

Dynamics of a Subterranean Trophic Cascade in Space and Time

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Abstract: Trophic cascades, whereby predators indirectly benefit plant biomass by reducing herbivore pressure, form the mechanistic basis for classical biological control of pest insects. Entomopathogenic nematodes (EPN) are lethal to a variety of insect hosts with soil-dwelling stages, making them promising biocontrol agents. EPN biological control programs, however, typically fail because nematodes do not establish, persist and/or recycle over multiple host generations in the field. A variety of factors such as local abiotic conditions, host quantity and quality, and rates of movement affect the probability of persistence. Here, we review results from 13 years of study on the biology and ecology of an endemic population of *Heterorhabditis marelatus* (Rhabditida: Heterorhabditidae) in a California coastal prairie. In a highly seasonal abiotic environment with intrinsic variation in soils, vegetation structure, and host availability, natural populations of *H. marelatus* persisted at high incidence at some but not all sites within our study area. Through a set of field and lab experiments, we describe mechanisms and hypotheses to understand the persistence of *H. marelatus*. We suggest that further ecological study of naturally occurring EPN populations can yield significant insight to improve the practice and management of biological control of soil-dwelling insect pests.

Key words: entomopathogenic nematode, *Hepialus californicus*, *Heterorhabditis marelatus*, long-term persistence, *Lupinus arboreus*, metapopulation dynamics, biocontrol, trophic cascade.

Food webs have long played a prominent role in community and population ecology (Elton, 1927; Polis and Winemiller, 1996; Polis et al., 2005). Complex predator-prey interactions that drive food webs have been immensely useful for studying population regulation, community structure, and their ramifications for ecosystem properties (Winemiller and Polis, 1996). Trophic cascades—where predators alter biomass of primary producers as an indirect consequence of their direct effects on herbivores—represent a central theme in food web ecology (Pace et al., 1999). Trophic cascades can act as an important mechanism for the maintenance of plant biomass, species diversity and ecosystem function in a variety of ecosystems (Shurin et al., 2002; Stenseth et al., 2002; Schmitz, 2006). Trophic cascades are exemplified by classical biological control programs, in which natural enemies of invasive insect pests are introduced to increase crop production or yield (Gaugler et al., 1997; Snyder and Wise, 2001; Costamagna et al., 2007). An understanding of the conditions which favor cascading interactions is therefore critical.

Recent reviews and meta-analyses have made considerable inroads into understanding patterns in the strength and prevalence of trophic cascades (Schmitz et al., 2000; Halaj and Wise, 2001; Shurin et al., 2002; Borer et al., 2005). These syntheses lend support to the conjecture (Strong, 1992) that trophic cascades are

stronger and more prevalent in aquatic than in terrestrial systems (Shurin et al., 2006). Moreover, systems in which the size differences between consumers and their resources are great (Loeuille and Loreau, 2005) and/or where resources have a much shorter generation time than their consumers experience stronger cascades (Borer et al., 2005). Typical to studies in these reviews, the top predator is much larger than its prey and consumes more than one prey individual over the course of its lifespan (Lafferty and Kuris, 2002). Smaller organisms which don't fit this framework, such as parasites, parasitoids and diseases, also can induce cascades, but empirical data are limited primarily to a small set of cases in which introduced pathogens decimated mammalian herbivore populations with cascading consequences for vegetation (Sinclair, 1979; Dwyer et al., 1990). The long-term outcomes in such cases may differ from 'typical' trophic cascades because i) the consumers are typically smaller than prey, making them highly susceptible to vagaries of the abiotic environment (Gubbins and Gilligan, 1997), and ii) smaller organisms are limited in their spatial extent (Kotliar and Wiens, 1990).

Entomopathogenic nematodes (EPN) are widespread in soil on all continents except Antarctica (Hominick, 2002) and are potent natural enemies of many insects with soil-dwelling stages (Klein, 1990). EPN can protect vegetation (Strong et al., 1999; Denno et al., in press), are integral to rhizosphere food webs (Duncan et al., 2007) and are increasingly important as innoculative agents in integrated pest management (Lewis et al., 1998). Their broad host-range and ease of propagation and application make EPN promising candidates for classical or conservation biological control (Ehlers and Hokkanen, 1996; Lewis et al., 1998; Shapiro-Ilan et al., 2006). However, successful examples of persistent EPN-mediated control of insect pests in the field remain rare (Gaugler et al., 1997; Georgis et al., 2006). Biocontrol failures can result from a combination of biotic and abiotic factors that limit

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establishment, persistence and/or recycling. On the abiotic end, soil structure and moisture availability (often mediated by vegetation structure) affect EPN persistence and their subsequent impact. At the biotic end, variation in quality and abundance of hosts affects EPN reproduction and thus long-term persistence.

