Review

Ecology of belowground biological control: Entomopathogenic nematode interactions with soil biota

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Maxwell S. Helmberger[a,*], Elson J. Shields[b], Kyle G. Wickings[a]

[a] Department of Entomology, New York State Agricultural Experiment Station, Cornell University, New York, USA
[b] Department of Entomology, Cornell University, New York, USA

A R T I C L E   I N F O

A B S T R A C T

Entomopathogenic nematodes (EPNs) have potential to control many soil-dwelling insect pests but have been limited in their usage, partly by their unpredictable field performance. Numerous abiotic and biotic factors are thought to contribute to this poor predictability, but the exact impacts and relative importance of these factors in affecting EPN performance in the field are not well understood. Previous studies have highlighted diverse interactions between EPNs and other members of the soil community, from plants and fungi to arthropods and annelids. These interactions may help or hinder EPNs in a variety of ways. However, current research has yet to determine how many of these interactions influence EPN performance under field conditions, specifically, if they contribute to the variability limiting EPN efficacy and wide-scale adoption. Here we outline current knowledge of these interactions as well as challenges and avenues for future research, such as greater integration of EPN research with soil animal and rhizosphere ecology, that will better elucidate the potential, limitations, and proper use of EPNs in pest management.

1. Introduction

Since the discovery of entomopathogenic nematodes (EPNs) in 1923 and their first commercialization sixty years later, thirteen EPN species of the genera *Steinernema* and *Heterorhabditis* have been commercially cultivated and marketed for use in a wide array of agricultural and horticultural systems (Lacey et al., 2015). EPN infective juveniles (IJs) invade insect bodies through the mouth, anus, spiracles, or cuticle (Lewis et al., 2006; Wang and Gaugler, 1998) and release their bacterial symbionts (*Xenorhabus* spp. bacteria for *Steinernema* spp. nematodes, and *Photorhabdus* spp. bacteria for *Heterorhabditis* spp. nematodes) into the insect's hemolymph. The bacteria release toxins to kill the insect, though sometimes are aided by venom proteins and anti-immune agents produced by the nematodes themselves (Lu et al., 2017), and proliferate in the cadaver. The IJs consume the bacteria, complete their development, and reproduce. After one or more generations of nematodes inside the cadaver, new IJs leave to seek new hosts in the soil (Kaya and Gaugler, 1993; Lewis and Clarke, 2012).

When using EPNs against pests in agricultural and horticultural systems, IJs are commonly applied onto soil as an aqueous suspension sprayed through the same kind of device used to apply a chemical pesticide. Many other application techniques exist, such as applying EPNs through drip irrigation systems or applying them contained

within bait capsules or already-infected insect cadavers (Shapiro-Ilan and Dolinski, 2015). EPNs can effectively provide a non-toxic, environmentally benign alternative to chemical insecticides for the control of some soil-dwelling pests, including white grubs (Grewal et al., 2005), citrus root weevil (Shapiro-Ilan et al., 2005, 2002), and mole crickets (Parkman et al., 1996). However, despite these and other successes (Georgis et al., 2006), extensive use of EPNs in agriculture is limited to a few markets, including citrus orchards (Shapiro-Ilan et al., 2005) and vegetables in greenhouses (Dolinski et al., 2012; Lacey and Georgis, 2012). Despite the safety of EPNs for humans, other vertebrates, and many non-target invertebrates (Georgis et al., 2006; Lacey and Georgis, 2012), their variable performance and persistence remain important factors restricting their adoption by pest managers (Georgis et al., 2006; Georgis and Gaugler, 1991; Shapiro-Ilan et al., 2002). For instance, many studies of EPN efficacy against scarab grubs in turf and nursery crop systems report highly variable control even within the same EPN species (Georgis et al., 2006; Grewal et al., 2005). Increasing knowledge of how abiotic and biotic soil characteristics affect and contribute to variability in EPN performance and persistence will be a crucial task to better optimize EPNs for soil pest management. In addition, while many applied EPNs do not persist in soil longer than a few weeks or months (Ebssa and Koppenhöfer, 2011; Gaugler et al., 1997; Smits, 1996; Susurluk and Ehlers, 2008), some native EPN populations,

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adapted to a particular environment, have been shown to persist over multiple years when isolated, cultured, and applied to the soil (Koppenhöfer and Fuzy, 2009; Shields et al., 1999). This interest in using persistent EPN populations underscores the need for understanding the biotic and abiotic factors that limit or promote EPN persistence.

Many abiotic factors influencing the ability of EPNs to survive and locate hosts in soil have been identified, and will be covered here only briefly. Soil type (Koppenhöfer and Fuzy, 2006; Kung et al., 1990a) and moisture (Grant and Villani, 2003; Kung et al., 1991) affect EPN performance, both having been correlated with EPN performance not only in laboratory settings but also in the field over regional scales (Campos-Herrera et al., 2013b). The small pore spaces of finely textured soils restrict EPN movement, soils that are too dry lack the water films that EPNs require for movement, and EPNs may face oxygen stress in saturated soils. Soil temperature is another abiotic constraint, with each EPN species possessing an optimal temperature range typically somewhere between 5 and 35 °C (Kung et al., 1991). Salinity (Thurston et al., 1994b) and pH (Kung et al., 1990b) also affect EPN performance, though usually at levels outside what would be found in a typical agricultural soil. UV light and humidity are especially important factors when EPNs are applied to a soil, as UV light rapidly inactivates EPNs (Gaugler et al., 1992; Smits, 1996) and low humidity renders them vulnerable to desiccation (Smits, 1996), hence the common recommendation that EPNs be applied to soil at dusk (Ebssa and Koppenhöfer, 2011; Shannag and Capinera, 1994).

Despite awareness of the abiotic characteristics that limit EPN efficacy against soil-dwelling pests, the ways in which EPNs are impacted by biotic soil factors have received less attention. EPNs must share the soil with enormous biodiversity beyond the pest insect they are deployed against (Fig. 1), and numerous beneficial and detrimental interactions between EPNs and soil organisms other than their hosts have been documented (El-Borai et al., 2005; Eng et al., 2005; Rasmann et al., 2005; Timper et al., 1991; Ulug et al., 2014) (Table 1). Along with abiotic soil properties, these interactions may affect the ability of EPNs to survive, move through soil, locate hosts, and reproduce (Fig. 2). However, they have been less well studied in field settings, where their potential impacts on EPN performance are most relevant.

Whether or not interactions with the soil community can produce noticeable increases or decreases in EPN field performance remains an open question, though some studies show evidence for the primacy of abiotic soil properties over biotic characteristics. For example, Campos-Herrera et al. (2016) found that abiotic properties, such as soil moisture and pH, were stronger determinants of EPN occurrence than the abundance of fungal and nematode natural enemies in Florida mixed forests and old fields. However, McGraw and Schlossberg (2017) found no association between soil moisture and EPN occurrence at fine spatial scales in turfgrass, and suggested that biotic factors may take precedence. Overall, the extent and impact of biotic interactions as well as their relative importance in influencing EPN survival and performance against pests remain poorly understood. Here we review the known and potential effects of soil organisms on EPNs through both direct and indirect ecological interactions. Some interactions have been studied under field conditions, others have been characterized in laboratory settings but lack description in the field, and still others are unobserved but still possible given current knowledge of soil ecology (Table 1). In addition, we highlight key questions that are not yet fully answered and propose avenues of future research by which clearer knowledge of organisms' effects on EPN performance can be obtained.

