



Does plant richness alter multitrophic soil food web and promote plant-parasitic nematode regulation in banana agroecosystems?



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ABSTRACT

Agroecosystem plant diversification at the field scale has been shown to enhance ecological pest regulation. We explored the effects of plant community composition and soil properties on the soil nematode community, with a particular interest in the regulation of banana plant-parasitic nematodes (PPN). We monitored banana phytometers (Cavendish Grande Naine cultivar) in 85 plots distributed along a plant richness gradient. Plant community composition, soil properties, abundance of bacterivorous, fungivorous and proportion of predaceous soil free-living nematodes, and abundance and damage of PPN (*Radopholus similis*, *Pratylenchus coffeae*, *Helicotylenchus multicinctus*, and *Meloidogyne* spp.) in phytometer roots were measured. We used structural equation modeling to investigate ecological processes leading to PPN regulation. Low-stratum plant species richness, but not high-stratum, was positively related to microbivore nematode abundances, supposedly because it promoted qualitative diversity of organic inputs and micro-climatic effects supporting more soil microorganisms. *Musa* genotype and low-stratum plant species richness induced associational susceptibility because of differential susceptibility of *Musa* genotypes to PPN and because of polyphagia of PPN spreading outside the *Musa* family, respectively. We found no regulation of PPN by predaceous nematodes, probably because food web complexity prevented trophic cascades from propagating. Ultimately, fungivorous nematode abundance was negatively related to PPN abundance, suggesting apparent competition or increased regulation by antagonistic fungi. Our results suggest that, when facing generalist pests, cropped plant communities should be diversified to promote pest regulation but must be carefully assembled to limit pest susceptibility heterogeneity among crop genotypes and to exclude alternative host plant species.

1. Introduction

According to the “resource concentration hypothesis” (Root, 1973), monocultures are prone to pest and disease infestation. Since the 1990’s, agroecosystem plant diversification is increasingly considered a promising way to restore positive interactions among plants and promote ecological pest regulation (Altieri, 1999; Malézieux et al., 2009; Tschamtkke et al., 2012; Leakey, 2014; Isbell, 2015). Meta-analyses have shown that field-scale agroecosystem plant diversification might be associated with regulation of diverse pests (Quijas et al., 2010; Letourneau et al., 2011; Boudreau, 2013; Dassou and Tixier, 2016), including plant-parasitic nematodes (PPN). In some cases, however, plant diversification may favor pests (Schroth et al., 2000; Norris and Kogan, 2005) leading to increased damage (Quijas et al., 2010; Letourneau et al., 2011).

Plant diversification can have positive, negative or neutral effect on PPN abundance in agroecosystems (Boudreau, 2013). Several studies have demonstrated that the effect of primary resource diversification on the soil food web depends on the identity of the plants and is more likely attributable to the complementarity in resource quality than to an increase in total resource quantity (Wardle et al., 2003; de Deyn et al., 2004; Djigal et al., 2012). In these studies, authors compared the soil food webs before and after an artificial change in vegetation during short experiments (from 8 to 28 months). Therefore, they rather assessed the effect of perturbations on nematode communities than the influence of plant diversity or richness on these communities in perennial cropping systems. *A fortiori*, nematodes belong to the below-ground compartment of ecosystems, which presents inertia in responding to changes in the plant community (Korthals et al., 2001;

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Eisenhauer et al., 2010; Wardle and Jonsson, 2014). Because of their direct dependence on plant resources, PPN are more responsive to changes in vegetation than nematodes belonging to other trophic groups (Korthals et al., 2001). Short-term studies may therefore observe transitive community states rather than the final consequence of plant diversification on the soil food webs and ultimately on PPN regulation.

Banana-based agroecosystems provide a good model to study the effect of plant community diversity on the soil food web and the regulation of PPN since bananas are grown as semi-perennial or perennial crop under wide ranges of plant community structure and composition. Among the most damaging pests in banana agroecosystems are the PPN (Gowen et al., 2005) which reduce yields by disrupting soil resource uptake and by causing banana plants to topple (Quénéhervé, 2008). Banana roots are attacked by various PPN species presenting different parasitic modes (Gowen et al., 2005; Quénéhervé, 2008). The main banana PPN are the migratory and strict endoparasites *Radopholus similis* and *Pratylenchus coffeae* which perform their entire cycle within the central cylinder of the roots (Gowen et al., 2005), the migratory semi-endoparasite *Helicotylenchus multicinctus* which is confined to the cortical cells of the roots (Orion et al., 1999), and the sedentary endoparasite *Meloidogyne* genus, in which females form root galls before releasing juveniles in the soil. In export banana production, nematicides have been widely used to control PPN resulting in 5–267% yield increases (Quénéhervé, 2008). However, nematicides represent a threat to beneficial nematodes (Timper, 2014), human health and the environment (Matthews, 2006), and their efficiency may decrease with repeated application (Moens et al., 2004). In French West Indies, nematicides have led to water, soil and reef pollutions (Bocquéné and Franco, 2005; Cabidoche et al., 2009) with consequences on human health and ecosystem functioning. To control PPN more sustainably, growers may adopt cultural practices to interrupt PPN population growth such as fallow or rotation with non-host crops and clean material replanting (Quénéhervé, 1993). Unfortunately, these practices did not lead to economic and environmental benefits in all farm contexts (Blazy et al., 2009). Elsewhere, cultural practices relying on biodiversity, i.e. mixed crops or cultivars, the introduction of antagonistic or trap plants or the use of resistant cultivars, have emerged in subsistence agriculture where farmers cannot afford nematicides (Bridge, 1996). Such field-scale spatial diversification practices have been reported to enhance PPN regulation for several crops but rarely for bananas.

