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Original article

Soil nematode assemblages indicate the potential for biological regulation of pest species

Hanne Steel [a, b, *], Howard Ferris [a]

[a] Department of Entomology and Nematology, University of California Davis, One Shields Avenue, Davis, CA 95616-8751, USA
[b] Nematology Research Unit, Department of Biology, Ghent University, K.L. Ledeganckstraat 31, 9000 Ghent, Belgium

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ABSTRACT

In concept, regulation or suppression of target nematode pest species should be enhanced when an abundance of predator species is supported by ample availability of bacterial- fungal- and non-damaging plant-feeding prey species. We selected soils from natural and managed environments that represented different levels of resource availability and disturbance. In microcosm chambers of each soil, in its natural state or after heat defaunation, we introduced test prey species not already resident in the soils (*Meloidogyne incognita* and *Steinernema feltiae*). Survival of the test prey was determined after a 5-day bioassay exposure. Across the soils tested, predator abundance and biomass were greater in undisturbed soils with plentiful resources and lower in soils from agricultural sites. Suppressiveness to the two introduced species increased with both numerical abundance and metabolic footprint of the predator assemblages. The magnitude of the increase in suppressiveness was greater at low numbers of predators then dampened to an asymptotic level at greater predator abundance, possibly determined by temporal and spatial aspects of the bioassay system and/or satiation of the predators. The more resource-limited the predators were and the higher the metabolic predator footprint, the greater the suppressiveness. The applied implications of this study are that soil suppressiveness to pest species may be enhanced by increasing resources to predators, removing chemical and physical constraints to their survival and increase, and altering management practices so that predators and target prey are co-located in time and space.

1. Introduction

Soil health and ecosystem functioning are important topics in current ecological and agricultural research. Doran et al. (1996) defined soil health as “the continued capacity of soil to function as a vital living system, within ecosystem and land-use boundaries, to sustain biological productivity, maintain the quality of air and water environments, and promote plant, animal and human health”. Soil suppressiveness, either general or specific, is an important function of a healthy soil (van Bruggen and Semenov, 2000) to which physical, chemical and biological factors might contribute (Janvier et al., 2007). Most of the research on indicators of soil suppressiveness focusses on microbial communities and is often performed with an experimental design in which few factors are varied (Postma et al., 2008). Many soil mesofauna, including nematodes in several trophic levels, are one or two steps higher in the food chain than microbes. Their generation time (weeks to months) is longer than that of the metabolically-active microbes (hours to days), making them more temporally stable rather than fluctuating with ephemeral nutrient flushes (Nannipieri et al., 1990; Neher, 2001). Moreover, nematodes have been used extensively as indicators of soil biodiversity and functioning (Ferris and Tuomisto, 2015; Neher, 2001) and as indicators of environmental disturbances (Bongers and Ferris, 1999; Ferris et al., 2001; Yeates, 2003).

Soil ecosystem services are benefits derived from ecosystems that are necessary to maintain soil health and productivity; they are delivered by the ecosystem functions of soil organisms (Brussaard, 2012). Guilds of soil biota are closely associated with different ecosystem functions, for example, Carrascosa et al. (2014) reported a positive and significant relationship between soil suppressiveness, soil food web structure and nematode diversity. Suppression of pest and disease organisms is an ecosystem service that is the outcome of the ecosystem function of biological population

* Corresponding author. K.L. Ledeganckstraat 35, 9000 Ghent, Belgium.
E-mail address: Hanne.Steel@UGent.be (H. Steel).

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regulation (Brussaard, 2012). Suppression might be induced by adding biocontrol agents (e.g. Jaffee, 2000) but in the absence of specific predator-prey associations, higher trophic levels might generally enhance suppression by predation on plant-feeding species (Sánchez-Moreno and Ferris, 2007). In that case, target species could be regulated by controlled increases in bacterial-, fungal- and non-damaging plant-feeding nematodes, which will provide resources to enhance predator abundance and promote important and useful population interactions. System level regulation of soil pest species might be obtained by providing additional resources to predators through a trophic web of carbon and energy exchange. For this system to work, some criteria need to be fulfilled. First, the carbon and energy flow must be available to the relevant soil organisms and second, chemical and physical constraints to the survival and population growth of the specialist or generalist predators must be alleviated. Most studies on natural regulation by predator nematodes have focused on the direct top-down effect on the prey (Bilgrami et al., 2005; Khan and Kim, 2005) or on the impact of resources on predator and consequently also on prey guilds (Ferris et al., 2012a, 2012b). In those studies, additional resources (e.g., those provided by cover crops and organic amendments) not only affected organisms at the entry level of the food web (prey guilds) but were also transferred to higher trophic levels (predator guilds) which consequently increased top-down pressure on herbivore nematodes (Ferris et al., 2012b).

