

Potential for Entomopathogenic Nematodes in Biological Control: A Meta-Analytical Synthesis and Insights from Trophic Cascade Theory

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Abstract: Entomopathogenic nematodes (EPN) are ubiquitous and generalized consumers of insects in soil food webs, occurring widely in natural and agricultural ecosystems on six continents. Augmentative releases of EPN have been used to enhance biological control of pests in agroecosystems. Pest managers strive to achieve a trophic cascade whereby natural-enemy effects permeate down through the food web to suppress host herbivores and increase crop production. Although trophic cascades have been studied in diverse aboveground arthropod-based systems, they are infrequently investigated in soil systems. Moreover, no overall quantitative assessment of the effectiveness of EPN in suppressing hosts with cascading benefits to plants has been made. Toward synthesizing the available but limited information on EPN and their ability to suppress prey and affect plant yield, we surveyed the literature and performed a meta-analysis of 35 published studies. Our analysis found that effect sizes for arthropod hosts as a result of EPN addition were consistently negative and indirect effects on plants were consistently positive. Results held across several different host metrics (abundance, fecundity and survival) and across measures of plant performance (biomass, growth, yield and survival). Moreover, the relationship between plant and host effect sizes was strikingly and significantly negative. That is, the positive impact on plant responses generally increased as the negative effect of EPN on hosts intensified, providing strong support for the mechanism of trophic cascades. We also review the ways in which EPN might interact antagonistically with each other and other predators and pathogens to adversely affect host suppression and dampen trophic cascades. We conclude that the food web implications of multiple-enemy interactions involving EPN are little studied, but, as management techniques that promote the long-term persistence of EPN are improved, antagonistic interactions are more likely to arise. We hope that the likely occurrence of antagonistic interactions in soil food webs should stimulate researchers to conduct field experiments explicitly designed to examine multiple-enemy interactions involving EPN and their cascading effects to hosts and plants.

Key words: biological control, crop yield, EPN, food-web dynamics, intraguild predation, interspecific competition, meta-analysis, multiple-enemy interactions, pest suppression, trophic cascade.

The objective of biological control in production agriculture is to maximize the effectiveness of the natural-enemy complex in suppressing pests and ultimately in enhancing crop yield (DeBach and Rosen, 1991; Norris et al., 2003). Thus, pest managers seek a strong trophic cascade whereby natural-enemy effects permeate down through the food web to increase crop production (DeBach and Rosen, 1991; Rosenheim et al., 1995; Polis et al., 2000; Snyder et al., 2005). In an ecological context, “trophic cascades” are predator-prey interactions that indirectly alter the abundance, biomass or productivity of a community across more than one trophic link in a food web (Carpenter and Kitchell, 1993; Pace et al., 1999; strict definitions are concerned only with biomass responses, see Polis et al., 2000; Shurin et al., 2002). Many factors, however, can alter the strength of trophic cascades and the extent to which natural-enemy effects on lower trophic levels either attenuate or propagate (Schmitz et al., 1997, 2000; Halaj and Wise, 2001; Finke and Denno, 2004; Gruner, 2004; Borer et al., 2005; Finke and Denno, 2006). These factors include multiple natural-enemy interactions (e.g., intraguild predation and predator complementarity), the peculiarities (i.e., identity) of predators or parasitoids, the spatial and temporal dynamics of predator-prey and parasite-

host interactions, interspecific competition, the presence of alternative prey, habitat structure, physical disturbance, and the quantity or quality of abiotic resources (Hochberg, 1996; Chalcraft and Reseraris, 2003; Borer et al., 2005; Finke and Denno, 2005; Wilby et al., 2005; Casula et al., 2006; Finke and Denno, 2006; Schmitz, 2007; Otto et al., 2008).

For example, in the arena of biological control, a longstanding debate considers whether better pest suppression is achieved by releasing or encouraging one vs. several natural enemies (DeBach and Rosen, 1991; Rosenheim, 1998; Denoth et al., 2002; Cardinale et al., 2003; Stiling and Cornelissen, 2005; Snyder et al., 2006). The issue remains controversial and system-specific because there is extensive evidence both for (Heinz and Nelson, 1996; Riechert and Lawrence, 1997; Symondson et al., 2002; Snyder et al., 2006) and against (Rosenheim et al., 1993, 1995; Snyder and Wise, 1999; Snyder and Ives, 2001; Prasad and Snyder, 2004) the proposition that multiple enemies are more effective than single enemy species in reducing pest populations. The key to understanding when and where a natural-enemy complex promotes or relaxes prey suppression likely lies in the sign and strength of interactions among the predators themselves. For example, multiple enemies can interact synergistically to enhance prey suppression (Soluk, 1993; Losey and Denno, 1998) additively (Chang, 1996; Straub and Snyder, 2006) or antagonistically, whereby they consume each other (intraguild predation) or interfere with each other’s capture success (Rosenheim et al., 1995; Finke and Denno, 2003; Prasad and Snyder, 2004). In some cases, however, complex-structured habitats provide spatial refuges from intraguild preda-

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tion and increase the effectiveness of the predator complex (Finke and Denno, 2002; Denno and Finke, 2006; Finke and Denno, 2006). Such evidence provides encouragement to pest managers that the effectiveness of the natural-enemy complex can be enhanced via habitat manipulations (Landis et al., 2000; Gurr et al., 2004).

Most studies of multiple-enemy interactions have assessed their consequences for prey density or parasitism rate but they have not examined how such interactions propagate to enhance or reduce plant biomass or yield, a question of paramount importance in agriculture and biological control. Importantly, there are some studies showing that the effects of multiple-enemy interactions cascade down to basal resources with variable consequences for plant biomass and yield. For instance, intense intraguild predation in a system can relax prey suppression and dampen the potential cascading effects of enemies on plant biomass (Finke and Denno, 2005). In contrast, if enemies complement one another and thus act in concert to suppress prey, enemy effects can cascade to primary producers, resulting in increased yield (Snyder and Wise, 2001; Casula et al., 2006).

