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Entomopathogenic nematode food web assemblages in Florida natural areas



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ABSTRACT

In Florida citrus orchards, root weevil herbivory is tempered by four native entomopathogenic nematode (EPN) species whose spatial patterns are associated with soil properties related to water content. Manipulation of these variables could affect the efficacy and conservation of native EPNs for control of root weevils. The diversity of EPNs in non-agricultural areas it is unknown. We speculated that, whereas different species composition may occur in some natural areas by virtue of non-citrus niche adaptations, similar soil properties and environmental conditions should shape the communities in both systems. We characterized EPN food web assemblages during summer-fall 2011 in 91 sites comprising five naturally occurring botanical groups (oak, pine, palm and palmetto, mixed and other) and two ecoregions (central ridge and flatwoods). We used species-specific qPCR probes for 13 EPN species, two species of Paenibacillus (ectoparasitically associated with EPNs), seven species of nematophagous fungi (NF), an oomycete pathogen of citrus (Phytophthora nicotianae) and free-living bactivorous nematodes (Acrobeloidesgroup), some of which compete with EPNs. Seven EPN species were detected at frequencies about 60% of that reported from citrus. Additional species detected were Steinernema glaseri and Heterorhabditis floridensis, whereas citrus inhabitants Steinernema riobrave and Steinernema scapterisci, were absent, suggesting a possible niche adaptation. EPN recovery frequency did not differ between two ecoregions, except for Heterorhabditis indica which was detected at more sites in the flatwoods than on the central ridge and Heterorhabditis zealandica exhibiting the opposite pattern for detection frequency and abundance. Nor did the botanical habitats much affect EPNs other than H. indica which occurred with greatest frequency and abundance in abandoned citrus orchards. Soil moisture appeared to be important in modulating these subterranean communities, with groundwater depth, organic matter, soil clay and pH explaining significant EPN variability between sites. There was little evidence that regional or habitat differences in natural enemy occurrence affected the EPN spatial patterns. Indeed, numerous significant direct associations between species of nematodes and nematophagous fungi suggested that the local abundance of the r-selected EPN and Acrobeloides-group nematodes is an important resource modulating population growth of these trapping and endoparasitic fungi. Congruent relationships between EPN spatial patterns and soil properties that affect water potential in both natural areas and citrus orchards suggests that soil moisture drives these patterns and modulates the regulation of root herbivores by EPNs in this part of the Florida peninsula. Consequently, management of soil moisture by manipulating these properties has the greatest potential to enhance and conserve EPN services.

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1. Introduction

Subterranean trophic cascades in which plant species were shown to be protected from herbivorous insects by indigenous entomopathogenic nematodes (EPNs) have been characterized







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both in a natural area of California (Strong et al., 1999; Preisser, 2003) and in agricultural fields in Florida (Duncan et al., 2003a, 2007). *Heterorhabditis marelatus* (Rhabditida: Heterorhabditidae) is an EPN that preys on ghost moth (*Hepialus californicus*, Lepidoptera: Hepialidae) larvae in the Bodega Marine Reserve (California, USA). Root herbivory by ghost moth larvae weaken and kill the yellow bush lupine, *Lupinus arboreus* (Fabales: Fabaceae), but primarily in sites with few *H. marelatus* (Strong et al., 1999; Preisser, 2003). Similarly, the root weevil *Diaprepes abbreviatus* (Coleoptera: Curculionidae) is a major pest of citrus in Florida (USA). The weevil population size and its damage to citrus (*Citrus* spp., Sapindales: Rutaceae) are least in eco-regions that support diverse EPN communities which inflict high larval mortality, and are greatest in eco-regions where EPNs are less diverse and effective (Duncan et al., 2003a, 2007).

The geospatial patterns of the EPNs, food webs and soil properties in both the Bodega Reserve and Florida citrus orchards continue to be studied in some detail in order to understand properties of habitats that are conducive to trophic cascades. Identifying conducive properties could enable the novel pest management approach of habitat modification to conserve and enhance the services of naturally occurring EPNs. Soil moisture was identified as a key factor associated with the survival/abundance of H. marelatus. The nematode must persist during the dry summer months in the Mediterranean climate of the California coast until winter rains and hatching ghost moth eggs provide adequate soil moisture and host prey. The effects of climatic cycles, vegetation cover and soil depth on soil moisture combine with individual survival heterogeneity to modulate the survival rates of the nematode between sites in the reserve (Ram et al., 2008; Dugaw and Ram, 2011). It is interesting that the geospatial patterns of EPN species in humid, subtropical Florida citrus orchards may also derive largely from variation in soil moisture. Campos-Herrera et al. (2013a) reported that deep groundwater, low soil water holding capacity, low clay and organic matter content were positively associated with the occurrence of Steinernema diaprepesi (Rhabditida: Steinernematidae) and Heterorhabditis zealandica (Rhabditida: Heterorhabditidae) and inversely related with a Steinernema sp. in the glaseri-group. Variables related to soil moisture were not associated with the spatial pattern of the nearly ubiquitous Heterorhabditis indica (Rhabditida: Heterorhabditidae). The responses (persistence and orientation) of these four species to soil moisture gradients in laboratory assays were consistent with their natural relationships (El-Borai et al., unpublished). Studies such as these suggest that manipulation of soil moisture by irrigation methods, mulching, or alteration of planting substrate can function to conserve or enhance the services provided by EPNs (Duncan et al., 2013; Campos-Herrera et al., 2014).