Highly variable abiotic conditions impose stresses that can drastically alter the ability of natural enemies to suppress prey in freshwater, marine and terrestrial systems (Briggs and Godfray, 1996). Spatial and temporal variability in environmental stressors can decouple the strong consumer-resource interactions that yield trophic cascades. In the soil environment, the primary abiotic stressors are extremes of temperature and moisture. Critical thresholds of soil moisture are essential for EPN movement, dispersal and ultimately survival; unlike many nematode clades, EPN lack an anhydrobiotic stage and are desiccation-intolerant (Womersley, 1990; Kaya and Gaugler, 1993; Grant and Villani, 2003b). During seasonally warm and dry periods, EPN populations can experience local extirpation in surface soils. Although soil aggregates that remain moist can serve as refugia in which EPN can persist under harsh conditions, EPN movement into such refuges is impeded as temperatures rise and soil moisture declines.

Biotic factors also play an important role in regulating EPN populations. Much like human and animal diseases, EPN can go locally extinct despite their strong impacts on host populations (Strong, 2002). Certain viral diseases, for example, can disappear when all susceptible individuals are either killed or immunized (Holmes et al., 1997). Field populations of EPN also can be extirpated if hosts are inaccessible or insufficient in density and/or size for EPN reproduction and population persistence. These dual risks of over- and under-exploitation, which are characteristic of many host-pathogen systems, combine to narrow the window of EPN persistence (Smith et al., 2003; Dugaw et al., 2005).

In this review, we summarize findings from 13 years of research on a naturally occurring, EPN-mediated subterranean trophic cascade in a California coastal prairie ecosystem. Through laboratory and field experiments and dynamic models, we have identified mechanisms that allow EPN to persist in heterogeneous habitats where abiotic conditions and host availabilities vary.

Natural history of the subterranean trophic cascade

The Bodega Marine Reserve (BMR, Sonoma County, CA; 38.32°N, 123.07°W) has a Mediterranean climate with much of the rainfall restricted primarily to the winter months. With only 147 ha of land area, the reserve spans a range of soil types, from sand dunes to grassland areas in which loam and sand are mixed with organic matter ((Barbour et al., 1973). The dominant vegetative habitat on the reserve is coastal prairie com-

posed primarily of a mix of native and exotic annual herbs. Naturally treeless, the site contains only four woody species: *Baccharus pilularis*, *Ericameria ericoides*, *Lupinus chamassonis* and, the most abundant in this coastal prairie, the yellow bush lupine *Lupinus arboreus* (Fabaceae). Yellow bush lupines are fast-growing nitrogen fixers that mature in two to three years and flower from early spring through summer, with seedset in the fall. Shrubs grow up to a height of three meters with an average life span of about seven years (Davidson and Barbour, 1977).

Foliar-feeding western tussock moths (*Orgyia vetusta*; Lepidoptera: Lymantriidae) can defoliate adult lupine bushes in outbreak years; however, such occurrences are localized, uncommon and do not ordinarily kill mature plants (Harrison and Maron, 1995). Numerous other insects attack lupine flowers and seed pods, thereby affecting total seedset; however, stem- and root-boring ghost moth caterpillars (*Hepialus californicus*; Lepidoptera: Hepialidae) are probably the most important cause of adult lupine mortality in this system (Strong et al., 1995; Maron, 1998). Because they damage important plant transport tissues such as xylem and phloem, even a few ghost moths can have a disproportionately large effect on an individual plant (Preisser and Bastow, 2006). Widespread lupine die-offs can lead to colonization of nitrogen-enriched soil by invasive grasses and forbs and result in species turnover and regime shifts of the plant community (Maron and Connors, 1996; Maron and Jefferies, 2001).