The great majority of terrestrial studies testing evidence for enemy-propagated trophic cascades have focused on arthropods or vertebrates as predators in aboveground food webs (Rosenheim et al., 1995; Schmitz et al., 2000; Halaj and Wise, 2001; Shurin et al., 2002; Snyder et al., 2005). Soil-dwelling organisms comprising belowground food webs have been virtually ignored (but see Mikola and Setälä, 1998; Wardle et al., 2005). Nematodes, despite their prevalence in both agricultural habitats and natural systems (Sohlenius, 1980; Sasser and Freckman, 1987; Stanton, 1988), are highly under-represented in studies of population and food-web dynamics and in particular in those investigating trophic cascades (Stuart et al., 2006). A notable exception involves the entomopathogenic nematode (EPN) *Heterorhabditis mavelatus* and its ghost moth host *Hepialis californicus* that bores in the roots of bush lupine (*Lupinus arboreus*) in sand-dune habitats of coastal California (Strong et al., 1996, 1999; Preisser, 2003; Ram et al., 2008a). In this natural system, soil moisture promotes EPN survival, which inflicts widespread mortality on root borers that in turn releases bush lupines from herbivory. Under this scenario, bush lupines thrive, providing a clear example of how EPN can induce a trophic cascade in a natural, belowground food web.

Entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae have been used to suppress populations of pest insects in a variety of agroecosystems, and in several cases their positive effects on crop yield have been shown (Lewis et al., 1998; Mráček, 2002; Georgis et al., 2006). Thus, there is evidence for strong trophic cascades initiated by EPN in

agroecosystems. Moreover, EPN are known to interact antagonistically with other competitors, such as entomopathogenic fungi (Barbercheck and Kaya, 1991), as well as predaceous nematodes, arthropods, parasitoids and nematophagous fungi (Kaya and Koppenhöfer, 1996; Sher et al., 2000; Mráček, 2002; Stuart et al., 2006), and soil factors can influence EPN-host interactions (Portillo-Aguilar et al., 1999; Gruner et al., 2007). However, the literature on the subject is widely scattered, and we know little about how EPN interact with other natural enemies in the system and habitat structure (e.g., soil characteristics) to affect prey suppression with cascading effects to plants. Based on our knowledge of aboveground arthropod food webs, such information is critical for understanding when and under what conditions EPN might act as effective biological control agents.

Toward synthesizing the available information on EPN and their ability to suppress prey and affect plant damage and yield, we surveyed the literature and performed a meta-analysis of the data. Meta-analysis is a statistical method that combines results from independently conducted experiments (Gurevitch and Hedges, 1999). Meta-analysis allows for the estimation of the magnitude of effect sizes (e.g., log ratios) across studies and can be used to determine if the overall effect (EPN augmentation in this case) is significantly different from zero. Our study was designed to test the effect of EPN on lower trophic levels. Specifically, we calculated effect sizes to quantitatively assess the impacts of EPN on: (i) herbivore/pest density or mortality, (ii) herbivore damage, or plant growth, biomass, survival or yield, and (iii) the strength of the correlation of these two factors. In line with trophic cascade theory, we hypothesized that EPN additions should have net negative effects on host population parameters and net positive effects on plants. We also expected these effects to be negatively correlated, such that stronger host suppression leads to more positive cascading effects on plants. We then review the major factors expected to attenuate or enhance the strength of cascading interactions based on our limited knowledge of soil ecology and more extensive ecological experimentation from aboveground systems. We also consider how the unique life history traits of EPN (e.g., restricted dispersal ability and foraging strategies) might influence the spatial coupling of EPN-host interactions and thus the probability for trophic cascades. Altogether, our meta-analytical approach aims to integrate our current understanding of the important role entomopathogenic nematodes play as drivers in food-web dynamics and biological control.

MATERIALS AND METHODS

Criteria for identifying and selecting studies for meta-analysis: Published studies testing for EPN indirect impacts on plants were compiled using several different

approaches. First, we surveyed the literature from previous reviews of experimental studies where EPN were supplemented to a system or not (e.g., Lewis et al., 1998; Mráček, 2002). Next, we used the database Web of Science to identify all studies that cited EPN review papers. Last, we performed keyword searches on Web of Science pairing ‘[entomog* or entomopath*] and nematode*’ with various combinations of the following terms: prey suppression, pest density, biological control, and plant biomass, damage, or crop yield. Searches revealed numerous experimental studies with quantitative impacts on arthropod hosts and possible indirect effects on plants. Because meta-analysis requires quantitative data on experimental outcomes (minimally, means; ideally, variances and sample sizes), published studies with incomplete designs or qualitative response variables were discarded.

Additionally, we applied the following a priori conditions for the inclusion of studies in our analysis: (i) EPN manipulated at one or more application levels, with an appropriate control lacking EPN addition; (ii) experiments performed in the field or in large mesocosms (e.g., glasshouse)—laboratory microcosm experiments were excluded; (iii) EPN applied only to soil environments (i.e., experimental foliar sprays were excluded); (iv) some measure of plant above- or below-ground biomass, production, yield, damage or mortality reported. These criteria narrowed considerably the number of studies that could be included in the analyses, and they limit our inference to broad trends. We also included three studies in which primary producers were commercial fungi and compared these results with plants for any strong deviations. Given the above criteria, our search resulted in a total of 35 studies of EPN indirect effects on plants or fungi extracted from 22 publications (see Table 1 for a list of all studies used in our meta-analysis).