Functional interactions between predators and prey can only occur if the organisms are in the same place at the same time and are thus highly affected by the patchiness of the component populations. Previous studies on this topic (e.g. Carrascosa et al., 2014; Ferris et al., 2012b; Min and Toyota, 2013; Sánchez-Moreno and Ferris, 2007), were based on composited and mixed bulk samples which essentially eliminates the spatial component of the above criteria. Therefore, we tested in intact soil cores the hypothesis that the numerical, biomass or functional abundance of predator nematodes, either specialists or generalists, are useful indicators of suppressiveness of opportunistic plant-feeding species. Differing abundance of resident prey and predator populations in each core led us to the hypothesis that soil patches with hungry (i.e., resource-restricted) predators are likely to be more suppressive than patches with abundant available prey and satiated predators. In that case, suppression is not only a function of predator abundance but also the availability of resident prey per predator. As a caveat to the experimental bioassay design and observations, we emphasize that besides their direct effects on the prey and their active involvement in succession within the soil food web, the predator nematodes are also indicators of the presence of predation and regulation by all organisms in the system that have similar life course characteristics and that participate in the ecosystem function (Stirling, 2014b; Yeates et al., 2009). Through their comparable function, response to resources and sensitivity to disturbances, many different types of organisms contribute to the same ecosystem services (Sánchez-Moreno et al., 2009). Consequently, our intact and undisturbed microcosm experiments potentially provide a proof of concept that can be translated to field scale application.

2. Materials and methods

Single soil patches, from a variety of soils and inhabited by a range (both in number and taxa) of naturally occurring predatory nematodes, were tested in 5-day bioassays inoculated with a constant number of introduced prey (*Steinernema feltiae* and *Meloidogyne incognita*).

2.1. Sampling methods and soil characteristics

To obtain a wide range of abundance and diversity of both predatory nematodes and prey, samples were collected from both natural and agriculturally-influenced sites in California, USA, representing a wide range of edaphic conditions and levels of disturbance (Fig. 1). The sites included seven natural and apparently undisturbed habitats: under a manzanita bush (*Arcostaphylos* sp.) (U-MAN) and a horse-chestnut tree (*Aesculus californica*) (U-HCT) at the Audubon Bobcat Ranch Reserve in western Yolo County at 38° 32.309′N, 122° 02.937′W and 38° 32.307′N, 122° 02.921′W, respectively, in the UC Davis Putah Creek Riparian Reserve (U-PCR1 and 2) at 38° 31.743′N, 121° 46.867′W and 38° 31.249′N, 121° 46.183′W, under a boxwood hedge (*Buxus* sp.) on the UC Davis campus near Hart Hall (U-HHH) at 38° 32.442′N,121° 45.072′ W, from undisturbed soil of the Field of Dreams (U-FOD) in which alfalfa (*Medicago sativa*) was the predominant plant (38° 31.743′ N, 121° 52.273′ W) at the UC Davis Russell Ranch Sustainable Agriculture Facility and from moist soil near a natural spring on Creekside Drive in Shingle Springs (U-SS) in Eldorado County at 38° 38.731 N, 120° 55.909′ W. To represent agriculturally-influenced and thus disturbed habitats, samples were collected from four locations: untreated and yard-waste-amended plots of an organic amendment experiment (no crop at time of sampling) at the Hansen Agricultural Research and Extension Center (D-HAR) (34° 19.575′ N, 119° 06.459′ W) near Santa Paula, Ventura County, from a wheat field (D-RR) (38° 31.743′ N, 121° 52.273′ W) in a long-term cropping systems project at the UC Davis Russell Ranch Sustainable Agriculture Facility, and from two grape vineyards, one in Lodi, San Joaquin County (D-GVL) (rootstock cv Freedom, 38° 10.693 N, 121° 13.800′ W) and one in Dunnigan, Yolo County (D-GVD) (rootstock cv 101-14, 38° 51.181′ N, 121° 55.452′ W).

At each site, intact cores were collected in metal cylinders (depth 5 cm, diam. 5 cm, volume 98.2 cm^3) to ensure that patches of soil and organisms remained intact and undisturbed. Cylinders were pushed into the soil and then carefully excavated and covered top and bottom with plastic petri dishes to hold the soil in place during transportation. The rationale for this sampling strategy was to assemble microcosms with a diversity of predator/prey ratios by taking advantage of the patchy distribution of nematodes in soil. Between 3 and 15 pairs of cores were taken at each site. Each pair of cores was considered more likely to represent the same or similar soil patches than would be the case with individual cores positioned at random. In the laboratory, the soil in one core of each pair was heat-defaunated (DF), the other remained non-defaunated (NDF). The purpose of the DF cores was to obtain a measure of the suppressiveness of the physical and chemical component of the soil in the absence of resident biological activity while that of the NDF cores was to assess the additional suppressiveness of the biological component. Three additional samples from each site were used to check for natural occurrence of the test nematodes (i.e., *M. incognita* and *S. feltiae*), for abiotic soil measures (DOC, %N, % C, C/N, %silt, %sand, %clay, moisture %, pH), and microbial biomass carbon (MBC). All cores of soil were transported to the laboratory in insulated containers and stored at 4 °C until processed.

Dissolved organic carbon (DOC) was determined from unfumigated extracts and MBC was the difference between DOC in unfumigated and fumigated extracts (Brookes et al., 1985; Vance et al., 1987). Organic C in 0.5 M K_2SO extracts was measured after dilution (1:10) with a Phoenix 8000 UV enhanced-persulfate digestion TOC analyzer (Dohrmann [Tekmar-Dohrmann], Manson, OH) according to the method of Wu et al. (1990). Samples were air-dried, sieved (<2 mm) and ground in a mortar and pestle. Weighed subsamples of approximately 30 mg were analyzed for C and N content using an elemental combustion analyzer (Costech Analytical