial scales, and that contribute to an improved ecological topology for EPNs.

Beginning with host finding by IJs, a number of early studies focused on understanding the soil environment and characteristics that influence host searching behavior (reviewed by Kaya and Gaugler, 1993; Lewis et al., 2006; Stuart et al., 2006). For example, soil physical characteristics can influence the movement of IJs toward insect hosts in the soil. Host finding behavior was recognized to vary among nematode species and potentially requires somewhat different functions for each in representing host encounter rates. Studies on host invasion provide additional needed biological information to model invasion and mortality rates of insect hosts by EPNs. The broad host community associated with EPNs (Peters, 1996; Georgis et al., 2006) and variation in the physical or behavioral barriers to entry among hosts (Eidt and Thurston, 1995; Gouge et al., 1999) require careful treatment of the potential for infection and reproduction as a function of a particular host community coalescing in space and time. Tritrophic interactions (described above) between nematodes, insects and host plants influence host finding as well as host invasion rates. Furthermore, complexity in invasion rates has been observed as a result of the presence of endophytic fungi and their influence on the plant-insect-nematode interaction (Grewal et al., 1995). Data on the impact of physical and chemical factors on the susceptibility of insect hosts can also contribute to quantifying invasion rates (e.g. Eidt and Thurston, 1995; Grewal et al., 2001). Additionally, it has been demonstrated that EPN IJs vary over time in the proportion of the population that infects, which potentially requires accounting for the age structure of the population (Bohan and Hominick, 1997) or tracking the conditions under which IJs develop (Jagdale and Gordon, 1997). This variation in the nematodes themselves might represent a means for increasing the odds of survival for populations of IJs (Campbell et al., 1999).

Data on reproductive rates of EPN has been reported as a function of host species (Wang and Bedding, 1996; Boff et al., 2000a) and environmental conditions in the insect host (Grewal et al., 1994; Boff et al., 2000b; Bornstein–Forst et al., 2005), as well as in relation to density dependent effects within the host (Selvan et al., 1993; Ryder and Griffin, 2002). Despite the availability of data for some of these key parameters, this is

a relatively weak area that needs to be further investigated in modeling studies. Most of the research on EPN development has been conducted using *Galleria mellonella* as the standard rearing host rather than considering representative species from other insect orders (some exceptions are cited above). Mortality within the host and emergence of nematode progeny has been described as a function of environmental conditions, in particular temperature and humidity (Brown and Gaugler, 1997; Koppenhöfer et al., 1997), and also limited to *G. mellonella* as the insect host model.

Dispersal of IJs in the absence of hosts has been described both as passive or phoretic (Lacey et al., 1995; Shapiro et al., 1995) and active processes (Del Valle et al., 2008). Active dispersal has been studied in laboratory settings, and has considered different EPN species (Grewal et al., 1994) and various soil conditions and depths (Hsiao and All, 1996; Anderson et al., 1997; Portillo–Aguilar et al., 1999; Del Valle et al., 2008). These studies have been conducted in field and laboratory experiments (Ferguson et al., 1995; Hsiao and All, 1998). Studies of dispersal have been complemented by studies on spatial distribution (Stuart and Gaugler, 1994; Campbell et al., 1998; Bohan, 2000), and provide important background information for comparisons with the spatial distributions of insect hosts and habitat conditions. Below we provide a few examples of these interactions.

Predators and pathogens of IJs are common mortality factors that can be included in a model, as described in detail above (Frontier 3). Delayed emergence of IJs from cadavers can be interpreted as a survival mechanism that helps maintain EPN populations in the absence of insect hosts and also when there are unfavourable environmental factors (Koppenhöfer et al., 1997). A mathematical interpretation of these interactions could be used in refining rates of transition in a dynamic population model.

Since 2000, researchers have delved more deeply into these individual components of basic EPN population biology and ecology, and several studies have combined these data to develop population models. For example, analytical population models were developed to explore strategies for application of EPNs in crop protection (Fenton et al., 2000, 2001, 2002; Fenton and Rands, 2004). Such models are based on mathematically tractable sets of a few differential equations; in this case, three equations that describe the change in IJs, uninfected hosts, and infected cadavers over time. The models incorporated previous data on reproduction and mortality rates for many species. Although both precise in their solutions and general in their description of EPN dynamics, such models tend to require simplification of a great deal of the biological complexity to maintain tractability in the equations. Similarly, Wilson et al. (2004) developed a model using the slug parasitic nematode *Phasmarhabditis hermaphrodita* to optimise slug control based on descriptive rather than mechanistic functions that relate nematode and slug numbers to damage over time. Such descriptive models have been extended to include spatial effects (Stuart et al., 2006) and better describe observed populations in field surveys. However, more mechanistic models that incorporate additional details of described EPN biology have not yet been attempted to our knowledge, and could provide a needed complement to simple descriptive models (Van Nes and Scheffer 2005).