We defined a study as a temporally and spatially distinct experiment with consistent controls. Multiple studies could be reported from within one publication if the same experimental treatments were performed in different years or in multiple, independent locations with differing physical and/or biological conditions. When multiple response measures were reported over time from the same experiment, we used the last temporal sample. Numerous studies used multiple EPN application rates and/or crossed these treatments with additional factors (e.g., fertilization, watering). When multiple application levels were used for any EPN treatment, we used results from the treatment combinations with the highest application rates. We assessed additional treatment combinations case by case. In studies where treatments were immaterial to our study, we excluded inappropriate levels (e.g., treatments lacking hosts). In cases where no a priori decisions could be made (e.g., application of EPN by drip irrigation vs. soil

drenches), we calculated effect sizes for each and used the mean value for the study.

We accepted the following treatment response categories: abundance or fecundity (hosts); biomass, damage, growth or yield (plants); and percent mortality or survival (both hosts and plants). Log response ratios could be constructed if variables were measured with the same units in any treatment comparison. Where multiple acceptable measures were reported, or reported for different life history stages (larvae and adults), we included all acceptable measures and calculated mean standardized response ratios for each study. Data were extracted from tables or digitized figures using the GrabIt! XP add-in for Microsoft Excel (Datatrend Software Inc.).

Calculation of effect sizes: The impacts of EPN on host and plant variables were assessed by calculating an effect size for each pair-wise treatment (EPN addition and control). Because it was necessary to compare responses using different response measurements and units, we standardized comparisons among experiments using log response ratios ($\ln[\text{EPN treatment/control}]$). The log response ratio (*LRR*) is one of the most commonly used effect metrics in ecological meta-analysis (Hedges et al., 1999; Lajeunesse and Forbes, 2003). Another commonly used metric, Hedge’s *d*, requires a measure of sample variability and weights individual studies by this variance. This requirement would disqualify many studies that were otherwise appropriate but did not report variability (e.g., % mortality). Log response ratios require only the means of any measurement for treatment and control groups. Moreover, distributions of log ratios typically conform to normality assumptions, making them suitable for a wide range of parametric statistical tests (Hedges et al., 1999).

The control group was designated as the ambient environment, whereas the treatment group received supplemental EPN. Thus, we hypothesized that EPN addition should result in negative effect sizes for arthropod host population abundance, fecundity or survival, and these negative host impacts should result in positive indirect effects on plant biomass, growth, yield or survival. Negative population variables, such as mortality or plant damage, were multiplied by (–1) to be directly comparable with positive population effect sizes.

Analyses of effect sizes: The aggregate univariate *LRR* for plant and insect host responses were tested against the null hypothesis that effects did not differ from zero. We used simple 1-sided, one-sample t-tests, expecting a priori that host effects would be less than zero and plant responses would be greater than zero, as expected by trophic-cascade theory. We restricted these tests to the aggregate summaries because of sample size limitations within smaller response categories (e.g., host mortality $n = 1$). We also examined the bivariate association be-

tween host and plant *LRR*, fitting a linear regression to this relationship. Thus, we assessed if the strength of the adverse effect of EPN on hosts was associated with an increasing positive effect on plant survival or yield. All analyses were run in the R package (R Development Core Team, 2008).

RESULTS

Our search yielded a total of 35 studies of EPN indirect effects on plants or fungi extracted from 22 publications. In these studies, a range of EPN species were added as augmentative treatments in concentrations up to 500,000 individuals/m². A variety of steinernematid (*S. feltiae*, *S. carpocapsae*, *S. riobrave*, *S. scapterisci*) and heterorhabditid (*H. bacteriophora*, *H. marelatus*, *H. sp.*) nematodes were added to suppress a diversity of insects in four orders (Table 1).

As hypothesized from trophic-cascade theory, effect sizes for arthropod hosts as a result of EPN addition were consistently negative (overall 1-sided $t = 7.18$, $df = 32$, $p < 0.0001$) and indirect effects on plants were consistently positive (overall 1-sided $t = -5.1593$, $df = 22$, $p < 0.0001$). These results held across several different metrics for hosts (abundance, fecundity, survival and - [mortality]; Fig. 1A) and across numerous plant parameters as well (biomass, growth, yield, survival, - [damage], and - [mortality]; Fig. 1B). However, sample sizes for some response categories were too small for statistical analysis. The two studies that measured yield of fungi (Grewal and Richardson, 1993; Grewal et al., 1993) showed similar impacts on hosts but minimal effects on mushroom yield (average $LRR_{\text{host}} = -2.39$; $LRR_{\text{plant}} = 0.024$) and did not respond as did the bulk of plant studies. Therefore, these studies were not included in analyses of plant responses to EPN additions.

The relationship between plant and host effect size was strikingly and significantly negative, as expected by the mechanisms underlying trophic cascades ($R^2 = 0.39$, $df = 18$, $p = 0.003$; Fig. 2). That is, the measured positive impact on plant responses generally increased as the negative effect of EPN on hosts strengthened.

DISCUSSION

Evidence for EPN-generated trophic cascades

Results of our meta-analysis of experimental field studies provide strong evidence that EPN can reduce populations of their insect hosts by adversely affecting host fecundity and survival (Fig. 1A). Our analysis also shows that EPN effects often cascade to benefit basal resources in both natural and agricultural systems (Fig. 1B). For example, applications of *Steinernema feltiae* effectively reduced populations of the cabbage root flies *Delia radicum* and *D. floralis*, which in turn resulted in a two- to three-fold increase in cauliflower yield (Schroeder et al., 1996; Vänninen et al., 1999). How-

ever, EPN do not always promote trophic cascades, and reductions in plant damage do not always translate into increased crop yield. Applications of *Steinernema carpocapsae*, for instance, can reduce carrot weevil damage by 59% (Belair and Boivin, 1995), but such EPN applications do not necessarily result in increased carrot survival or yield (Miklasiewicz et al., 2002). Moreover, there are cases in which applications of EPN in cropping systems fail to inflict significant host mortality or enhance yield (Mráček, 2002; Georgis et al., 2006).

