Consequences of *Melaleuca quinquenervia* Invasion on Soil Nematodes in the Florida Everglades

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Abstract: The tree *Melaleuca quinquenervia* invades all types of habitats of South Florida leading to up to 80% loss of aboveground diversity. To examine impacts on the belowground ecosystem, we investigated the composition and diversity of nematodes from soils dominated by the invasive tree and compared them with soils supporting native plant communities at six locations across the Florida Everglades over three years. Despite the significant differences in soil type, hydrology, and native plant composition of the sites, there were consistent differences in nematode communities between soil environments under the native and invaded plant communities. The total abundance and diversity of nematodes in soils dominated by *M. quinquenervia* was 60% and 80% of adjacent soils under native plants. Fungal-feeding and plant-parasitic nematodes were twice as abundant under native plants as under *M. quinquenervia*. Nematode communities under *M. quinquenervia* were bacterivore-dominated, while under native vegetation plant-parasite dominated. The overall diversity of nematodes was 20% lower under the exotic than under native plants, with plant parasites being 36% and fungivores being 30% less diverse. Soil moisture, % of Ca, Mg, and clay particles and total soil C and N were greater in *M. quinquenervia* soils, but plant-available concentrations of P, K, Ca, and Mg as well as CEC were reduced. Overall, data suggests that the invasion process may modify soil biotic and abiotic conditions that in turn promote the advancement of the exotic *M. quinquenervia* and displacement of the native plants.

Key words: diversity, ecology, enemy release, exotic plant, Florida Everglades, invasive, *Melaleuca quinquenervia*, nematode community, nematode diversity, plant-soil feedback, soil chemistry

Exotic plant invasions threaten managed and natural ecosystems worldwide (Chapin, 2000). In natural systems, invasions can alter ecosystem function through changes in native biodiversity and trophic structure (e.g., Vitousek et al., 1997; Belnap and Phillips, 2001; Forys and Craig, 2002), ecosystem processes (e.g., Vitousek and Walker, 1989; Mack and D'Antonio, 2003) and disturbance regimes (Evans et al., 2001). There are many theories to explain the extraordinary success of invasive plants (e.g., species richness of native plant communities (Elton, 1958), life history traits (Rejmánek and Richardson, 1996), release from enemies (Elton, 1958; Mitchell and Power, 2003; Callaway et al., 2004), or disturbance (Myers and Bazely, 2003)), but rarely has it been suggested that the interaction between plant and its soil environment plays an important role in plant invasions.

Complex interactions and feedbacks at the aboveground-belowground interface represent potentially important factors regulating ecosystem processes and properties (Wardle et al., 2004). Positive feedbacks may occur when changes in the soil community induced by a plant species promote growth and dominance of that species, while under negative feedbacks, the relative growth rate of a plant is reduced (Bever, 1994; Bever et al., 1997). Negative feedbacks are hypothesized to result from accumulation of root pathogens and parasites and are suggested to operate in native plant communities. Dominant and invasive plants are presumed to function under more positive feedbacks that are associated with mutualistic symbionts and/or lower root pathogen pressure (Klironomos, 2002; Reinhart et al., 2003).

Melaleuca quinquenervia (Cav.) S. T. Blake was introduced to Florida in the late 1800s. In its native range of Australia, *M. quinquenervia* occurs in coastal, seasonally flooded wetlands. Fire adaptation, thick bark saturated with water, root and trunk bud sprouting, fire-induced seed release and seed wind dispersal (Serbesoff-King, 2003) enabled *M. quinquenervia* to adapt to the fire-driven Florida Everglades. *Melaleuca quinquenervia* is on a Federal Noxious Weed List, USDA, 7 CFR-360 (Plant Protection and Quarantine, 1999) because it has invaded all types of terrestrial and wetland habitats, including undisturbed pine flatwoods, sawgrass-dominated communities and cypress swamps (Bodle et al., 1994), but also roadsides, pastures and urban sites (Turner et al., 1998). Thus far, the invasion has converted >200,000 hectares of South Florida ecosystems to closed-canopy *M. quinquenervia* forests (dense *Melaleuca* trees) with limited understory vegetation. With 60 to 80% loss of native biodiversity (Austin, 1978; Mazzotti et al., 1985; O'Hare and Dalrymple, 1997), these invaded habitats are ecologically and functionally very different from the native communities (Van et al., 2000). Due to the effects *M. quinquenervia* has on the native diversity aboveground, we hypothesized that similar effects would be observable belowground and that the changes in the soil environment (biotic and abiotic) could potentially result from the presence of less negative feedbacks.