Spatial and temporal models: Research described above provides the context for developing a mechanistic understanding of the relationships between EPNs, habitats, and host communities. Although the relationship between EPNs and soil or habitat characteristics has been examined in the studies cited above, the analytical methods used have not always been designed to relate multiple species of entomopathogenic and free–living nematode species to multiple environmental variables in combination such as in the study by Hoy et al. (2008). Statistical techniques for relating species to environmental variables, described only briefly here, include both direct and indirect methods. ***Indirect methods*** are those that focus on a single set of variables (typically related to the environment), and seek a set of linear combinations of those variables that captures the variation within and among them. Principle Components Analysis (PCA) is a common example. A typical approach might be to use PCA to examine variation within a set of edaphic factors in sites where EPN were surveyed, factors hypothesized to be important in EPN distribution (e.g., Alumai et al., 2006; Kanga et al., 2012). The PCA, however, would provide insight into the variation among the edaphic variables, and those variables only. The methodology offers no direct evidence for how nematode species relate to that variation, other than strictly post hoc attempts by inspection of where sites with nematodes fall on axes representing a linear combination of the edaphic variables that maximizes the variation within and among them. By contrast, in ***direct methods*** the relationship between species and environment is included in the statistical model. In this type of model, the environmental/ soil variables (explanatory variables, predictors) are used to explain the variability observed in species (dependent variables, response variables that might be quantitative, semiquantitative or qualitative). The direct methods restrict the analysis of variation among environmental variables describing sites to only the variation that is associated with the variation among species. A second consideration in the selection of the model relating species to environment is whether the relationship is ***linear*** (i.e. abundance strictly increasing or decreasing as a function of the environmental variable) or ***unimodal*** (i.e. an optimum in the environmental

variable exists above and below which species abundance declines). Examples of the latter are pH and temperature.

Several studies have suggested direct gradient analysis, including Redundancy Analysis (RDA, linear model) and Canonical Correspondence Analysis (CCA, unimodal model) (Ter Braak, 1986) as more useful methods to relate the presence and abundance of free–living nematode taxa to multiple soil conditions (Fiscus and Neher, 2002; Neher et al., 2005). Several studies have used RDA to examine EPN relationships with habitat variables, and included soil characteristics (Kanga et al. 2012), tillage (Greenwood et al., 2011), plant cover and the abundance of suitable insect hosts (Mráček et al., 2005). Hoy et al. (2008) used CCA to relate edaphic conditions with a wide range of free–living nematode species and two EPN species. In this study, the presence and abundance of nematodes, and EPNs in particular, were associated with a unique combination of the many edaphic biotic and abiotic factors that have been identified and described individually in the literature reviewed above, with respect to community coalescence, ecological memory, and emergent properties. Furthermore, this study demonstrated that the edaphic conditions associated with EPNs were different from those associated with the other nematode taxa, possibly a function of unique life history traits. Such studies of EPNs and their relationship to the environment could be enhanced in two ways: with more mechanistic understanding of the relationships between species and environmental variables and with more inclusive consideration of the biotic community assemblages that form the environment for EPNs. Steps are being taken to elaborate on the relationships between species and environmental variables using more sophisticated statistical techniques as described above and in terms of more sensitive detection of EPNs and other nematodes and more detailed measurement of environmental variables that are related.

Studies of EPN communities are becoming more detailed (Spiridonov et al., 2007) and better focused on naturally occurring host communities rather than strictly focusing on potential biological control targets. Studies relating EPNs to both soils and soil management are taking a more holistic approach (e.g., Campos–Herrera et al., 2008). Use of quantitative real time PCR as a means for detecting and enumerating EPN presence without baiting soil (Torr et al., 2007; Campos–Herrera et al., 2010) or in comparison with soil baits (Campos–Herrera et al., 2011a) offers new insights. Interactions between EPNs and soil food webs are also becoming more detailed and are leading to a more complete understanding of these communities (El–Borai et al., 2005; Duncan et al., 2007; Karagoz et al., 2007; Strong, 2007). In addition, use of molecular techniques is contributing to more detailed information on the role of EPN in food webs (Read et al., 2006; Campos–Herrera et al., 2011b, Pathak et al., 2012).

Research on EPN dispersal mechanisms and their role in spatial distribution continues to increase. Factors such as different species or strains (Lacey et al., 2001; Rolston et al., 2006), and sex variation within species (Fujimoto et al., 2007; Alsaiyah et al., 2009) have been studied in relation to dispersal mechanisms. Moreover, factors such as soil conditions (Jabbour and Barbercheck, 2008) and biotic community effects have been investigated for their effect on both active and phoretic movement of EPNs (Eng et al., 2005).

Research related to mass production has also taken a population dynamics approach (Hirao and Ehlers, 2010). Trait selection for factors important in population dynamics, such as host location, could have direct application in insect control (Mukuka et al., 2010; Salame et al., 2010), although the focus of these studies has been technological rather than ecological. More recently, ecological genetics has been used to investigate EPN distribution in natural settings (Crossan et al., 2007; Bashey and Lively, 2009). Research with this focus should lead to a better understanding of EPN populations dynamics.

The research described above has enhanced our understanding of EPN population dynamics in both natural and managed ecosystems. Future research should consider other parameters such as habitat conditions associated with EPN presence and abundance to provide snapshots of EPN dynamics in space and time. Inclusion of environmental conditions in models will further improve our understanding of EPN population dynamics.

Conclusions

Use of modeling to understand EPN interactions in the environment is contributing significantly to the key frontiers of ecology (Thompson et al., 2001). The dynamics of coalescence in ecological communities are being explored extensively to understand the relationships between EPNs and the abiotic and biotic soil habitat. To better understand EPN associations with the environment and other members of the soil community, methods for recovering and validating new isolates and for rapid identification should be standardized. This effort is particularly important for biogeographical studies because EPNs are introduced as biological control agents and might displace native, undescribed species. The ecological memory underlying EPN life histories will continue to provide a context for ongoing research on their systematics and biogeography. In particular, the increasing discovery rate of these nematodes has prompted the need for rapid and more accurate methods for species diagnostics through molecular biology methods. Quantitative and mechanistic analyses of EPN populations and their relationship to habitat

characteristics are identifying emergent properties in their unique life history traits. Finally, as studies and techniques are combined into a more comprehensive view of naturally occurring EPN populations and their dynamics in space and time, an ecological topology for EPNs and their ecosystems is beginning to emerge.

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