Thus, we can ask what factors influence the probability for EPN-induced trophic cascades. The answer likely lies in unraveling the complex biotic interactions involving EPN that exist in soil-based food webs and in elucidating how abiotic factors mediate the strength and spatial extent of these biotic interactions. In above-ground terrestrial systems, multiple-enemy interactions (e.g., omnivory and intraguild predation), resource competition, habitat structure and physical disturbance are known to alter the impact of arthropod enemies on herbivores and their indirect effects on plants (Fagan, 1997; Rosenheim, 1998; Chalcraft and Reserants, 2003; Finke and Denno, 2005; Casula et al., 2006; Finke and Denno, 2006; Snyder et al., 2006; Schmitz, 2007). We lack the field studies needed for a quantitative review of the interactive effects of multiple EPN species, or of the interactions among EPN and other soil-dwelling predators, pathogens and competitors (all factors which could diminish potential EPN effects on hosts and dampen trophic cascades) while also measuring impacts on primary producers. Thus, we now explore what characteristics of soil ecosystems might contribute to variation in the strength of EPN-induced trophic cascades and highlight areas of research needed to understand these complex food-web interactions.

Antagonistic interactions involving EPN and the likelihood for trophic cascades

A diverse array of organisms in multiple trophic levels can influence the abundance and distribution of EPN in soil communities (Stuart et al., 2006) and thus their potential to kill hosts and initiate trophic cascades. From the perspective of an EPN, a broad range of host and non-host arthropods, competitors, predators and pathogens can influence their survival (Epsky et al., 1988; Sayre and Walter, 1991; Timper et al., 1991; Koppenhöfer et al., 1996; Kaya, 2002; Stuart et al., 2006; Karagoz et al., 2007). However, specific interactions among these component players are poorly studied, even though omnivory is considered widespread in soil communities, potentially resulting in both direct and indirect impacts on EPN (Walter, 1988; Walter et al., 1989; de Ruiter et al., 1996; Stuart et al., 2006). In general, omnivory is thought to dampen top-down effects on prey populations, for instance when predators

TABLE 1. Summary of studies, EPN species added, affected insect host species and plants, and log response ratios (*LRR*) of effect sizes. In cases where multiple studies are used from single reports, the notes column defines the reason for treating them as independent estimates.