2. Antagonism

2.1. Predation

Predation is one of the most extensively studied interactions between EPNs and the existing soil community. In laboratory settings, many springtail and mite species consume EPNs (Epsky et al., 1988; Gilmore and Potter, 1993; Ulug et al., 2014), often to the point of reducing infection of the model host insect *Galleria mellonella* (L.) (Epsky et al., 1988; Gilmore and Potter, 1993). Although these studies provide insight into predation effects, few of them have evaluated the effects under natural conditions. Under field soil conditions, many factors could influence the strength of predation by soil animals on EPNs. Field soils possess greater structural complexity than laboratory arenas, which has been shown to reduce predation pressure by providing refuges for prey animals in aquatic systems (Grabowski, 2004; Humphries et al., 2011) and soil (Hohberg and Traunspurger, 2005). In addition, field soils possess a wide array of alternate animal and microbial food sources for predators to consume. Even strict nematophages have other nematode prey available. Total nematode abundance in soil lies in the millions of individuals per square meter (Ruess, 1995; Yeates, 2003, 1979) (Fig. 1), of which EPNs are only a small fraction under natural conditions (Park et al., 2014). EPN application rates in published studies vary widely, ranging between 7400 and 1,500,000 infective juveniles (IJs) per square meter (Forschler and Gardner, 1991; Shields et al., 1999; Shields and Testa, 2015; Susurluk and Ehlers, 2008), with 250,000 IJs per square meter being a common recommended rate for commercial applications (Koppenhöfer et al., 2015). Thus, even after an
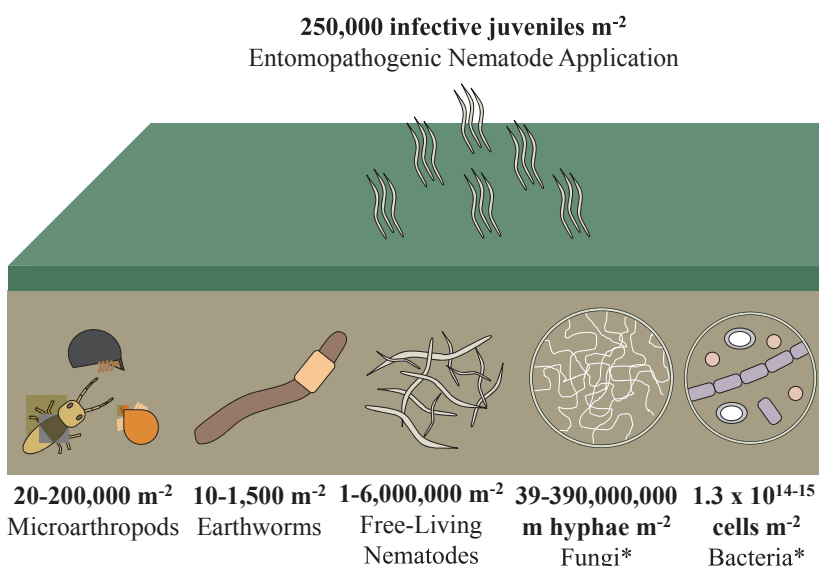

250,000 infective juveniles m⁻²
Entomopathogenic Nematode Application

20-200,000 m⁻²
Microarthropods

10-1,500 m⁻²
Earthworms

1-6,000,000 m⁻²
Free-Living Nematodes

39-390,000,000 m hyphae m⁻²
Fungi*

1.3 x 10¹⁴⁻¹⁵ cells m⁻²
Bacteria*

Fig. 1. A selection of some of the other organisms entomopathogenic nematodes (EPNs) are exposed to when they are applied to a soil. Citations for organismal abundance are as follows: mites and springtails (Giller, 1996; Koehler, 1999), earthworms (Ivask et al., 2007; Timmerman et al., 2006), fungi* (Bardgett et al., 1993; Christensen, 1989), free-living nematodes (Ruess, 1995; Yeates, 1979), bacteria* (Gelsomino et al., 1999), common EPN application rate (Koppenhöfer et al., 2015).
*Per m² abundances calculated from per g values to a soil depth of 10 cm, assuming an average soil density of 1.30 g cm⁻³ (Beylich et al., 2010).

Table 1
List of most known or potential interactions between EPNs and other soil organisms, potentially affecting the ability of EPNs to survive, move through the soil, and infect hosts. Broad taxonomic groups (*e.g.*, fungi, mites) are listed in bold with several examples of more specific groups or species below.

Interaction Type	Tested taxa (examples)	Citations
Predation/ infection	**Fungi**[a]	
	Arthobotrys gephyropaga, Catenaria sp.	El-Borai et al. (2011)
	Protists[c]	
	Cryptodifflugia operculata	Geisen et al. (2015)
	Nematodes[c]	
	Family Mononchidae	Moore et al. (1988); Sayre and Walter (1991)
	Earthworms[c]	
	Lampito mauritii	Dash et al. (1980)
	Mites[a]	
	Gamasellodes vermivorax, Tyrophagus putrescentiae, Pilogalumna cozadensis	Epsky et al. (1988)
	Sancassania polyphyllae	Ekmen et al. (2010b)
	Springtails[a]	
	Folsomia candida	Gilmore and Potter (1993)
	Hypogastrura scotti	Epsky et al. (1988)
Exploitation	**Bacteria**[a]	
	Paenibacillus spp.	Campos-Herrera et al. (2012b); and Enright and Griffin (2005)
Competition	**Bacteria**[b]	
	Bacillus thuringiensis	Kaya and Koppenhöfer (1996)
	Fungi[b]	
	Beauveria bassiana	Tarasco et al. (2011)
	Nematodes[a]	
	Pellioditis sp., *Acrobeloides* spp.	Duncan et al. (2003)
	Oschieus spp.	Blanco-Pérez et al. (2017)
	Mites[a]	
	Sancassania polyphyllae	Ekmen et al. (2010b)
	Insects[b]	
	Linepithema humile, Formica pacifica	Baur et al. (1998)
	Tetramorium chefketi, Labidura riparia	Ulug et al. (2014)
Amensalism	**Plants**[b]	
	Tagetes spp.	Kanagy and Kaya (1996)
Phoresy	**Earthworms**[b]	
	Eisenia fetida	Campos-Herrera et al. (2006)
	Lumbricus terrestris	Shapiro-Ilan and Brown (2013)
	Mites[b]	
	Hypoaspis sp., *Gamasellodes vermivorax, Pilogalumna cozadensis*	Epsky et al. (1988)
	Isopods[b]	
	Porcellio scaber	Eng et al. (2005)
Mutualism	**Plants**[a]	
	Pisum sativum	Hiltpold et al. (2015)
	Thuja occidentalis	Van Tol et al. (2001)
	Zea mays	Rasmann et al. (2005)
Facilitation	**Bacteria**[b]	
	Paenibacillus popilliae	Thurston et al. (1994a)

