



The evaluation of entomopathogenic nematode soil food web assemblages across Switzerland reveals major differences among agricultural, grassland and forest ecosystems



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ABSTRACT

Entomopathogenic nematodes (EPNs) occur in natural and agricultural soils and contribute to the control of soil dwelling insect pests. Ecosystems differ in their soil parameters (pH, moisture, texture, etc.) and microhabitat conditions (presence of roots, plant cover, belowground fauna, etc.), which can affect the EPN soil food web assemblage in an unpredictable manner. By comparing soils that represent different ecological scenarios, we can link the natural distribution of the EPN to abiotic and biotic factors that shape the assemblages of soil food web to unravel the factors that determine EPN abundance and activity. We hypothesized that the EPN soil food web assemblages are affected by agricultural management practices and that this should be reflected when compared to natural ecosystems, such as forests and grasslands. By combining traditional and state-of-the-art molecular tools, we targeted 25 soil organisms to explore EPN food web in 40 Swiss georeferenced sites that can be categorized as “agricultural area”, “forest”, and “grassland”. EPNs abundance, richness and diversity did not vary among the different ecosystems. However, EPN activity (capability to kill insects) was higher in grasslands. Similarly, the free-living nematodes (FLNs) that compete with EPN for the cadavers were much more abundant in grassland, while reduced in the forest soils, suggesting contrasting conditions between these two natural areas. Nematophagous fungi (NF) were more diverse and present in agricultural areas, suggesting that the abiotic conditions in the agricultural areas may favor NF presence. Six soil properties and environmental factors shaped the EPN soil food web in Swiss soils (pH, elevation, clay content, soil water content, temperature, and rainfall), which explained 54% of the community variation in multivariate analysis. These observations were consistent with the key abiotic variables described for subtropical and Mediterranean regions. Identifying the links between the abiotic and biotic factors in very distinct areas can be the basis for predicting EPN soil food web assemblages. Such information can be of value for developing strategies to favour EPN resilience in a changing environment and enhance their capacity as biocontrol agents.

1. Introduction

The diversity and abundance of soil organisms such as bacteria, fungi, protists, micro-arthropods, nematodes and earthworms are reliable indicators of soil ‘health’ (Kennedy and Smith, 1995; Singh et al., 2011). Many of these provide key services in agroecosystems such as decomposition of the organic matter, aeration of the soil, and the control of pests and diseases (Garbach et al., 2014).

Entomopathogenic nematodes (EPNs) have been studied extensively because of their high potential as biological control agents and they are highly suitable as model organisms for ecological research (Lewis et al., 2006; Stuart et al., 2006; Campos-Herrera et al., 2012a; Stock, 2015). EPNs belonging to the Steinernematidae and Heterorhabditidae families are parasite of insects (Dillman et al., 2012). They live freely in the soil in the form of infective juveniles (IJs) in search of a host to penetrate. They penetrate the host, and once inside, the IJs release their

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associated bacteria, which proliferate in the insects' homeocel. This causes septicemia and leads to host death within 2–5 days (Dillman et al., 2012; Stock, 2015). Inside the host, EPNs will multiply over several cycles until the resources inside the cadaver are depleted. Then, nematodes develop a new generation of thousands of IJs that leaves the host to pursue the same cycle over again.

In the soil, IJs have to cope with the pressure of abiotic conditions such as water content, temperature, pH, and soil texture (Stuart et al., 2006, 2015; Lewis et al., 2015). In addition, EPN populations are strongly affected by the presence of natural enemies such as nematophagous fungi (NF), certain microarthropods (mites, collembolans) and protists that prey upon EPN. In addition, ectoparasitic bacteria in the genus *Paenibacillus* can limit EPN movement and scavengers such as certain free-living nematodes (FLNs) can compete for insects as a resource (Kaya and Koppenhöfer, 1996; Kaya, 2002; Duncan et al., 2003; El-Borai et al., 2005; Enright and Griffin, 2005; Stuart et al., 2006, 2015; Campos-Herrera et al., 2012a,b, 2015a; Geisen et al., 2015; Lewis et al., 2015; Blanco-Pérez et al., 2017; Helmberger et al., 2017). Various studies that employed the traditional insect-bait technique have linked the presence of EPNs to abiotic factors (Hominick and Briscoe, 1990; Hara et al., 1991; Liu and Berry, 1995; Stock et al., 1999; Sturhan and Lisková, 1999; Griffin et al., 2000; Hazir et al., 2003; Mráček et al., 2005; Hatting et al., 2009; Campos-Herrera et al., 2007, 2008). Much rarer are the studies evaluating the impact of biotic factors on EPN presence using traditional techniques (Duncan et al., 2003, 2007; Ram et al., 2008). Nowadays, the employ of molecular tools such as quantitative real time PCR (qPCR) has proven to be an efficient method to expand our ability to study the presence and the abundance of EPNs and their related soil food web in different soil systems (Campos-Herrera et al., 2011a,b, 2015b). The combination of a molecular approach with the conventional baiting method, provides additional information on the suppressive potential of the soil and the various interactions between EPN and their natural enemies and competitors (Campos-Herrera et al., 2015a; Jaffuel et al., 2016).