Although the potentially devastating impact of underground herbivory by *Hepialus californicus* larvae on *Lupinus arboreus* had long been recognized (Barbour et al., 1973), the existence and potential impacts of EPN on this interaction remained unknown until the early 1990s. EPN were discovered by chance at BMR when an undergraduate student in a field ecology course discovered a reddish-orange ghost moth larva in a lupine root that, although dead, did not appear to be decaying (D. Strong, pers. comm.). Closer examination revealed that the ghost moth larva had been infected by a previously undescribed species of heterorhabditid nematode. This species was named *Heterorhabditis hepialus* to signify its primary host at BMR (Stock et al., 1996). This name was preempted by Liu and Berry (1996), who, working without knowledge of the BMR discovery, isolated the same species from coastal marshes in Oregon and named it *Heterorhabditis marelatus*. Although two species of EPN, *H. marelatus* and *Steinernema feltiae* (Filipjev) (Steinernematidae) have been isolated from BMR soils (Gruner et al., 2007), *S. feltiae* is widespread but locally uncommon on the reserve. No infections of *Hepialus* by *S. feltiae* have been documented from the field, and competition experiments in the lab suggest *H. californicus* is not a favored host for *S. feltiae* (Gruner et al., unpublished data).



Field evidence for the trophic cascade

Early research linked widespread bush lupine die-offs (>10,000 mature individuals) to periodic outbreaks of ghost moth herbivory that removed root tissue and effectively girdled the plants (Strong et al., 1995). Strong and colleagues also noted that ghost moth caterpillars suffered high mortality from *Heterorhabditis marelatus* (=unnamed EPN at that time) and speculated that this species might be responsible for the patchily distributed nature of lupine mortality at BMR. A follow-up study (Strong et al., 1996) used a combination of lab work and field surveys to demonstrate that i) *H. marelatus* is found disproportionately in the soil surrounding lupine roots (the 'rhizosphere') at BMR, and ii) *H. marelatus* is an effective ghost moth predator capable of producing >420,000 offspring from a single infected *H. californicus* cadaver. They also documented an inverse correlation between EPN and *H. californicus* densities across the reserve and noted that areas with high EPN densities did not experience *H. californicus* outbreaks (Strong et al., 1996).

Subsequent field experiments demonstrated the causal mechanism of trophic cascades, confirming that *H. marelatus* could indirectly benefit *L. arboreus* through its suppression of underground *H. californicus* herbivory (Strong et al., 1999; Preisser, 2003; Preisser and Strong, 2004). Strong et al. (1999) exposed potted lupine seedlings to a range of *H. californicus* densities (0, 8, 16 or 32 caterpillars) in the presence or absence of *H. marelatus*. In the absence of *H. marelatus*, lupine mortality sharply increased as a function of *H. californicus* density; however, even high *H. californicus* densities did not affect lupine survival in the presence of *H. marelatus*. This was the first published research to confirm that trophic cascades occurred in belowground systems.

In a larger-scale field experiment, Preisser (2003) manipulated the presence/absence of *H. marelatus* underneath mature adult lupines exposed to a standard density of 24 *H. californicus* larvae/bush. The effect of *H. marelatus* on lupine fitness was both rapid and dramatic: *H. marelatus* presence increased lupine seed set by 44% in three months and trunk growth by 67% over an eight-month period. The large effect of *H. marelatus* documented by this research suggested that this cascade was capable of playing an ecologically important role in the BMR coastal prairie system, a result confirmed by dynamical models (Dugaw et al., 2004).

Although this work was generally interpreted as supporting a 'food-chain' approach to soil food webs, other research found no evidence that the densities of nematode-trapping fungi and *H. marelatus* were inversely correlated and therefore rejected the hypothesis of a four-level trophic cascade (Jaffee et al., 1996; Koppenhöfer et al., 1996). Subsequent lab microcosm studies showed that even large numerical responses of nematode-

trapping fungi (*Arthrobotrys oligospora* and *Myzocytiopsis glutinospora*) were insufficient to regulate *H. marelatus* swarms issuing from cadavers (Jaffee and Strong, 2005; Jaffee et al., 2007).

Variation in EPN incidence

EPN are patchy by nature (Stuart and Gaugler, 1994; Wilson et al., 2003; Stuart et al., 2006) and are likely to exist as metapopulations. To establish the patterns of occurrence of *H. marelatus* at BMR, we surveyed lupine bushes at six pre-established sites across the reserve, representing the range of habitats in which EPN could occur. Since 1993, we have continuously monitored presence/absence (hereafter incidence, sensu (Boag, 1993)) in a cluster of marked bushes at each site. The bushes were dispersed throughout each site to capture inherent variation. We assayed soil samples from each rhizosphere using standard *Galleria mellonella* baiting techniques (Bedding and Akhurst, 1975).