Properties such as soil moisture affect other organisms in food webs that might indirectly modulate EPN population dynamics. El-Borai et al. (2007, 2009) demonstrated in laboratory microcosms of citrus soils the potential for EPN population regulation by naturally occurring nematophagous fungi (NF) and that the effects of various NF species on EPN species were highly specific. Spatial-temporal patterns of H. zealandica and S. diaprepesi were significantly related with those of trapping NF in a citrus orchard, suggesting a role for these fungi in EPN regulation (Duncan et al., 2007). By contrast, NF abundance was unrelated to the spatial patterns of H. *marelatus* in the Bodega Reserve (Jaffee et al., 1996). Despite being abundant and actively preying on the nematode, NF did not appear to regulate these nematodes to an important extent (Jaffee and Strong, 2005; Jaffee et al., 2007). Nevertheless, given the specificity with which NF and EPNs interact, and the diversity of EPN species that prey on D. abbreviatus in Florida orchards, it is reasonable to ask whether habitats affect NF communities in ways that modulate EPN spatial patterns (Stuart et al., 2008). Conversely, EPNs and some free living nematodes that compete with EPNs represent remarkably abundant resources for NF as they emerge from insect cadavers (Jaffee and Strong, 2005). Habitat modulation of EPN occurrence and efficacy could, therefore, shape the spatial patterns of NF.

Until recently, attempts to quantify the level of nematophagy by NF in nature were complicated by the fact that most NF species are saprophagous and only facultatively nematophagous (Stirling, 2014). Molecular tools are now available that simultaneously identify and quantify EPNs and selected members of the soil food web (Campos-Herrera et al., 2011a, 2011b, 2012a, 2013a; Pathak et al., 2012). Presumably nematophagy is better distinguished from saprophagy by measuring NF DNA recovered from samples of nematodes extracted from soil (Pathak et al., 2012). Molecular tools were used to find linkages between EPNs, some of their natural enemies and selected soil properties that might explain different patterns of herbivory in two different ecoregions in Florida, the central ridge (higher altitude, deep, well-drained sandy soils) and the flatwoods (altitude near sea level, shallow, poorly-drained sandy soils) (Campos-Herrera et al., 2013a, 2013b). They were also used to evaluate how newly adopted citriculture methods alter the soil food web and severity of a pest-disease complex (Campos-Herrera et al., 2013c, 2014) and how soil organisms responded to cultural practices in organic orchards (Campos-Herrera et al., 2015a). Results of these studies provide a basis to explore habitat modifications for conservation biological control involving EPNs (Campos-Herrera et al., 2015b).

Studies of EPN food webs in natural areas are rare (reviewed by Ram et al., 2008). Moreover, with the exception of Torr et al. (2007), who used qPCR to describe the occurrence of native EPNs in forest and grassland, previous studies used traditional culturing methods to quantify microorganisms. Our aim in the present study was to use qPCR methods to characterize landscape-scale spatial patterns of EPNs, some natural enemies of EPNs and soil properties in natural areas within the geographic boundaries reported for a citrus orchard survey (Campos-Herrera et al., 2013a). We hypothesized that different species would occur in natural areas by virtue of noncitrus niche adaptations, but that similar soil properties and environmental conditions would shape the communities in both systems. Our objectives were to *i*) validate the habitat properties associated with different EPN species reported by Campos-Herrera et al. (2013a) and search for evidence that ii) NF predation modulates EPN spatial patterns at a landscape scale and/or iii) EPN spatial patterns modulate those of their NF predators.

2. Materials and methods

2.1. Regional survey scheme, sampling methods and soil properties analyses

Ninety-one natural area sites were surveyed during summer and early autumn 2011. A composite sample of 30 single soil cores (2.5 cm dia. x 30 cm deep, ca. 1400 cm³ soil per sample) was collected per locality in an area about 0.5 ha. The samples were transported in coolers to the laboratory, where they were processed within 16-32 h. The localities were selected to encompass the local natural plant diversity, categorized by botanical groups as oak (*Quercus* spp., Fagales: Fagaceae) (n = 20), pine (*Pinus* spp., Pinales: Pinaceae) (n = 16), palmetto and palm (Arecales: Arecaceae) (n = 12), mixed habitats (comprising oak, pine and/or palmetto/palm, n = 26) and other plant species (n = 17) such as longabandoned orchards and grasses. The sampling localities were in ecoregions designated as central ridge (n = 31) or flatwoods 60) (http://www.plantmaps.com/interactive-florida-(n)=

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