Publication	EPN	Insect host	Host <i>LRR</i>	Plant	Plant <i>LRR</i>	Notes
Belari and Boivin, 1995	<i>S. carpocapsae</i>	<i>Listronotus oregonensis</i> (Coleoptera: Curculionidae)	-1.133	carrot	0.898	1989 experiment
Belair and Boivin, 1995	<i>S. carpocapsae</i>	<i>Listronotus oregonensis</i> (Coleoptera: Curculionidae)	-0.693	carrot	0.209	1990 experiment
Canhilar and Carner, 2006	<i>S. carpocapsae</i> , <i>Heterorhabditis</i> sp.	<i>Melittia cucurbitae</i> (Lepidoptera: Sesiidae)	NR	squash	0.989	1997 Trial 1
Canhilar and Carner, 2006	<i>S. carpocapsae</i> , <i>Heterorhabditis</i> sp.	<i>Melittia cucurbitae</i> (Lepidoptera: Sesiidae)	NR	squash	0.924	1997 Trial 2
Canhilar and Carner, 2006	<i>S. carpocapsae</i> , <i>Heterorhabditis</i> sp.	<i>Melittia cucurbitae</i> (Lepidoptera: Sesiidae)	NR	squash	0.555	1997 Trial 3
Canhilar and Carner, 2006	<i>S. carpocapsae</i> , <i>S. feltiae</i>	<i>Melittia cucurbitae</i> (Lepidoptera: Sesiidae)	NR	squash	1.556	1998 Trial 1
Canhilar and Carner, 2006	<i>S. riobrave</i> , <i>S. feltiae</i>	<i>Melittia cucurbitae</i> (Lepidoptera: Sesiidae)	NR	squash	1.423	1998 Trial 2
Canhilar and Carner, 2006	<i>S. riobrave</i> , <i>S. feltiae</i>	<i>Melittia cucurbitae</i> (Lepidoptera: Sesiidae)	-1.869	squash	1.258	1999 Trial 1
Canhilar and Carner, 2006	<i>S. riobrave</i>	<i>Melittia cucurbitae</i> (Lepidoptera: Sesiidae)	-0.511	squash	1.057	1999 Trial 2
Capinera et al., 1988	<i>S. feltiae</i>	<i>Agrotis ipsilon</i> (Lepidoptera: Noctuidae)	NR	corn	0.614	—
Cottrell and Shapiro-Ilan, 2006	<i>S. riobrave</i> , <i>S. carpocapsae</i>	<i>Synanthedon exitiosa</i> (Lepidoptera: Sesiidae)	NR	peach	1.085	—
Glazer and Goldberg, 1993	<i>H. bacteriophora</i>	<i>Maladera matrida</i> (Coleoptera: Scarabaeidae)	-0.589	peanut	0.539	1989 experiment
Glazer and Goldberg, 1993	<i>S. carpocapsae</i>	<i>Maladera matrida</i> (Coleoptera: Scarabaeidae)	-0.673	peanut	0.762	1991 experiment
Grewal et al., 1993	<i>S. feltiae</i>	<i>Lycoriella mali</i> (Diptera: Sciaridae)	-2.797	mushroom	0.033	—
Grewal and Richardson, 1993	<i>S. feltiae</i>	<i>Lycoriella auripila</i> (Diptera: Sciaridae)	-1.977	mushroom	0.0160	—
Legaspi et al., 2000	<i>S. riobrave</i>	<i>Eoreuma loftini</i> (Lepidoptera: Pyralidae)	0.838	sugarcane	-0.387	—
Levine and Oloumi-Sadeghi, 1992	<i>S. carpocapsae</i>	<i>Agrotis ipsilon</i> (Lepidoptera: Noctuidae)	NR	corn	1.197	—
Loya and Hower, 2002	<i>H. bacteriophora</i>	<i>Sitona hispidulus</i> (Coleoptera: Curculionidae)	-1.417	alfalfa	0.237	—
Miklasiewicz et al., 2002	<i>S. carpocapsae</i> , <i>H. bacteriophora</i>	<i>Listronotus oregonensis</i> (Coleoptera: Curculionidae)	0.234	parsley	0.032	—
Morse and Lindegren, 1996	<i>S. carpocapsae</i>	<i>Asynonychus godmani</i> (Coleoptera: Curculionidae)	-1.535	orange	0.817	—
Mráček et al., 1993	<i>S. feltiae</i>	<i>Otiorynchus sulcatus</i> (Coleoptera: Curculionidae)	NR	rhododendron	0.950	—
Parkman et al., 1994	<i>S. scapterisci</i>	<i>Scapteriscus</i> sp. (Orthoptera: Grylotalpidae)	-0.403	grass (golf course)	0.484	—
Preisser, 2003	<i>H. marelatus</i>	<i>Hepialus californicus</i> (Lepidoptera: Hepialidae)	-0.656	bush lupine	0.395	—
Preisser and Strong, 2004	<i>H. marelatus</i>	<i>Hepialus californicus</i> (Lepidoptera: Hepialidae)	-0.128	bush lupine	0.199	—
Schroeder et al., 1996	<i>S. feltiae</i> , <i>S. riobrave</i> , <i>H. bacteriophora</i> , <i>S. carpocapsae</i>	<i>Delia radicum</i> (Diptera: Anthomyiidae)	-0.267	cabbage	0.139	Trial 1 greenhouse
Schroeder et al., 1996	<i>S. carpocapsae</i> , <i>H. bacteriophora</i> , <i>S. feltiae</i>	<i>Delia radicum</i> (Diptera: Anthomyiidae)	-0.884	cabbage	0.243	Trial 2 greenhouse
Schroeder et al., 1996	<i>S. feltiae</i>	<i>Delia radicum</i> (Diptera: Anthomyiidae)	-3.044	cabbage	0.467	Trial 3 greenhouse
Schroeder et al., 1996	<i>S. feltiae</i>	<i>Delia radicum</i> (Diptera: Anthomyiidae)	NR	cabbage	0.450	Field experiment
Shapiro et al., 1999	<i>S. carpocapsae</i>	<i>Agrotis ipsilon</i> (Lepidoptera: Noctuidae)	NR	corn	2.063	—
Shields et al., 1999	<i>H. bacteriophora</i>	<i>Otiorynchus ligustici</i> (Coleoptera: Curculionidae)	-1.807	alfalfa	0.844	—
Strong et al., 1999	<i>H. marelatus</i>	<i>Hepialus californicus</i> (Lepidoptera: Hepialidae)	NR	bush lupine	0.241	—
Vänninen et al., 1999	<i>S. feltiae</i>	<i>Delia radicum</i> (Diptera: Anthomyiidae)	-0.146	cabbage	0.199	1987 experiment
Vänninen et al., 1999	<i>S. feltiae</i>	<i>Delia radicum</i> (Diptera: Anthomyiidae)	NR	cabbage	0.012	1990 experiment
West and Vrain, 1997	<i>S. feltiae</i> , <i>S. carpocapsae</i>	<i>Actebia fennica</i> (Lepidoptera: Noctuidae)	-2.0123	black spruce	1.899	1993 experiment
West and Vrain, 1997	<i>S. feltiae</i> , <i>S. carpocapsae</i>	<i>Actebia fennica</i> (Lepidoptera: Noctuidae)	-0.453	black spruce	0.398	1994 experiment

consume one another in addition to their shared prey (Fagan, 1997; Finke and Denno, 2003).

The abundance of nematophagous fungi, bacteria, protozoa, predaceous nematodes, mites, collembolans

and other micro-arthropods in the soil, and the high rates of mortality they can impose in the laboratory, suggests that these consumers might generate significant negative impacts on EPN populations in the field