The study found that incidence of *H. marelatus* varied considerably among sites (Ram et al., 2008). Three of the sites ('high sites': Mussel Point, Cove and Dune) had high long-term EPN incidence while the remaining three ('low sites': Lower Draw, Upper Draw and Bayshore) had low long-term incidence. Incidence between the highest and lowest sites varied by an order of magnitude. These differences arose despite the lack of any apparent differences in lupine cover (Strong et al., 1996) or variation in ghost moth abundance (Strong, unpublished data). The surveys clearly indicated that *H. marelatus* populations wax and wane dramatically. They become locally extinct in lupine rhizospheres, colonize new rhizospheres and re-colonize rhizospheres, suggesting that local movement and dispersal are important for long-term persistence.

Mechanisms for persistence

Several mechanisms could generate such patterns of dynamic persistence in the field. Here we review a set of mechanisms that could explain patterns of long-term occurrence observed at BMR.

I. Survivorship

For microparasites that suppress herbivores, survivorship of the free-living stage is essential for the protection of vegetation via a trophic cascade (Polis and Strong, 1996). EPN are distinctive among microparasites in having a long-lived IJ stage that is at the mercy of both the biotic and abiotic environment (Stenseth et al., 2002). IJ survival is quite sensitive to soil moisture, and models demonstrate that extended drought conditions readily contribute to local extinction of these microparasite populations (Dugaw et al., 2005). The inter-annual differences in dry season soil moisture generated by El Niño—Southern Oscillation (ENSO) climate variation can affect IJ survival, creating tempo-



ral differences in the strength of the trophic cascade driven by these microparasites (Preisser and Strong, 2004). Evidence that *H. marelatus* affected *H. californicus* density and lupine survival spurred research into the factors affecting *H. marelatus* distribution and relative abundance. Although *H. marelatus* survival proved largely density-independent under field conditions (Preisser et al., 2005), watering experiments revealed that soil moisture, through its effect on *H. marelatus* survival, played a critical role in the cascade (Preisser and Strong, 2004). Lupine rhizospheres that experienced the wet summer conditions that characteristically follow ENSO climatic events retained their *H. marelatus* populations; in contrast, rhizospheres exposed to the drier summer conditions typical of non-ENSO years quickly lost their resident *H. marelatus*. Simulations showed that relatively small changes in moisture content (1–2% by volume) proved critically important in facilitating the survival of a small fraction of *H. marelatus* IJ through the relatively dry BMR summers until the following winter, when ghost moth eggs are laid and their caterpillar hosts are again available (Dugaw et al., 2005).

Later research confirmed the primacy of soil moisture conditions in facilitating *H. marelatus* survival (Preisser et al., 2006). *Heterorhabditis marelatus* IJ buried under lupines experienced higher survival over the course of a typical BMR summer than those buried in nearby grasslands, a difference that disappeared under wet winter conditions. The seasonally varying protection afforded these IJ appears linked to soil moisture conditions; mature bush lupines possess a dense canopy and thick detrital layer that reduces desiccation and helps maintain a zone of relatively moist soil around their taproots. Models parameterized using this data showed that the moisture-driven increases in IJ survival in the lupine rhizospheres have far-reaching effects: some fraction of even a small cohort of *H. marelatus* IJ emerging into a lupine rhizospheres are likely to survive dry summer conditions, while the extinction of even large IJ cohorts in grassland soils is virtually guaranteed (Dugaw et al., 2005).

Ram et al. (2008) examined patterns of mortality at larger spatial scales by following a fixed cohort of *H. marelatus* in host-free tubes over one year at all six survey sites. This research enumerated surviving *H. marelatus* at three different time intervals (2, 6 and 12 months in the ground) to calculate mortality rates. Survival was greater under lupines than surrounding grasslands, corroborating previous work (Preisser et al., 2005, 2006). Nearly all of the sites studied had identical mortality rates despite considerable variation in incidence. Dune was the only outlier, with significantly higher mortality and the lowest moisture levels. Despite apparently harsh conditions for EPN survival, Dune paradoxically had the second highest long-term incidence of all the sites. The three high sites (Mussel Point, Cove and

Dune) spanned the entire range of moistures from low to high. The low sites spanned a narrower range of moistures. These data present a paradox of persistence, where neither local abiotic conditions nor mortality predict local persistence.