[a] Indicates interactions characterized in field settings.
[b] Indicates interactions characterized in laboratory settings, but not in the field.
[c] Indicates interactions characterized with free-living nematodes, but not EPNs specifically.

inundative application, EPNs are unlikely to comprise more than even half of a soil's total nematode community, and so may not be preyed upon as intensively as has been observed in simplified laboratory settings where they comprise the entire nematode community.
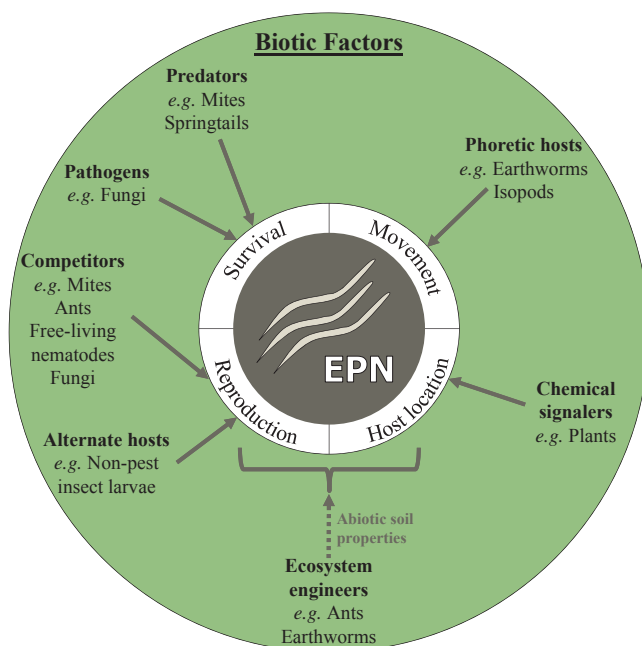

Fig. 2. Diagram of the many different types of soil organisms and their effects on different points in the EPN life/host infection cycle. Note that organisms can fit into multiple categories and thus affect EPNs in different ways. Ecosystem engineers may affect EPNs indirectly through their effects on soil abiotic properties.

Nevertheless, many studies indicate that EPNs are fed upon to some extent following inundative applications in the field, meaning that field predation still likely has some relevance. Surveys of field soil communities following EPN application reveal increases in the abundance of springtails, predatory mites, and higher predators like spiders and staphylinid beetles (Greenwood et al., 2011; Hodson et al., 2012; Jabbour and Barbercheck, 2011), indicating effects cascading up through the food web, likely spurred by the addition of EPNs as a food resource for lower-level consumers. In another field study, EPN DNA was detected in the guts of several oribatid mite species following an aqueous application of the nematodes (Heidemann et al., 2011), indicating that they can be found and consumed in field soils, even amidst the welter of other nematodes. These findings underscore the importance of studying predation and other interactions of soil organisms and EPNs in natural or semi-natural conditions.

The wider body of research surrounding predation on nematodes in general provides additional understanding of where EPNs fit into the broader soil food web. Some predatory nematodes and mesostigmatid mites specialize on nematodes (Moore et al., 1988), with some, such as the mite *Gamasellodes vermivorax* Walter, requiring nematode prey to reproduce (Walter, 1988). In addition, many generalist soil predators and even supposed detritivores will consume nematodes when available (Heidemann et al., 2014a, 2011; Muraoka and Ishibashi, 1976; Walter et al., 1986). In laboratory tests, predatory mites often prefer nematodes to arthropod prey (Walter et al., 1987) and the springtail *Folsomia candida* Willem prefers them to fungus (Lee and Widden, 1996). Protozoa, flatworms, and tardigrades are additional predators of nematodes (Geisen et al., 2015; Sánchez-Moreno et al., 2008; Sayre and Walter, 1991). Although these non-arthropod predators are often mentioned as predators of EPNs (Ekmen et al., 2010b; Raja et al., 2015; Read et al., 2006), they are rarely studied in that specific context. Earthworms can also consume nematodes, though whether this behavior can truly be called 'predation' is questionable, as EPNs can pass through the gut of earthworms without necessarily being harmed (Shapiro et al., 1995, 1993), though reductions in viability can occur (Campos-Herrera et al., 2006). However, other studies have shown reductions in (overall) nematode abundance in soils containing

earthworms (Dash et al., 1980).

Despite the parallels that can be drawn between free-living nematodes and EPNs, two aspects of EPN biology distinguish them as a food resource from most other nematodes: their symbiosis with pathogenic bacteria and their association with insect cadavers. EPNs and their symbionts can kill a wide variety of arthropod taxa, including ticks (Samish et al., 1999; Samish and Glazer, 2001), prostigmatid mites (Bussaman et al., 2006), isopods (Bathon, 1996; Sicard et al., 2014), and millipedes (Bathon, 1996), so it is clear that the EPN bacterial symbionts, *Xenorhabdus* and *Photorhabdus*, are toxic to more than just insects. Epsky et al. (1988) saw poor survival of the nematophagous *G. vermivorax* feeding on *Heterorhabditis heliothidis* (=*bacteriophora*) Poinar IJs and total inability of eight other mite species to fully develop on *Steinernema feltiae* Filipjev, a notable finding given that the mites originated from colonies raised on bacterial-feeding nematodes. EPNs have only rarely been observed to infect microarthropods (Epsky et al., 1988), but their bacterial symbiont may nevertheless render EPNs harmful to microarthropod predators. Thus, in some cases, microarthropods may prefer to consume non-entomopathogenic nematodes, such as free-living bacterivores, plant parasites, and predatory nematodes. Heidemann et al. (2011) noted that oribatid mites were less likely to consume the EPN *S. feltiae* than the snail and slug parasite *Phasmarhabditis hermaphrodita* Schneider, with 3 of the 7 tested mite species consuming live *S. feltiae* and 5 of the 7 consuming dead *S. feltiae*, whereas all mites consumed live and dead *P. hermaphrodita*. In contrast, *G. vermivorax* shows no preference between *S. feltiae* and nematodes of the bacterial-feeding genus *Acrobeloides* (Walter and Ikonen, 1989). This indicates that feeding response may vary between predator taxa, or between specialist predators and opportunistic omnivores. Feeding response may also differ depending on the type of EPN being preyed upon, as *Steinernema* spp. and *Heterorhabditis* spp. differ both in the species of their bacterial symbionts and those symbionts' placement within the EPN gut (Goodrich-Blair and Clarke, 2007). However, more research is needed to confirm any repellent or toxic effects of the EPN symbiont on animals consuming IJs.

The association of EPNs with insect cadavers also sets them apart from most other nematodes. The spatial distribution of EPNs in soil varies from nearly uniform immediately following an aqueous application to patchy, aggregated swarms of IJs (Campbell et al., 1998; Shapiro-Ilan et al., 2014) to the extreme aggregation of IJs within an insect cadaver. Cadavers may attract scavenging animals that would not be significant threats to IJs in the soil, but when drawn to a cadaver may consume the resident or emerging IJs. Ekmen et al. (2010b) found that while just ten individuals of the astigmatid mite *Sancassania polyphyllae* Zachvatkin could consume 96% of IJs emerging from cadavers, they were less able to find and prey upon IJs occurring freely in the soil, as they were drawn primarily to the cadaver and not the IJs (Ekmen et al., 2010a).