In banana agroecosystems, the mixture of banana genotypes is likely to affect PPN abundances, as banana genotypes are more or less susceptible to PPN (Quénéhervé et al., 2009, 2011). The addition of cover crops has been showed to affect the abundance of multiple nematode trophic groups (Djigal et al., 2012). Moreover, the composition of the plant community may determine the quality and quantity of organic matter and interfere with the composition of the soil community (detritivore micro-organisms and nematodes) and affect PPN regulation (Tabarant et al., 2011). Trophic links may be involved in the regulation of PPN (Khan and Kim, 2007; Holtkamp et al., 2008). Recent studies using molecular gut analysis confirmed that predaceous nematodes were feeding on PPN, especially when in contact with the rhizosphere, (Cabos et al., 2013; Wang et al., 2015). However, the efficacy of predaceous nematodes as biological control agent may depend on their abundance relatively to that of PPN, the length of their life cycle, their sensitivity to soil perturbations and their degree of specialization (Neher, 2010). Antagonistic fungi trapping or feeding on PPN are also expected to play a role in PPN regulation (Siddiqui and Mahmood, 1996; Dong and Zhang, 2006; Mendoza and Sikora, 2009).

In this study, we monitored multitrophic soil food webs including free-living and plant-parasitic nematodes in a gradient of plant species richness in farmers' banana fields established for more than two years. We used structural equation modelling to test for and understand the effects of plant richness (crop and non-crop) and soil properties on the soil food web, and ultimately on banana PPN regulation.

2. Methods

2.1. Study regions

We conducted a field study in the Lamentin Plain in the center of Martinique, French West Indies (14°28'–14°40' N, 60°54'–61°05' W) and in the Talamanca Reserve (9°00'–9°50' N, 82°35'–83°05' W) in south-eastern Costa Rica. These two tropical, humid regions have similar pedo-climatic conditions and cover complementary ranges of agroecosystem plant diversity, ranging from intensive monoculture to highly diversified agroforestry. In the Lamentin Plain, bananas and plantains are mainly grown as a monoculture on bare soil or with a cover crop; fields eventually include spontaneous cover or marginal crops or trees (e.g., citrus trees, coconut trees, sugar cane). In the Talamanca Reserve, banana agroecosystems mainly consist of agroforestry systems varying in terms of plant community structure and composition, but including monocultures. Agroforestry systems may contain a mix of cultivars and include remnant forest trees, cultivated trees (e.g., cacao trees), medicinal plants, ground crops (e.g. taro, cassava) and weeds. The mean annual temperature measured within our sampling zone during the study was 26.7 ± 0.4 °C in Martinique and 24.8 ± 0.3 °C in Costa Rica. The mean annual rainfall ranges from 1500 to 2500 mm from south to north on the Lamentin Plain (Duyck et al., 2012) and is about 3500 mm in the Talamanca Reserve (Deheuvels et al., 2012). Soils are alluvial soils or Ferrisols (Colmet-Daage and Lagache, 1965; Winowiecki, 2008).

2.2. Phytometers

We monitored a network of 85 twenty-meters diameter circular plots (29 plots in Martinique and 56 plots in Costa Rica) distributed in 9 heterogeneous banana-based farmers' fields. All fields were established for at least 2 years at the beginning of the experiment. Fields and plot locations were selected *a priori* to cover a wide range of plant species richness situations. We installed one *in vitro*-propagated banana plant (*Musa* AAA, Cavendish subgroup, Grande Naine cultivar) in the center of each plot as a phytometer (Fig. S1 in Supplementary material). The phytometers are standardized plants (genetically similar) initially free of nematodes and experimentally transplanted in contrasted situations to assess responses to environmental variables (Dietrich et al., 2013). Each phytometer was placed 1.5 m distant from an existing banana plant. Within one field, adjacent phytometers were at least 20 m apart so that two adjacent plots never overlapped. The study began in July 2014 and ended in January 2016. No chemical control of nematodes or soil perturbation occurred in any of the fields during the study. In each plot, we evaluated the abiotic properties of the soil, plant richness, *Musa* abundance and richness, abundance of free-living nematodes in the soil according to trophic group, PPN abundance in the phytometer roots and damage caused to the phytometer roots.

2.3. Plant community

Plant species richness is commonly used as an indicator of ecosystem plant biodiversity (Letourneau et al., 2011; Soliveres et al., 2016). Within each plot, we subdivided the plant community into a low stratum (plant height at top of the crown < 1.5 m) and a high stratum (plant height at top of the crown \geq 1.5 m) to account for differential effects related to differences in plant traits such as root depth and growth dynamics. Plant species richness of the high stratum was calculated as the number of plant species present in the plot after identification of each plant to species level. We evaluated the species richness of plants smaller than 1.5 m high along four transects of 10 m, going from the phytometer to the border of the plot and oriented toward the four cardinal points (Fig. S1). For each transect, we counted the number of plant species encountered along the transect within a 20-cm wide strip. Plant species richness of the low stratum was obtained by

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