II. Metapopulation and spatial dynamics

While EPN suppress hosts at the scale of individual rhizospheres (Strong et al., 1999; Preisser, 2003), this pattern did not necessarily extend to larger spatial scales. Many organisms exist as metapopulations, where extinction and colonization of local populations maintain the population at the landscape level (Hanski and Thomas, 1994). Colonists from persistent patches can re-invade extirpated patches and help maintain overall population densities. Using the same 13-year dataset, Ram et al. (2008) also calculated colonization and extinction rates for lupine rhizospheres at each BMR site. Sites at the high end of the incidence spectrum also experienced more frequent colonizations and extinctions. Dune, the site with the highest mortality and lowest moisture, also experienced the highest rate of colonization. Sites with low average incidence were rarely colonized and experienced infrequent extinctions.

The inherent patchiness and metapopulation structure of naturally occurring EPN populations may be a key to the persistence and stability of EPN-prey interactions (Stuart and Gaugler, 1994; Holyoak and Lawler, 1996; Wilson et al., 2003). The limited mobility of both EPN and host caterpillars, each interacting strongly and uniquely with abiotic and biotic properties of individual microsites, tends to reduce correlations among microsites within a landscape matrix. With increasing spatial scale, the signals from these microsites can be superimposed to yield phenomena with diminishing resemblance to the dynamics at microsite scales (De Roos et al., 1991). Since 2004, we have been monitoring the *H. marelatus*—*H. californicus*—*L. arboreus* interaction on a landscape matrix of 800+ lupine shrubs. Within a landscape where more than 70% of all monitored lupine rhizospheres were consistently occupied by *H. marelatus*, in excess of 50% of lupines died within the first two years after sustaining heavy root and stem herbivory by *Hepialus californicus*. Spatial autocorrelation functions showed that characteristic patch sizes of *H. marelatus* were larger than the scale of individual lupine rhizospheres, but that these dynamic ‘clouds’ of EPN swelled into grasslands during the wet season and retreated to lupine rhizospheres following dry summers (Gruner et al., unpublished data). The presence of *H. marelatus* was a poor predictor of lupine survival on the spatial scale of this landscape, where abiotic and biotic variables were not uniformly homogenous as in smaller-scale experiments.

III. Local and long-distance dispersal

Measuring dispersal in the field is often quite difficult and may appear essentially impossible with inconspicuous

ous organisms such as EPN. To our knowledge, no published studies have measured EPN dispersal in the field. Estimates derived from the few existing laboratory-based studies may not be ecologically relevant since dispersal clearly varies with soil characteristics, moisture and host cue availability (Moyle and Kaya, 1981; Lewis, 2002). Since IJ have fixed lipid reserves, energetic demands also impose limits on long-distance dispersal. One possible mechanism that could allow EPN to disperse over large distances is phoresy, whereby EPN hitch a ride on non-host cursorial organisms. Terrestrial isopods (*Porcellio scaber*) occur in very high densities (Justin Bastow, unpublished) at BMR and frequently visit remnant galleries of ghost moths. High densities of *P. scaber* at BMR coupled with their frequent occurrence inside lupines make them ideal agents of phoresy. Although Eng et al. (2005) demonstrated that these isopods can transport EPN in a laboratory setting, the extent to which phoretic dispersal occurs in the field remains unknown.

Soil drying during the warm summer months may largely extirpate *H. marelatus* populations from surface soils and grasslands. Pockets of soil that remain moist may serve as refugia where EPN can persist under harsh summer conditions. Wet winter conditions increase soil moisture levels, making it favorable for EPN to disperse and seek hosts. Given their strong dependence on soil moisture for movement, EPN are able to seek hosts and reproduce only in the wet winter, while remaining inactive in dry summer months (Grant and Villani, 2003a, 2003b). As EPN cannot move and infect hosts in dry summer soil, they must survive through a dry summer in the absence of hosts. Given that EPN have limited dispersal (Ram, unpublished, McLaughlin and Strong,

unpublished) and unknown phoretic range (Eng et al., 2005), a reasonable hypothesis is that EPN retreat into deeper, moist soil refugia during dry summer months. In one study, *Heterorhabditis* species occurred more frequently in deeper soil layers (>20 cm) than sympatric *Steinernema* species (Ferguson et al., 1995), but few field studies have tested soils deeper than 40 cm (but see Mauleon et al., 2006).