2.2. Fungal pathogenesis

Nematophagous fungi (NF) are perhaps the most prominent and well-studied pathogens affecting EPNs. A few instances of microsporidian pathogens of EPNs and phages attacking their symbiotic bacteria have been noted (Kaya, 2002), but have not been extensively studied. NF can be divided into two categories: endoparasitic fungi that attach as conidia to the nematode cuticle and grow into the body cavity; and nematode-trapping fungi that catch nematodes in specially structured hyphae (Kaya and Koppenhöfer, 1996). EPN species differ in their morphological and behavioral defenses against NF. For example, IJs of the genus *Heterorhabditis* retain the cuticle of their previous juvenile stage more readily than do those of the genus *Steinernema*, which sometimes (but see El-Borai et al., 2009) affords greater protection from endoparasitic NF and suggests that heterorhabditid EPNs would be the best species to employ in soils high in these pathogens (El-Borai et al., 2009; Timper and Kaya, 1989). Also, EPN species differ in their

responses to different species of NF, with EPNs potentially being repelled, attracted, or unaffected depending on fungal species (El-Borai et al., 2011). Nematode-trapping species in particular exhibit variable lifestyles, alternating between predatory and saprotrophic behavior (Cooke, 1963; Pathak et al., 2012) in response to competition from other saprotrophic fungi (Quinn, 1987). Therefore, the danger posed by trapping NF to EPNs may vary depending on soil fungal community structure, as well as the specific NF species present and EPNs employed at a given site (El-Borai et al., 2009). Understanding characteristics of soil fungal communities that control this switch to trapping behavior in NF would again aid in assessing a soil's suitability for EPN application, and conversely, in efforts to employ NF against plant-parasitic nematodes (Kerry, 2000).

Both trapping and endoparasitic NF have been studied as EPN antagonists in field settings (Campos-Herrera et al., 2016; Jaffee et al., 1996; Pathak et al., 2012). However, whereas laboratory studies found reduced infection of *G. mellonella* in soils with NF (Koppenhöfer et al., 1996b), and though earlier studies did not show the same effect in the field (Jaffee et al., 1996), modern molecular methods have allowed for more accurate detection and measurement of NF populations in relation to EPNs in field settings. These methods are able to detect NF in samples of nematodes or bulk soil (Campos-Herrera et al., 2016; Pathak et al., 2012) and have shown spatial associations between EPNs and NF (Jaffuel et al., 2016; Pathak et al., 2017), though not always the negative associations that would be expected if NF substantially reduced EPN populations (Duncan et al., 2013; Pathak et al., 2017). Thus, NF may not always be major limiters of EPN performance. However, Duncan et al. (2007) found higher EPN infection of the citrus root weevil *Diaprepes abbreviatus* in soils mulched with animal manure, a treatment that also decreased populations of trapping NF, indicating that NF may still be a worthwhile target for management programs seeking to increase EPN efficacy.

2.3. Plant amensalism

In addition to their prominence aboveground, plants are pivotal members of the soil community in most terrestrial (and all agricultural) ecosystems. Plant roots alter soil structure and chemistry, provide resources for soil animals and microbes, and produce a wide variety of secondary metabolites to sculpt the surrounding community for their own benefit (Hinsinger et al., 2009; Philippot et al., 2013). Although plants usually benefit from the presence of EPNs and some (discussed below in Section 3.1) secrete EPN-attracting chemicals into the rhizosphere (Rasmann et al., 2005), other root exudates can act as deterrents or toxins (Kaya and Koppenhöfer, 1996). The thiophene α-terthienyl, an extract of marigold (Asteraceae) roots, has long been known to suppress plant-parasitic nematodes, and marigolds have even been incorporated into some agricultural systems as cover crops or green manures for this exact purpose (Chitwood, 2002; Hooks et al., 2010). However, α-terthienyl also displays toxicity to EPNs at high concentrations, causing decreased survival and lower numbers of nematodes penetrating hosts (Kanagy and Kaya, 1996). Interestingly, EPNs did not perform better or worse in the presence of marigold roots than in their absence, perhaps indicating that natural concentrations of the exudate suppress plant-parasitic nematodes but not EPNs. However, this interaction has not been extensively studied with marigold or any other plant. Many plants, including other asters, brassicas, and sorghum grasses, also produce nematicidal compounds to combat plant-parasitic nematodes (Chitwood, 2002), which may also reduce EPN infectivity against insect pests when incorporated into management practices. For example, mustard green manures tilled into a potato field reduced infection of *Galleria mellonella* larvae by a wide range of EPN species (Ramirez et al., 2009). However, the use of mustard as a cover crop did not significantly reduce EPN abundance compared to other cover crops or bare soil (Jaffuel et al., 2017). Thus, the potential for plant antibiosis should be studied in more detail and in a wider variety of crop systems.

In some cases, the benefits of plant-parasitic nematode suppression by toxic root exudates may outweigh any detriments of reduced EPN infectivity against insect pests. Attempts to reduce the presence or effects of these exudates would perhaps be best suited for cropping systems in which plant-parasitic nematodes are not economically important pests, or else for situations in which the plants producing the exudates toxic to EPNs are cover crops or weeds rather than the main crop.

2.4. Competition

An EPN-killed insect, burgeoning with bacterial biomass, is an excellent food resource for many organisms outside of the EPN-bacteria partnership. *Xenorhabdus* and *Photorhabdus* bacteria produce compounds that deter a wide range of scavengers, such as beetles (Foltan and Puza, 2009; Jones et al., 2015), ants (Baur et al., 1998), and even vertebrates (Fenton et al., 2011; Jones et al., 2017; Raja et al., 2017). However, ants, cockroaches, mites, and earwigs have still been found to feed on EPN-infected cadavers (Baur et al., 1998; Ulug et al., 2014). Scavengers can directly consume the developing and/or emerging EPNs within (Ekmen et al., 2010b) or simply break open the cadaver and leave the EPNs vulnerable to desiccation (Baur et al., 1998). Free-living and necromenic nematodes can also compete for the bacterial resources within an EPN-killed cadaver, substantially reducing the number of IJs that eventually emerge (Blanco-Pérez et al., 2017; Duncan et al., 2003), though susceptibility to bacterivore competitors can vary between EPN species (Blanco-Pérez et al., 2017; Campos-Herrera et al., 2015). EPNs can face similar conflicts with saprotrophic microbes that compete for cadaver resources and impede the growth of both EPN and symbiotic bacteria (Navarro et al., 2014a).