Materials and Methods

Study area: With no comparable native populations of plants to *M. quinquenervia* with its ability to invade all types of ecosystems, the sampling sites (Fig. 1, C–Clewiston, CS–Corkscrew Swamp Sanctuary, FM–Fort Meyers, HP–Holiday Park, LW–Lake Worth and PP–Prairie Pines) were selected to include a variety of environmental conditions under which the exotic tree thrives, and these included different types of native plant communities, hydrological patterns and geographical locations within South Florida (Table 1). A common feature to all sites was long-term (20–50 yr) presence of *M. quinquenervia*, prior to anthropogenic disturbance (for both invaded and noninvaded sites), and the presence of biological control agents (*Boreioglycaspsis melaleucae* [Moore] and *Oxyops vitiosa* [Pascoe]) released in earlier years to limit the invasive potential of the exotic.

Sampling design and variables: Within each of the six sites, one random survey plot (200 m × 200 m) was selected in invaded plant community (dominated by *M. quinquenervia,* called Melaleuca Plot or MP) and one random survey plot in an adjacent site under native vegetation (Native Vegetation Plot or NVP). Inferences from the analyses are based on the assumption that all sites were equally vulnerable to invasion. In fact, individual *Melaleuca* tree islands and the progress of the invasive edge into the native sites can be observed. Within each plot, four 12-m long replicate transects separated by at least 10 m were laid out. Soil samples were collected at 1-m intervals along each transect, resulting in a composite soil sample of 12 soil cores (2-cm-diam. × 10-cm-depth). Each core was taken through any organic horizons present. Within 1 m of soil coring, plant identity was registered. To account for year-to-year climatic variability, the surveys were repeated in

2004 and 2006, but always before the rainy season (Table 1). Samples were kept in a cooler and away from direct exposure to sunlight during transport to the laboratory at FLREC and stored at 4°C until processing. Each soil sample was analyzed for nematodes, soil moisture, chemistry and texture.

Sample processing: Nematodes were extracted from 100 cm^3 soil subsamples using the sugar flotation-centrifugation procedure (Jenkins, 1964) and enumerated and identified to genus level using an inverted microscope. Nematodes were classified to trophic groups following Yeates et al. (1993) as bacterial and fungal feeders, plant parasites (nematodes feeding on plant roots), omnivores/predators (nematodes feeding at several trophic levels) and strict predators (mainly Mononchida). Tylenchida with unconfirmed feeding habits (plant parasites/fungal feeders) were considered plant parasites. Diversity indices (Shannon-Weaver and Simpson's) at genus and trophic level and ratio of fungal- to bacterial-feeding nematodes (F/B) were calculated.

Approximately 10 g of soil was dried in an oven at 100°C for 48 hr to determine soil moisture (Jackson et al., 2000). The remaining soil was air-dried and passed through a 2-mm sieve to remove plant debris. Two grams of soil was ground to a fine powder using a ball mill, and subsamples (~0.250 g) were analyzed for total C and N using Perkin Elmer CHN Elemental Analyzer (PerkinElmer, Inc., Shelton, CT). The Walkley Black method was used to determine soil organic matter. Plant-available concentrations of P, Ca, Mg and K were estimated from Mehlich III soil extracts by Inductively Coupled Plasma Spectrophotometry. Hydrogen-ion activity (pH) was measured in 1:1 soil to water dilution and buffer pH using Adams Evans buffer. A hydrometer method was used to determine soil particle size distribution. Detailed methods can be found in Methods of Soil Analyses (Black et al., 1997).