Characterizing EPN soil food web assemblages in distinct habitats, we can reveal patterns of interdependence and key soil properties susceptible to modifications that favor the presence and activity of EPNs as biological control. For example, studies carried out in Florida compared the presence and abundance of EPNs, FLNs and NF in natural areas and in citrus orchards for two different ecoregions: central ridges (sandy soils, well-drained areas) and flatwoods (variable texture, tendency for saturated soils). Overall, EPN abundance was found not to differ between ecoregions, but abiotic parameters such as ground water depth, pH, and clay content consistently shaped the EPN soil food web assemblage (i.e. EPN, FLN into *Acrobeloides*-group and NF) (Campos-Herrera et al., 2013a, 2016a). It was proposed that in these ecoregions in Florida, the local abundance of nematodes is an important factor modulating population growth of NF (bottom-up effect), but not *vice-versa*, which is in agreement with a subsequent study by Pathak et al. (2017) that focused on NF spatial distribution. Similarly, another study carried out in Murcia (Spain) comparing agricultural, natural and polluted areas in a gradient established in a mining district, reported that certain soil parameters (water content, P/K, pH and organic matter content) affected the assemblage of the soil community members (FLN, NF, EPN) (Campos-Herrera et al., 2016b).

In agroecosystems, the management practices can significantly modify soil properties and disturb the presence of beneficial soil organisms (Fraser, 1994; Filser et al., 1995; Bunemann and McNeill, 2004). Intensive management, such as tillage, and the employ of agrochemicals may have a negative impact on the naturally occurring EPN (Rovesti et al., 1988; Campos-Herrera et al., 2008; Susurluk and Ehlers, 2008; Laznik and Trdan, 2014; Lewis et al., 2015; Shapiro-Ilan and Dolinski, 2015; Stuart et al., 2015). Also, the type of crop, for instance annual *versus* perennial, may affect soil properties that are important for EPN proliferation (Campos-Herrera et al., 2008). Indeed, studies on annual crops in Switzerland revealed some differences

among crops, whereas management practices did not affect EPN presence or activity (Campos-Herrera et al., 2015b; Jaffuel et al., 2016), possibly due to low overall numbers of EPN, or low densities of potential host or the combination of both (Shapiro-Ilan et al., 2006; Koppenhöfer, 2007). Good knowledge of the underlying mechanisms is needed if we wish to improve soil conditions in agroecosystems such that they favor the presence and activity of natural enemies of pests (Tschamtko et al., 2007).

We hypothesized that the different characteristics of the soil in an ecosystem influence the EPN food web assemblage. In agroecosystems, the disturbances due to management practices (in annual crops) may limit the presence and the abundance of EPNs in the soil as compared to more natural areas such as forests and grasslands. Similar to EPNs, members of the associated food web (e.g. NF and FLN that compete for the cadavers) might also be affected by the differential soil conditions in agricultural areas, thereby indirectly influencing the EPN presence and abundance. The aim of this study was to get new insights into the biotic and abiotic factors that drive the presence and diversity of EPNs, as well as that of their natural enemies in distinct ecosystems in Switzerland. We studied this in wheat field and broader agricultural-managed plots, as well as more naturalized areas such as forests and grasslands.

2. Material and methods

2.1. Survey design, soil sampling and measurements of abiotic parameters

From February to June (after the thaw) 2014 and 2015 we sampled soils from different Swiss sites categorized as “agricultural area” (n = 10), “forest” (n = 10) and “grassland” (n = 10). The geo-referenced localities of the sampling sites are part of the Swiss Soil Monitoring Network (NABO, www.nabo.ch). Ten extra geo-referenced “wheat field” sites spread across Switzerland (NRP68-nematode project, <http://www.nrp68.ch/en>) were also sampled from April to June in 2013 and 2015 (Fig. 1). Whenever possible, the sampling order was altered in the second year (Supplementary material 1). At each site, we randomly took two independent composited soil samples consisting of 20 cores from the top 20 cm of soil, and transported to the laboratory and kept at 4° C until use. Various soil parameters were measured: soil organic content (SOC), calcium carbonate (determined by digestion with sulphuric acid and volumetric metering of the CO₂ produced, FAL, 1996), clay content and pH (CaCl₂) (FAL, 1996; measured only once) and bulk density. The soil water content was measured for 180 g of fresh soil of each sample by drying at 40 °C for a week. The elevation was recorded with Google maps (<https://www.google.fr/maps>), whereas the mean annual precipitation and the temperature were obtained from a weather station nearest to each sampled site (<http://www.prevision-meteo.ch>).

2.2. Measurements of soil food web members and estimations of suppressive potential of the soil against insect pests

In the laboratory, each soil sample (n = 160 for the whole survey: 2 years each site × 40 sites × 2 samples per site) was thoroughly mixed to homogenize the 20 cores of the composite sample. Two fresh subsamples of 400 g were prepared from each of the composite soil samples. No later than 2–4 days after collection, one 400 g soil aliquot was used to extract nematodes and other soil organisms by sucrose centrifugation (Jenkins, 1964), to be used in real-time qPCR analyses (Campos-Herrera et al., 2015b). To test the suppressive potential of the soil, the second 400 g fresh soil aliquot was divided in two portion of 200 g and each baited with 5 final instar *G. mellonella* larvae (commercial stock, Au Pêcheur SARL Neuchâtel, Switzerland) in two independent rounds (modified from Bedding and Akhurst, 1975). After 4 days exposure, the dead *G. mellonella* larvae were recovered from the soil, rinsed with tap water, and individually placed in White traps

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