EPNs can also compete with other insect pathogens sharing their host. Competition with entomopathogenic viruses, bacteria, and fungi has been reviewed in depth by Kaya and Koppenhöfer (1996) and will be discussed only briefly here. Co-infection of EPNs and many bacterial and viral entomopathogens usually results in reduced viability of the next EPN generation, due either to resource competition (Kaya and Brayton, 1978) or to the other pathogen disintegrating the insect cadaver's cuticle and desiccating the developing EPNs (Kaya and Burlando, 1989). In contrast, effects of co-infecting entomopathogenic fungi (EPF) on EPNs are timing- and temperature-dependent, and in favorable circumstances, EPNs can exclude the fungi and develop normally (Barbercheck and Kaya, 1990). Compounds produced by EPF and EPN symbiotic bacteria are generally antagonistic to one another, although this can vary by individual EPF or symbiont species (Ansari et al., 2005; Tarasco et al., 2011). In rare instances, EPNs and EPF can colonize different parts of the same cadaver (Tarasco et al., 2011), though this would still decrease the amount of resources available to the EPNs. Interestingly, combined applications of EPNs and other entomopathogens (in management contexts) sometimes have additive or synergistic effects on pest mortality (Abdolmaleki et al., 2017; Ansari et al., 2006; Jabbour et al., 2011), yet this is sometimes dependent on the relative timing of both applications (Abdolmaleki et al., 2017). This indicates that the relationship between EPNs and other entomopathogens may be less adversarial when considering an entire population of hosts rather than their interactions within a single host. Though outside the scope of the present review, different EPN species can also compete with one another within the soil profile (Koppenhöfer et al., 1996a) and within single host cadavers (Koppenhöfer et al., 1995), with the victorious species usually being the one with faster development time or less specific bacterial symbiont association (Koppenhöfer et al., 1995).

Unlike predation, competition for cadaver resources can only reduce EPN recycling and thus their potential to persist over time, not the initial infectivity of an aqueous EPN application. However, the practice of applying EPNs within infected insects (Raja et al., 2015; Shapiro-Ilan et al., 2006), despite its advantages of increased EPN infectivity under typical circumstances (Shapiro-Ilan et al., 2003; Shapiro and Lewis, 1999), may not be suitable for soils unusually high in potential

scavengers.

2.5. Bacterial encumbrance

There is also evidence that EPNs can be negatively affected by soil microbes that exploit IJs for their own dispersal. The bacterium *Paenibacillus nematophilus* can attach itself to many *Heterorhabditis* EPN species and use them as phoretic hosts (Enright and Griffin, 2004), and an unidentified congener, *Paenibacillus* sp., attaches to *Steinernema diaprepesi* (El-Borai et al., 2005). Unlike many other *Paenibacillus* species, these bacteria are not entomopathogenic, but instead will proliferate inside of EPN-killed insects after reaching them as spores on the IJs. *Paenibacillus* presence does not significantly impact EPN reproduction or development inside of cadavers, but spores can reduce EPN mobility and ability to infect hosts in laboratory settings (El-Borai et al., 2005; Enright and Griffin, 2005). From an evolutionary perspective, bacteria that benefit from transportation to a host would not be expected to commonly overburden their source of transportation, as that would decrease their own fitness as well as the fitness of the EPN (Enright and Griffin, 2005). However, the *Paenibacillus*-EPN phoretic association itself has been repeatedly confirmed in natural soils via real time quantitative PCR (Campos-Herrera et al., 2016, 2011, 2012b), and increases in *Paenibacillus* spore encumbrance have been linked to reduced EPN abundance (Campos-Herrera et al., 2013a).

3. Facilitation

3.1. Plant root signaling

Due to the protection EPNs provide plants in both natural (Ram et al., 2008) and agricultural ecosystems (Chen et al., 2003; Toepfer et al., 2008), plants would be expected to benefit from the ability to attract EPNs to the site of belowground herbivory. As such, many plants secrete exudates in response to root feeding that can attract and mobilize EPNs against the feeding insects. Root exudates from citrus (Ali et al., 2012), pea (Hiltpold et al., 2015), conifers (Van Tol et al., 2001), and maize (Rasmann et al., 2005) all affect EPNs in this way, primarily attracting them to defend the plant from belowground attack. Pea root exudates can induce quiescence in both EPNs and plant-parasitic nematodes when present in high concentrations (Hiltpold et al., 2015; Jaffuel et al., 2015), but at low concentrations, the exudates increase EPN infectivity to *Galleria mellonella* while still subduing plant-parasitic nematodes (Hiltpold et al., 2015). Exudates from citrus roots have been found to enhance biological control even when applied to the soil in non-citrus cropping systems (Ali et al., 2012), though they also can attract free-living bacterivorous nematodes, which can compete with EPNs for cadaver resources (Ali et al., 2013). Conversely, the exudates can also modify EPN behavior in the presence of NF, reducing infection of the EPNs (Willett et al., 2017).

The interaction of EPNs with maize root exudates is the most intensively studied. Certain maize cultivars exude the sesquiterpene (*E*)-β-caryophyllene (EβC) from their roots in response to feeding damage from the western corn rootworm *Diobrotica virgifera* LeConte, thus attracting EPNs to kill the pest (Rasmann et al., 2005). EβC not only attracts EPNs, but also helps them navigate complex root architecture to locate hosts (Demarta et al., 2014). EPNs thus attracted can significantly reduce *D. v. virgifera* numbers and damage to maize roots (Hiltpold et al., 2010a,b,c). This interaction has led to extensive research into ways to select for EPN populations more responsive to the EβC signal (Hiltpold et al., 2010a,b) and, through genetic engineering, to restore the signal to maize cultivars that have lost it (Degenhardt et al., 2009). Interestingly, selecting for enhanced response to EβC resulted in greater *D. v. virgifera* mortality and decreased root damage when *Steinernema feltiae* and *Heterorhabditis megidis* Poinar, Jackson, & Klein were applied to the soil, but selection had no effect on the insect-killing or plant-protecting ability of *H. bacteriophora* (Hiltpold et al.,

2010c). This suggests that some EPN species may be less reliant on host plant chemical signals than other species, and so would be the optimal choice of EPN for use on crops and cultivars lacking those signals.

It must be noted that while these interactions have been intensively studied in a few crop plant systems, soil is an incredibly complex chemical environment, replete with volatile and solubilized compounds from plant and microbial sources, most of whose functions are unknown (Delory et al., 2016; Insam and Seewald, 2010; Leff and Fierer, 2008). Under natural conditions, the full importance of established chemical cues relative to other compounds remains to be unearthed. In addition, other physicochemical complexities of soil, properties such as moisture, texture, and pH, can affect how volatile chemicals disperse through the soil pore matrix (Chiriboga et al., 2017; Som et al., 2017), impacting the efficiency with which damaged plants can recruit EPNs (Chiriboga et al., 2017).