Statistical analysis: Prior to analysis, nematode data were transformed using log (x+1) to address heteroscedasticity. All data were subjected to 3-Way analysis of variance to test for effects of vegetation origin (exotic vs. native), location (6 sites) and year of sampling (2004 vs. 2006). All differences were considered significant at $P \leq 0.05$, and post hoc Sheffe's test was performed to separate differences between sites. *F* statistic values are reported as $F_{x,y}$, with *x* and *y* indicating treatment and error test degrees of freedom. Although statistical analyses (SAS Institute StatView 5.0) were performed on log transformed data, untransformed averages along with standard deviations (SD) are reported throughout the paper, tables and figures.

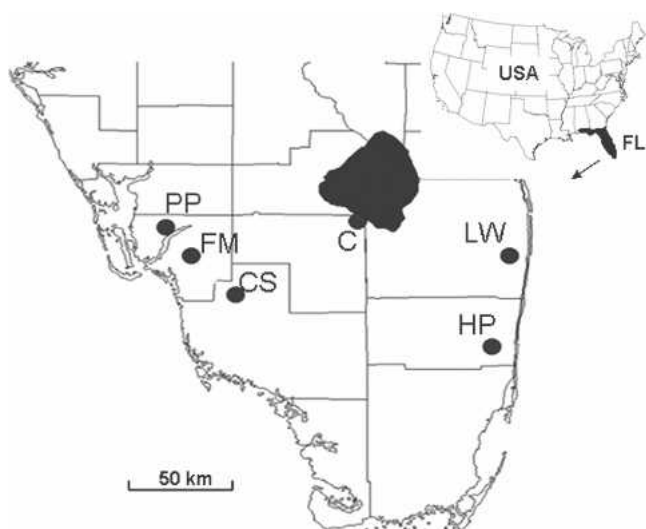FIG. 1. Distribution of the six sampling sites from across South Florida used in this study. Abbreviations are as follows: C–Clewiston, CS–Corkscrew Swamp Sanctuary, FM–Fort Myers, HP–Holiday Park, LW–Lake Worth, PP–Prairie Pines. An insert map of the United States illustrates the location of Florida.

Results

Nematode community: There were 86 nematode genera identified across all sites and years, out of which more

TABLE 1.   Description of the experimental sites used in the study. Sites were selected primarily to represent diversity of ecosystems prone to *Melaleuca* invasion. Site characteristics varied in relation to: 1. Hydrological patterns, 2. Type of native vegetation under the threat of *Melaleuca* invasion and the status of *Melaleuca* where the invasion has been well established, and 3. Years under *Melaleuca* invasion. In addition, total coverage area (ha), geographic location within Florida, and the exact dates of sampling are indicated in the "Site" column.

Site	Native vegetation plots	*Melaleuca* plots
Clewiston (**C**) 8.1 ha Central: 26.743 N, 80.889 W 6 May 2004, 7 June 2006	1. Seasonally flooded 2. Sawgrass marsh 3. Not invaded	1. Seasonally flooded 2. Dense mature trees 3. 30–40
Corkscrew Swamp Sanctuary (**CS**) 5.3 ha West: 26.378 N, 81.595 W 8 Jan 2004, 13 July 2006	1. Never flooded 2. Pine flatwoods 3. Not invaded	1. Never flooded 2. Dense saplings to mature trees 3. 40–50
Fort Meyers (**FM**) 15 ha West: 26.546 N, 81.786 W 16 Dec 2003, 6 July 2006	1. Never flooded 2. Cypress dome 3. Not invaded	1. Never flooded 2. Dense saplings 3. 20–30
Holiday Park (**HP**) 42.5 ha East: 26.057 N, 80.439 W 9 Jan 2004, 9 June 2006	1. Seasonally flooded 2. Sawgrass marsh 3. Not invaded	1. Seasonally flooded 2. Dense mature trees 3. 30–40
Lake Worth (**LW**) 1 ha East: 26.565 N, 80.132 W 2 Feb 2004, 30 June 2006	1. Never flooded 2. Pine flatwoods 3. Not invaded	1. Never flooded 2. Dense mature trees 3. 20–30
Prairie Pines (**PP**) 25.9 ha West: 26.726 N, 81.879 W 16 Dec 2003, 15 June 2006	1. Seasonally flooded 2. Pine flatwoods 3. Not invaded	1. Seasonally flooded 2. Saplings to mature trees 3. 20–30