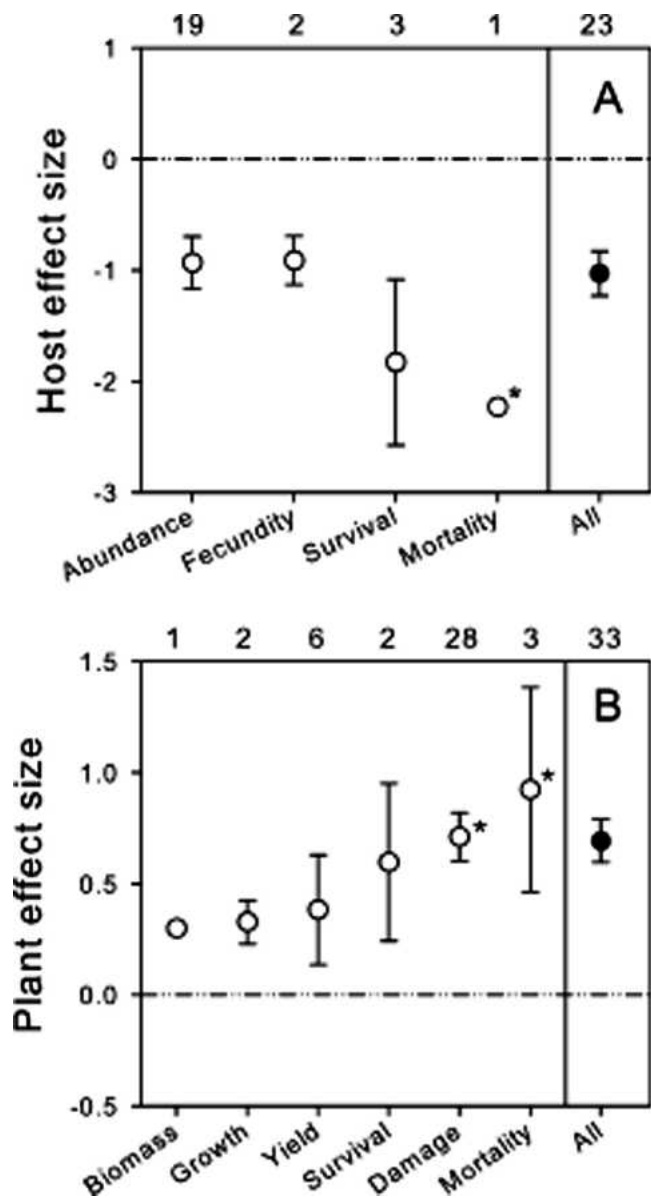


FIG. 1. Log response ratio effect sizes for EPN treatments on (A) host insect and (B) plant response categories. Effect sizes are presented as means (\pm SE) across independent studies that measure variables within the same response category, with sample sizes given above the top margin for each value. Averages across studies are presented with filled symbols (sample sizes do not sum because some studies reported multiple response categories). Asterisks denote effects that were adjusted (multiplied by -1) for the negative expectation for those variables (e.g., mortality expectation adjusted to same sign as survival). The dashed line shows the null hypothesis of no effect.

(Epsky et al., 1988; Gilmore and Potter, 1993; Kaya and Koppenhöfer, 1996; Stuart et al., 2006). However, there are surprisingly few manipulative studies involving EPN and their predators and pathogens in the field. In one experiment, infective juveniles placed in sterilized soil survive better than in “raw soil,” suggesting that predators and pathogens in non-treated soil adversely affect EPN survival (Timper et al., 1991; Kaya and Koppenhöfer, 1996). However, determining which specific an-

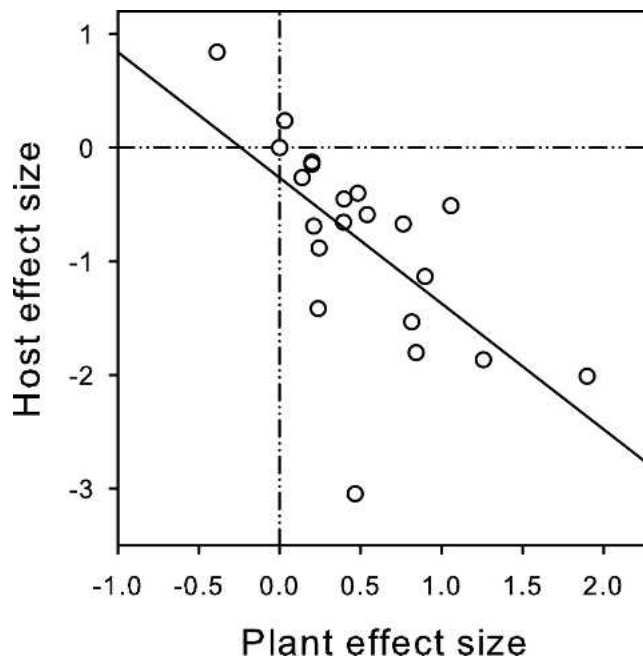


FIG. 2. Relationship between plant and host log response ratios (*LRR*) in EPN-addition studies in which both effects were reported. The signs of *LRR* with negative expectation (e.g., plant damage) were adjusted by multiplying each *LRR* by (-1). The solid line is the best fit linear regression ($LRR_{\text{host}} = -0.27 - 1.11[LRR_{\text{plant}}]$, $R^2 = 0.39$, $df = 18$, $p = 0.003$), and the dashed lines show the null hypothesis of no effect.

tagonists are responsible for reducing EPN density has proved challenging in a field setting.

Mites and collembolans can consume *Steinernema* and *Heterorhabditis* species in simple laboratory microcosms, an effect which relaxes EPN-inflicted mortality on hosts (Gilmore and Potter, 1993; Kaya and Koppenhöfer, 1996). However, in more complex-structured mesocosms with turf grass added, the collembolan *Folsomia candida* did not reduce the ability of *Steinernema glaseri* to kill larvae of the Japanese beetle, *Popillia japonica*. This study highlights how the structural complexity of the habitat can provide spatial refuges from predation and enhance overall top-down effects on hosts, a phenomenon shown in aboveground systems (Denno and Finke, 2006; Finke and Denno, 2006).

Nematophagous fungi, including nematode-trapping fungi and endoparasitic fungi, are among the best-studied natural enemies of EPN (Gray, 1988). Such fungi can kill EPN species in simple laboratory microcosms (Timper and Kaya, 1992; Kaya and Koppenhöfer, 1996; Karagoz et al., 2007). For example, nematode-trapping fungi protected mole crickets (*Scapteriscus borellii*) from infection by the EPN *Steinernema feltiae* in laboratory trials (Fowler and Garcia, 1989). However, even strong numerical responses of nematode-trapping fungi can be ineffective at suppressing the enormous numbers of EPN juveniles emerging from infected hosts (Jaffee and Strong, 2005; Jaffee et al., 2007). Thus, the explosive emergence of EPN from host cadavers

can swamp soil-dwelling predators and destabilize predator-prey interactions. Clearly, the conditions that promote EPN control by nematophagous fungi and other enemies are in need of more study (Kaya and Koppenhöfer, 1996).