3.2. Phoresy on soil animals

One of the principal challenges EPNs face is that of dispersing through the soil to locate patchily distributed insect hosts (Stuart et al., 2006). Soil moisture and texture limit the ability of EPNs to disperse independently through the soil matrix (Grant and Villani, 2003; Kung et al., 1990a), however, like many other microinvertebrates, nematodes are capable of dispersing phoretically on the surface of larger animals. EPNs can disperse phoretically both at and below the soil surface on isopods (Eng et al., 2005) and earthworms (Campos-Herrera et al., 2006; Shapiro-Ilan and Brown, 2013; Shapiro et al., 1995, 1993). Other macrofauna such as myriapods or slugs may also serve as phoretic hosts, but those taxa have not been tested. Microarthropods may also provide EPNs with transportation through the soil. Epsky et al. (1988) observed EPNs exploiting mites as phoretic agents, although the study was not conducted in soil, where EPNs may risk being abraded against mineral grains or scraped from the mite's exoskeleton as they move through the soil pore matrix. However, EPNs were seen clustering on the dorsal surface of mites, suggesting an active behavior of the nematodes that they would presumably perform in soil.

3.3. Entomopathogen commensalism

Unlike the entomopathogens discussed above in Section 2.3, *Paenibacillus popillae* (formerly *Bacillus popillae*), causative agent of the milky spore disease in Japanese beetle *Popillia japonica* Newman, not only avoids conflict with co-infecting EPNs, but also enhances EPN penetration of the midgut of infected grubs (Thurston et al., 1994a). Though this 'compensatory infection' may not result in greater insect mortality following EPN application, it could potentially increase EPN recycling and their ability to persist in controlling Japanese beetle over the course of a season. However, native milky spore disease is not often a major source of *P. japonica* mortality (Cappaert and Smitley, 2002; Hanula and Andreadis, 1988), though it can be a dominant pathogen at some sites (Redmond and Potter, 2010). In addition, commercial formulations of *P. popillae* are often ineffective (Redmond and Potter, 1995). It is therefore unlikely that exploiting the EPN-milky spore disease commensalism will lead to enhanced biological control strategies.

4. Host community interactions

Although many of the previously discussed interactions represent top-down pressures on EPN populations, some soil organisms could provide bottom-up effects on EPNs and their ability to infect pests. Obviously, characteristics of a pest population such as density (Ebssa et al., 2011), dominant life stage (Power et al., 2009), and individual pest species within a generalized group such as 'white grubs' (Koppenhöfer et al., 2006; Morales-Rodriguez et al., 2010) can affect the success of an EPN application. However, effects of other, non-target

insect hosts on EPN success against a pest have received little attention. Although some EPN species, such as *Steinernema scarabaei* Stock & Koppenhöfer and *S. scapterisci* Nguyen & Smart, specialize on single or limited numbers of related host species (Koppenhöfer and Fuzy, 2003; Nguyen and Smart, 1991), others, including many commercially available species, have wide host ranges and can infect organisms beyond the targeted pests (Bathon, 1996; Peters, 1996). This fact has received some attention in the context of assessing EPN effects on non-target organisms (Babendreier et al., 2015; Bathon, 1996). Less well understood are the effects of alternate hosts on EPN population dynamics, persistence in soil, and especially their ability to infect pests. Abundance of insect hosts, pest or otherwise, is predictably associated with increased occurrence of EPNs (Efron et al., 2001; Harvey and Griffin, 2016; Mráček et al., 2005; Mráček and Bečvář, 2000), though not in all cases (Campbell et al., 1995; Půža and Mráček, 2005). Susurluk and Ehlers (2008) found that persistence of *Heterorhabditis bacteriophora* was nearly doubled in cropping systems with high availability of hosts throughout the course of the study compared to systems lacking viable hosts.

The effect of alternate hosts on EPN infection of pests is likely dependent on several variables, perhaps most importantly the relative timing of the alternate host and the pest life cycles. Alternate hosts present at the same time as the target pest could potentially reduce infection of the pest via apparent mutualism or increase pest infection via apparent competition, depending on a wide range of traits specific to the EPN, pest, and alternate host under consideration (Abrams et al., 1998; Holt and Lawton, 1994). In contrast, alternate hosts present at different times from target pests could enhance EPN persistence, providing a temporal stepping-stone to sustain the population through periods where pest insects are absent from the soil. This was observed by Sulistyanto and Ehlers (1996), which found that EPNs applied to control the scarab grub *Aphodius contaminatus* Herbst could control a second grub occurring later in the season, *Phyllopertha horticola* (L.), at a level high enough to suggest that recycling within the *A. contaminus* and not simple persistence of the original application had occurred.

5. Habitat modification by ecosystem engineers

Soil organisms act not only on one another, but also on the abiotic soil environment around them. Though abiotic properties may be more important controls of EPN performance than biotic properties in some systems (Campos-Herrera et al., 2016), abiotic properties can be shaped by the activities of living ecosystem engineers. Soil macrofauna, especially earthworms, can alter many of the soil properties important for EPN performance, notably soil moisture via burrowing-induced changes in porosity, water infiltration, and water storage (Bottinelli et al., 2015; Capowiez et al., 2009; Lavelle et al., 1997). Ants and termites can also cause similar changes both in their mounds and in surrounding soils (Frouz et al., 2003; Nkem et al., 2000). Some changes may be restricted to their mounds, such as increases in deep-soil porosity in ant mounds (Nkem et al., 2000), but other changes extend throughout their range of activity. In addition, ants and termites are both capable of increasing water infiltration rates through their tunneling activities (Mando et al., 1996), to the point where excluding these organisms can decrease crop yields in arid soils (Evans et al., 2011). A similar decrease in water infiltration might also reduce EPN performance, suggesting that the presence of these ecosystem engineers would be beneficial to EPNs.

Ecosystem engineers can also influence another major abiotic control of EPN performance, soil texture. Ingestion and passage through the guts of earthworms (Carpenter et al., 2007; Suzuki et al., 2003) and scarab larvae (Suzuki et al., 2003) can erode mineral grains to the point of converting coarse and medium sand grains into fine and very fine sand (Suzuki et al., 2003), though any potential effects of scarabs on soil texture at field scales are not well characterized. Earthworms can also alter the vertical distribution of a soil's mineral constituents (Resner et al., 2011), changing the soil profile that EPNs must penetrate

to reach the target pest. Ants similarly redistribute soil particles, as Nkem et al. (2000) found lower clay and higher silt and sand contents in ant-impacted soils, even five meters from the mounds and in foraging tracks extending farther. Any fauna-induced changes to soil texture would likely occur over timescales much longer than those of any direct ecological interaction such as predation. However, earthworms are prominent invasive species in certain parts of the world, such as the northern United States (Bohlen et al., 2004). Thus, their influence on soil physical properties would be a new addition to those ecosystems, one with potential to alter soils' suitability for EPNs over time.

Whether these and other fauna-induced changes are beneficial or detrimental to EPN performance would obviously depend on a variety of factors, such as engineer species, soil characteristics, EPN foraging strategy, and target pest. For example, earthworm burrow size, depth, and structure differ considerably across species and ecological groups (Capowiez et al., 2006), as do the size and distribution of ant and termite mounds (Greenberg et al., 1985), and so the activities of different species would likely have different effects on EPNs. Thus, no single 'engineer effect' is likely to exist. To date, we are not aware of a single study seeking to characterize indirect effects of faunal ecosystem engineering on EPN performance, although Shapiro-Ilan and Brown (2013) found higher dispersal and infectivity of *Steinernema carpocapsae* in soils containing the earthworm *Lumbricus terrestris* compared to soils without it, which the authors attributed primarily to phoresy but could have also been a result of more favorable soil conditions generated by the earthworms.