To test the plausibility of the hypothesis that EPN undergo vertical local migration in summer months, we surveyed EPN at different depths at each of our six study sites in summer 2006. Using a 15-cm diam. PVC pipe to prevent collapse and integration of shallow soils with deeper layers, we cored with vacuum extensions to 80 cm below the surface. We collected soil samples from the surface, and at 50 cm and 80 cm depths, at 10 replicate locations along a transect and measured incidence using standard baiting techniques (Bedding and Akhurst, 1975). When analyzed categorically by site groups (high- and low-incidence sites), the risk of infection at the surface was significantly higher in high sites as opposed to low sites (two sample, two-tailed binomial test: $n = 180$, $df = 1$, $p < 0.0001$, Fig. 1). High sites also had a significantly higher risk of infection at 50 cm and 80 cm below ground (two sample, two-tailed binomial test: $n = 360$, $df = 1$, $p < 0.0001$, Fig. 1). This difference remains significant even when the site with the highest historical population, Mussel Point, is removed from the analysis (two sample, two-tailed binomial test: $n = 240/n = 360$, $df = 1$, $p < 0.0001$; Fig. 2).

Only one infected bioassay was recovered below-ground from any of the low sites. At high sites, however, infection risk by deep EPN was proportional to or exceeded that at the surface. The presence of these deep

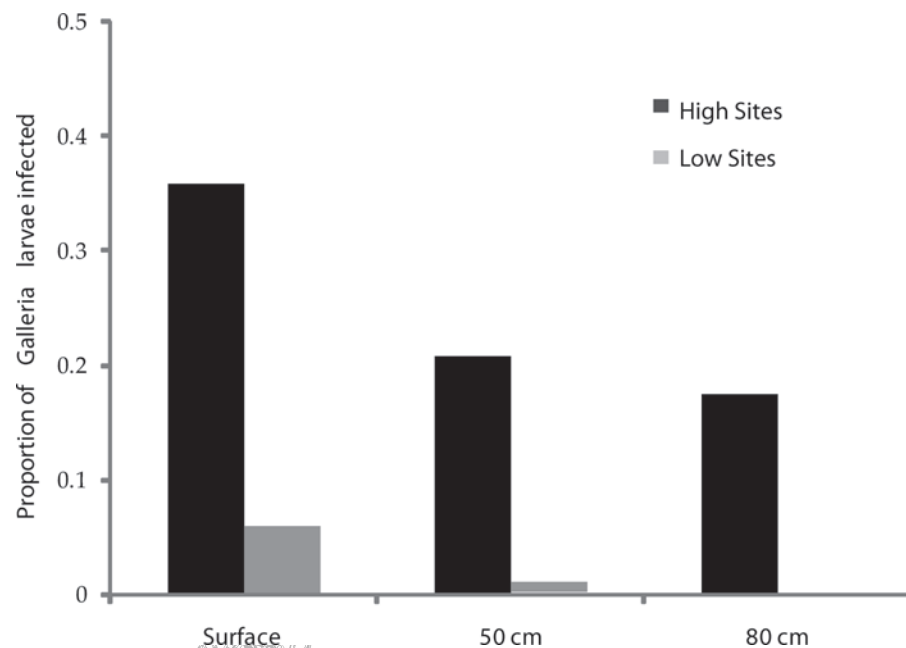


FIG. 1. Proportion of *Galleria* larvae infected at each depth ($n = 120$). No infections were recovered from 80 cm at any of the low sites.



FIG. 2. Map of long-term sites at the Bodega Marine Reserve (BMR). Incidence rates reported per site are from long-term surveys carried out from 1993–2006 (redrawn from Ram et al., in press). Lines point to the approximate center of each long-term site.

EPN populations in the summer suggests that they may undergo seasonal vertical migration in the soil column. This migration may aid local population persistence (Mauleon et al., 2006). The cooler temperatures and increased moisture content of deep soils may allow EPN to conserve their lipid to later ascend up to the host-rich upper layers ('A' and 'O' horizons) with the onset of winter rains. We are currently testing this hypothesis, particularly how variation in lipid levels affect survivorship.

DISCUSSION

Entomopathogenic nematodes clearly play important roles in both managed and natural soil ecosystems. Within a single rhizosphere, favorable abiotic conditions facilitate EPN involvement in powerful trophic cascades. This effect, however, becomes much less clear at much larger spatial scales. Metapopulation processes such as colonization and extinction, facilitated by phoretic or individual movement and patchy abiotic refugia, sometimes override local limitations and may enable EPN to persist despite seasonal and variable conditions at micro sites. Even sites with favorable local conditions may not have strong EPN-driven impacts on hosts if at low levels of EPN colonization. Moreover, our longer spatially explicit studies have demonstrated that the mere presence of *H. marelatus* does not guarantee a strong effect on hosts or subsequent protection of lupines. Future empirical work and models on local and long-distance movement will provide improved mechanistic explanations of how populations—and their cas-

cadic impacts on insect hosts and plants—vary in space and time.

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