Intraguild predation (sensu Polis et al., 1989), whereby one predator species (intraguild predator) consumes another (intraguild prey), can severely relax predation pressure on shared prey or host species at lower trophic levels and dampen trophic cascades (Schmitz et al., 2000; Halaj and Wise, 2001; Finke and Denno, 2004; Gruner, 2004; Finke and Denno, 2006). Such intraguild interactions involving EPN are poorly studied, but may prove to be a significant source of antagonism (Kaya and Koppenhöfer, 1996). For instance, protozoan parasites (microsporidians in the genera *Pleistophora* and *Nosema*) are pathogenic to both EPN and their hosts (Veremchuk and Issi, 1970). In this case of intraguild predation, however, it is not known if infected EPN (intraguild prey) are less pathogenic to their hosts.

Intraguild predation also occurs between the EPN *Steinernema carpocapsae* and the parasitic wasp *Diglyphus begini*, both of which attack larvae of the leafmining fly *Liriomyza trifolii* on chrysanthemums (Sher et al., 2000). Specifically, the EPN infects the host fly but also infects larvae of *D. begini*, and the presence of nematodes in mines decreases the chance of wasp survival to adulthood. Nonetheless, using both the parasitoid and EPN together results in greater overall mortality on leafminers than either agent inflicts alone, in part because the parasitoid avoids EPN-infected hosts for oviposition.

The occurrence of intraguild predation and interference among biological control agents has generated controversy over whether better pest suppression is achieved by one or multiple natural enemies (Rosenheim, 1998; Denoth et al., 2002; Snyder et al., 2006). In the above case involving *S. carpocapsae* and the parasitoid *D. begini*, intraguild predation was insufficient to reduce survival of their shared leafminer host. Similarly, the use of *Heterorhabditis marelatus* to suppress Colorado potato beetle larvae had no effect on the parasitism rate or emergence of the common larval parasitoid *Myiopharus doryphorae* from beetle larvae (Armer et al., 2004). Both of these examples suggest that EPN and insect parasitoids complement one another to suppress their host in additive fashion. As a cautionary note, both examples involve interactions between EPN and insect parasitoids in the aboveground food web and should not be taken as representative of the potential for intraguild predation in the belowground soil community, especially between EPN and pathogens.

Two or more EPN species often occur sympatrically, commonly infect the same host individual, and thus have the potential to compete interspecifically for a shared host resource and adversely influence each oth-

er's survival (Kaya and Koppenhöfer, 1996; Stuart et al., 2006). The possibility for exploitative competition between two EPN is enhanced because there is little evidence that infective juvenile EPN avoid hosts previously infected by another genus or species of EPN (Lewis et al., 2006). In the laboratory, both intra-specific and inter-specific competition reduces EPN juvenile production, and inter-specific competition can cause local extinction of a nematode species (Alatorre-Rosas and Kaya, 1990; Kaya and Koppenhöfer, 1996). For example, in co-infected laboratory hosts, steinernematids usually exclude heterorhabditids, although the competitive outcome depends on inoculum size, colonization ratio and relative development rate. Studies of inter-specific competition between steinernematid species show that two species can co-infect a host individual, but that one EPN species will ultimately prevail to reproduction (Alatorre-Rosas and Kaya, 1990; Kaya and Koppenhöfer, 1996). However, multiple species can coexist in an environment if they possess different foraging strategies (e.g., ambushers vs. cruisers, Lewis et al., 2006), exhibit different levels of host specificity, exploit different spatial niches in the soil, or occur in aggregated distributions (Kaya and Koppenhöfer, 1996; Gruner et al. unpubl. data). Such species-specific differences in behavior and foraging niche may explain why various combinations of EPN species result in additive mortality of scarab beetle larvae (Choo et al., 1996; Koppenhöfer et al., 2000), suggesting weak interspecific competition in these cases. However, free-living bacterivorous nematodes can compete with the entomopathogenic nematodes in the insect host cadaver and may be significant regulators of nematode densities (Duncan et al., 2003a). Release of the exotic EPN *Steinernema riobrave* to control the root weevil *Diaprepes abbreviatus* resulted in the partial displacement of endemic EPN (Duncan et al., 2003b), but *S. riobrave* reproduced and persisted poorly in part due to competition with bacterivorous nematodes (Duncan et al., 2003a).

Altogether, there is extensive evidence that antagonistic interactions involving EPN can adversely affect their ability to suppress host populations. However, the EPN literature, unlike that for aboveground arthropod-based food webs (Rosenheim et al., 1995; Snyder and Wise, 1999; Finke and Denno, 2004; Prasad and Snyder, 2004), provides too few studies to examine quantitatively how multiple-enemy and competitive interactions might cascade to affect plant biomass or yield. Increased production or yield, in essence, is the ultimate objective of research striving for enhanced pest control. From the limited number of suggestive studies that exist, EPN-pathogen or EPN-predator interactions are likely to affect the extent that top-down effects will cascade to basal resources, at least at a local spatial scale.