6. Challenges and future goals

A common theme emerges when considering the literature surrounding ecological interactions between EPNs and other soil organisms, as does a question that should be on every pest manager's mind: do biotic interactions matter? Can the action of other soil organisms enhance or reduce the biological control potential of EPNs, either the initial infectivity of an application or the efficacy and dynamics of a persistent population? Soil organisms are well positioned to have a role in the variable field performance of EPNs. Their abundance and community composition are highly variable in time and space (Frey, 2015; Giller, 1996; Moore and de Ruiter, 1991), and also vary with soil management practices (Chu et al., 2007; Donnison et al., 2000; Gan and Wickings, 2017; Schon et al., 2008; Wickings and Grandy, 2013). For example, springtails and mites, two key groups of soil microarthropods with multiple potential effects on EPNs, range in abundance from hundreds to hundreds of thousands of individuals per square meter (Giller, 1996; Koehler, 1999). Thus, if these and other soil organisms can influence EPN performance, then their overall effect would be variable, and variable, unpredictable EPN performance would result. The temporal variation in soil communities would perhaps be especially important for management strategies seeking to establish persistent EPN populations, as those EPNs would be exposed to many different soil communities over the course of their time in the soil, which could affect the EPNs differently at different times.

However, the question of other soil organisms' effects on EPNs remains largely unanswered, as the majority of studies so far quantifying the impact of most ecological interactions on EPN performance have been conducted in laboratory settings. In studying predation, analyses of predator gut contents and soil community response to EPN application may identify animal groups that consume EPNs in the field, but cannot determine if predators impact EPN populations strongly enough to interfere with pest control. A few studies have, directly or indirectly, shed some light on this question, such as studies of biological control practices combining EPNs and *Hypoaspis* predatory mites, which are known to consume EPNs (Epsky et al., 1988). Borgemeister and Berndt (2003) suggested intraguild predation by mites on EPNs as an explanation for the not completely additive effect of EPNs and *Hypoaspis aculeifer* Canestrini mites on thrips mortality, but they did not assess

EPN infection of the thrips themselves and so could not directly tie the mites to decreased EPN efficacy *per se*. Wilson and Gaugler (2004) correlated springtail and mite abundance in turfgrass with declining EPN infection of *Galleria mellonella*, which could have been due to predation by the microarthropods, especially since the correlations were only present when EPNs were surface-applied as opposed to subsurface-applied. However, *G. mellonella* infection was assessed under laboratory conditions, not in the field. Similar knowledge gaps exist for other interactions. Duncan et al. (2003) observed reduced EPN emergence from field-collected cadavers in which free-living bacterivore competitors were also present, but the effect of this competition on future insect infection remains unknown. Phoresy of infective juveniles has never been examined in the field, nor have indirect effects of ecosystem engineers ever been explicitly tested (but see Shapiro-Ilan and Brown, 2013). To date, the only field studies assessing the effects of soil organism interactions on EPN performance against an agricultural pest have been those investigating root chemical signaling (Ali et al., 2012; Hiltpold et al., 2010b) nematophagous fungi infection (Campos-Herrera et al., 2014; Duncan et al., 2007), and *Paenibacillus* encumbrance (Campos-Herrera et al., 2014; Duncan et al., 2013). Still, previous studies under artificial conditions suggest that many other ecological interactions could have important effects on EPN performance in soil.

A concerted effort to quantify the effect of other soil organism interactions with EPNs under field conditions will help determine whether or not soil biota need to be taken into account when deciding to use EPNs as a pest control tool. Several avenues of research show promise. First, correlative studies associating biotic (and abiotic) soil properties with native EPN occurrence or applied EPN efficacy have provided understanding of which soil properties are most important (Campos-Herrera et al., 2016; Campos-Herrera et al., 2013a), as well as the relative importance of biotic and abiotic factors. In addition to informing targets for soil management, such findings could eventually help managers predict EPN performance in advance, reducing the likelihood of one's opinion being soured by an ineffectual application on a suboptimal soil. These studies should take wider ranges of soil biota into account, and be continued in a wider variety of agricultural systems and management regimes.

Continuing with the topic of management, soil biota could also be incorporated to a greater extent into studies examining the effects of agricultural management practices on EPNs, with the goal of determining if the downstream consequences of different agronomic, cultural, and pest management practices on soil communities comprises part of their overall influence on EPNs. Studies in Florida citrus orchards have already taken this approach, linking increased abundance of EPN natural enemies as a result of specific management practices to reduced EPN occurrence and increases in pest activity (Campos-Herrera et al., 2014; Campos-Herrera et al., 2013b). However, more general and widespread management practices have yet to receive attention of this kind. For instance, tillage both reduces densities of earthworms and microarthropods in soils (House and Parmelee, 1985; Reeleder et al., 2006; Winter et al., 1990), and has varying effects on EPN infection rates, including positive effects on *Steinernema riobrave* Cabanillas, Poinar, & Raulston (Millar and Barbercheck, 2002). Whether the effects of tillage on EPNs are entirely due to its abiotic changes to the soil or partly mediated by tillage's effects on the soil community remains to be determined. Pesticide use is another example of a management practice with potential indirect effects on EPNs. The direct toxicity of pesticides to EPNs varies by active ingredient, with effects ranging from 100% EPN mortality to no apparent harm (Krishnayya and Grewal, 2002; Navarro et al., 2014b; Rovesti et al., 1988). EPNs can even be applied in the same tank mix as certain pesticides, such as imidacloprid, with which some EPNs have a synergistic effect on scarab grub mortality (Koppenhöfer et al., 2000a), due to imidacloprid paralyzing the grub and preventing them from grooming themselves to remove EPNs (Koppenhöfer et al., 2000b). However, pesticides also have significant, and usually negative, effects on other soil biota, such as arthropods

(Kunkel et al., 1999; Peck, 2009) and saprotrophic fungi (Gan and Wickings, 2017), effects which could again have downstream implications for EPNs.

As a potential avenue beyond correlative analysis for gauging the relative importance of abiotic soil conditions and biotic communities for EPNs, the 'reciprocal transplant' experimental design commonly used by ecologists to determine the relative importance of abiotic (*e.g.* environmental) and biotic (*e.g.* genotypic) factors in governing organism or community characteristics (Hedderson and Longton, 2008; Meola et al., 2014; Pascoal et al., 2012) could be repurposed. Sterilized soils from each of multiple sites could be placed in permeable field mesocosms at each site, left for sufficient time to allow the sites' native biota to colonize, and be inoculated with EPNs and a host of interest. However, the effects of one site's community on another's soil and vice versa, separate from their effects on EPNs, would have to be accounted for, as factors such as soil pH are known to affect interactions between EPNs and other organisms (Campos-Herrera et al., 2014).