The spatial dynamics of EPN-host interactions and trophic cascades

The ability of natural enemies to suppress prey/host populations is intimately linked to spatial processes and metapopulation dynamics. For example, the ability of predators to disperse and aggregate in areas of increasing prey density are considered important attributes for effective prey suppression and biological control (Kareiva, 1990; Murdoch, 1990; Döbel and Denno, 1994), although the presence of alternate prey and intraguild predation can certainly affect the strength of a predator's numerical response (Lester and Harmsen, 2002). The infective juveniles (IJ) of EPN, however, have limited dispersal ability (Kaya and Gaugler, 1993; Lewis et al., 2006). IJ are highly susceptible to desiccation and are dependent on critical thresholds of soil moisture for movement and survival, which limits their effective dispersal to wet periods and restricts their distribution to moist refuges under plants or deeper soil strata (Kaya and Gaugler, 1993; Preisser et al., 2006; Stuart et al., 2006; Ram et al., 2008b). However, by hitching rides on non-host organisms (phoresy) and by using chemical cues from hosts or damaged plants to locate uninfected hosts, infective juveniles can extend their effective foraging ambit and colonizing ability (Lewis et al., 1992; Rasmann et al., 2005; Eng et al. 2005; Lewis et al., 2006).

Given their limited mobility and inability to persist locally due to desiccation and other factors, it is not surprising that EPN populations are patchy in nature and likely exist as metapopulations (Stuart and Gaugler, 1994; Wilson et al., 2003; Stuart et al., 2006). In natural systems, EPN populations expand and retract to spatial refuges depending on soil moisture and host availability (Stuart et al., 2006; Ram et al., 2008b). Although the patchiness and metapopulation structure of EPN populations can promote the long-term persistence and stability of EPN-host interactions, this spatial structure often restricts the occurrence of strong top-down control and EPN-driven trophic cascades in natural systems to local foci (Ram et al., 2008b). The frequent decoupling of EPN-host interactions due to limited dispersal ability, local extinctions, dramatic fluctuations in host density and a spatially constrained numerical response likely combine to explain the limited success of EPN in providing persistent biological control (Georgis et al., 2006).

Despite the inherent life-history constraints of EPN and the restricted occurrence of EPN-promoted trophic cascades in natural systems, our survey and meta-analyses identified numerous cases of EPN-induced trophic cascades in agricultural systems. Agricultural systems can be manipulated and thus provide the opportunity to achieve broad-scale pest suppression and enhanced crop yield using augmentative EPN releases or conservation biological control. Management

of soil moisture and structure (e.g., porosity and organic content) to favor EPN survival and long-term persistence is certainly possible. Moreover, minimizing soil disturbance via reduced tilling may foster the conservation and persistence of some EPN by preserving important spatial refuges in the soil (Lewis et al., 1998; Stuart et al., 2006). Coupled with their high reproductive potential, advances in EPN production and delivery methods and soil management practices may further increase the effectiveness of EPN in promoting trophic cascades in cropping systems (Georgis et al., 2006). Because discrepant dispersal abilities between predators (e.g., EPN) and their prey often lead to weak numerical responses and prey/host escape (Döbel and Denno, 1994), the appropriate timing of EPN releases could offset their inherent dispersal limitation and improve pest control (Georgis et al., 2006). Moreover, by selecting EPN species with foraging strategies that improve host tracking, better biological control might be achieved (Gaugler, 1999).

An improved understanding of how EPN interact with resident natural enemies in the soil food web to affect pest suppression is needed in the context of large-scale ecosystems. Because multiple-enemy interactions can relax top-down control and dampen trophic cascades, it becomes critical to assess how EPN and their associated soil-dwelling consumers (predators, pathogens and competitors) interact. Thus, determining which combinations of consumers provide complementary control and which combinations engage in intraguild predation or compete becomes essential information for improved pest management. Moreover, there is increasing awareness that strong linkages exist between aboveground and belowground food webs (Wardle, 2002; Wardle et al., 2004; Kaplan et al., in press), thereby increasing the complexity of multi-trophic interactions. For example, when young maize plants are infested with either the foliar lepidopteran *Spodoptera littoralis* or the root-feeding beetle *Diabrotica virgifera*, the parasitic wasp *Cotesia marginiventris* and the entomopathogenic soil nematode *Heterorhabditis megidis* are strongly attracted to their respective hosts (Rasmann and Turlings, 2007). However, attraction is significantly reduced if both herbivores feed simultaneously on the maize plant. Notably, the emission of the principal root attractant is reduced during double infestation. This example suggests that via plant mediation, players in the aboveground community can influence the strength of EPN-host interactions in the soil.

Prospectus and synthesis

Although we lack the experimental EPN studies to assess the effects of multiple-enemy interactions on trophic cascades, one could make a tentative argument that, even though omnivory is rampant in soil systems (Walter et al., 1989; de Ruiter et al., 1996; Stuart et al., 2006), we can hypothesize the effects of EPN on prey

and basal resources in a three trophic-level framework. We found evidence that EPN augmentation results in prey suppression, reduced plant damage and positive effects on plant yield and survival. Several factors likely contribute to this pattern.

First, although EPN are limited in their ability to move on their own power, they have a tremendous reproductive potential and often outstrip any numerical response of natural enemies (Jaffee and Strong, 2005; Jaffee et al., 2007). Moreover, large and well-timed augmentative releases of EPN in agricultural systems are likely to temporarily swamp any potential adverse effects natural enemies on EPN. Second, the majority of interactions among EPN individuals and species take place within their infected and shared host (Lewis et al., 2006), and, after colonization, intraguild predation is less prevalent (but see Veremchuk and Issi, 1970). Thus, EPN life history may reduce exposure to other natural enemies compared to arthropod predators that are exposed to top predators for a significant portion of their immature development. However, after colonizing the same host individual, EPN are more likely to engage in resource competition, both intraspecific and interspecific (Stuart et al., 2006). As management techniques that promote the long-term persistence of EPN are improved, antagonistic interactions among species and with other food web components are more likely to arise. This probability should spur researchers to conduct field experiments designed to evaluate the multitude of factors that dampen the strength of trophic cascades in belowground predator-prey interactions.

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