Further beyond the 'soft' manipulation of a reciprocal transplant study, experiments directly manipulating soil communities, either by excluding or augmenting different taxa, are commonplace in soil ecology and provide insight into the effects of soil organisms on community dynamics and ecosystem processes (Crowther et al., 2013; Soong et al., 2016; Uvarov and Karaban, 2015). Thus, alone and in combination with correlative studies, these will likely also be useful for understanding soil organism effects on EPN performance. One limitation of this approach is that it can do little to separate the effects of individual taxa and interactions on EPN performance (Fig. 3), especially in exclusion experiments where manipulating specific taxonomic groups instead of broad size classes is difficult. A single taxonomic group or even single species could interact with EPNs in multiple, possibly contrasting ways, and the magnitude and direction of each

group's effects, whatever they happened to be, would likely be difficult to determine. However, the relative strength of positive interactions versus negative interactions would be determinable by the overall effect on EPN performance of a community's presence or increased abundance of specific groups or overall community diversity. For example, Khan et al. (2016) observed decreased survival of four EPN species in soils containing organisms compared with sterilized soils, suggesting that negative interactions with members of that soil community predominated, regardless of individual species-level interactions.

Future studies should also investigate differences in interactions between soil biota and EPNs that occupy different ecological niches. For instance, EPNs vary between species (and sometimes within species depending on context, see Griffin, 2015) both in their movement behavior ('ambush' versus 'cruise' foragers) and their preferred foraging depths (Ferguson et al., 1995; Kaya and Gaugler, 1993; Neumann and Shields, 2006), potentially resulting in different EPN species encountering different biotic communities, as abundance and species composition of many soil organism groups, from bacteria to springtails, vary by depth (Frey, 2015). The different sizes of each EPN species' IJ stage may also affect their vulnerability to predators of different sizes. Of the thirteen commercially available EPN species, the largest, *Steinernema longicaudum* Shen & Wang, is nearly double the length of the smallest, *Heterorhabditis indica* Poinar, Karunakar, & David (Adams and Nguyen, 2002).

One particular area of research that has exploded in prominence in recent years, both within general soil ecology (Oburger and Schmidt, 2016; Philippot et al., 2013; van Dam and Bouwmeester, 2016) and the study of EPNs (Ali et al., 2013; Hiltpold et al., 2015; Jaffuel et al., 2015; Willett et al., 2017, also see Section 3.1 above), is the role of root exudates and volatiles in shaping complex community interactions belowground. These rhizodeposits provide food for soil animals (Garrett et al., 2001; Pollierer et al., 2007) and shape microbial communities, likely both by releasing anti-microbial compounds and again providing food resources (Brant et al., 2006; Broeckling et al., 2008). Research over the last two decades has advanced our awareness of the chemical complexity of plant rhizodeposition (Massalha et al., 2017) and has also begun to elucidate the role of root-derived compounds as info-chemicals mediating communication among plants, free-living and symbiotic microbes, and animals including root herbivores and EPNs (Huang et al., 2014; Lareen et al., 2016; Rasmann et al., 2005). These efforts have generated interest in the potential for manipulating plant rhizosphere traits in order to enhance belowground biological control (Degenhardt et al., 2009). However, soilborne exudates, especially volatile emissions, are variable in space and time (Dessureault-Rompré et al., 2007Peñaloza et al., 2002) and notoriously difficult to track, and our understanding of the impact of rhizodeposits on many other soil animal taxa is still limited to only a handful of studies (Eisenhauer et al., 2012; Ruf et al., 2006; Strickland et al., 2012). Thus, it will be critical to expand this knowledge base in order to fully gauge the influence of rhizodeposit-mediated interactions on the biological control capacity of EPNs. We see these potential effects as particularly interesting to investigate further and potentially applicable to a wider range of agricultural and horticultural systems and pest management scenarios. This is because such effects would be potentially relevant in situations beyond those in which EPNs are directly attracted to roots as a result of herbivory, such as cases in which roots do not secrete EPN-attracting chemicals when consumed, or in which the pest targeted by EPNs is a soil-dwelling stage of an aboveground feeder rather than a root feeder that would trigger release of root volatiles.

Difficulties may arise in separating the effects of multiple interactions with a single organism. For example, the overall effect of an earthworm on EPNs may be a combination of phoresy, predation, and ecosystem engineering effects. In field settings, the effects of multiple species on each other as well as on EPNs further confound the issue to potentially unmanageable levels. However, inventive experimental designs and use of modern observational techniques such as molecular
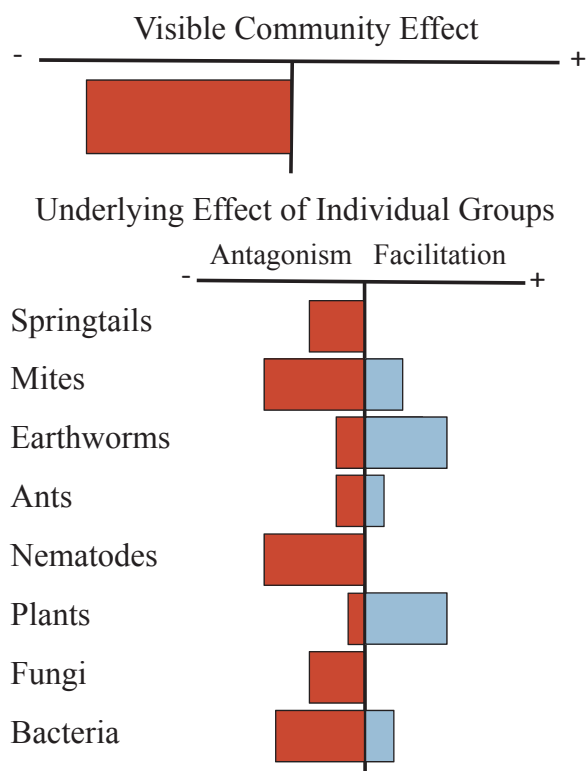

Fig. 3. Hypothetical positive (blue bars) and negative (red bars) effects of eight soil organism taxa on EPN performance contributing to and (perhaps) obscured by an overall community effect. Individual species within each taxon may have positive effects, negative effects, or varying degrees of both that contribute to their group's and the overall community's effect. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

gut content analysis, fatty acid analysis, real-time quantitative PCR, and stable isotope probing, which have proven excellent tools for characterizing belowground trophic ecology and species interactions in a wide variety of systems (Campos-Herrera et al., 2016, 2012b; Heidemann et al., 2014a, 2014b; Ruess and Chamberlain, 2010), should still provide information valuable to both pest managers and soil ecologists. Analytical procedures including path analysis, canonical correspondence, and structural equation modeling may also aid in teasing the directionality and relative importance of different biotic interactions between EPNs and complex soil communities (Campos-Herrera et al., 2012a).

7. Conclusions

EPNs interact with and are acted upon by a wide variety of soil organisms spanning the full breadth of soil's taxonomic diversity, and these interactions and their potential effects on EPN performance should be considered when studying the usefulness of EPNs against belowground pests. Despite the fact that EPNs can be applied to the soil in the same manner as a chemical pesticide, they are living organisms subject to all the biotic and abiotic pressures of the soil environment. Better understanding of these pressures, their relative importance, and the limits they may impose on EPNs will aid in successfully leveraging their pest control potential to its fullest extent.

Acknowledgements

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