than half were affected by either vegetation origin (native vs. exotic), year of sampling (2004 vs. 2006), site of sampling (C, CS, FM, HP, LW, PP), or their interactions (data not shown, available upon request). As expected, site characteristics and time of sampling had a major impact on a majority of the nematode measures; however, we will discuss these only in the context of the effects of vegetation origin, as this was the most important subject of our study.

Almost 80% of all identified nematode genera showed no response to *M. quinquenervia* invasion, and these included predominantly bacterial-feeding and omnivory/predatory nematode taxa. However, about 20% of nematode genera were responsive (a change of abundance or percent composition) to the shift of vegetation from native to *M. quinquenervia*-dominated, and they included representatives of all trophic groups except algivores. The overall effects of *M. quinquenervia* on the sensitive nematode genera were generally negative (Table 2), but the exact patterns were often dependent on the site and year of sampling (Table 2). From the responsive nematode genera, only *Cryptonchus* (bacterivore, $F_{1,71}$ = 5.6), *Diphtherophora* (fungivore, $F_{1,71}$ = 38.9), *Heterodera* and *Mesocriconema* (plant parasites, specialized and general feeders, respectively; $F_{1,71}$ = 45.1 and 41.2) showed a consistent decrease of abundance under the influence of *M. quinquenervia* regardless of the site and year of sampling (Table 2). Other nema-

tode genera were site-specific. For instance, *Hemicycliophora* (plant parasite, $F_{1,71}$ = 4.7) was generally suppressed by the presence of *M. quinquenervia* at five out of six sites, but at one site (FM) the pattern was reversed. In contrast to typically negative responses to *M. quinquenervia* presence, two nematode genera (*Acrobeles*, bacterivore, $F_{1,71}$ = 10.9 and *Dorylaimellus*, omnivore [but see Yeates et al., 1993], $F_{1,71}$ = 7.8) increased their abundances under *M. quinquenervia*, but again the exact patterns were site- and year-specific. The extent of the impact by *M. quinquenervia* invasion on nematodes varied considerably among nematode genera and ranged from 50% (e.g., *Hemicycliophora*) to 2,000% (e.g., *Mesocriconema*) reduction as the soil environment shifted from the influence of the native vegetation. The abundances could be reduced by a factor ranging between 1 and 100, with fungal feeders experiencing the most consistent reductions (2–5 times), and plant parasites the most severe reductions (e.g., the density of *Helicotylenchus* was reduced to zero under *M. quinquenervia* from an average of 376 and 658 individuals/100 cm^3 under the native vegetation in years 2004 and 2006, respectively).

The decrease of densities at the genus level was also observable at the level of a trophic group (Table 2). Overall nematode abundance was reduced by 40% by the influence of *M. quinquenervia* ($F_{1,71}$ = 13.1), with fungivores ($F_{1,71}$ = 8.2) and plant parasites ($F_{1,71}$ =

TABLE 2.   The direction of change (increase: +, decrease: –) in the biotic (abundance at the genus and trophic level, percentage of trophic groups and richness of nematode genera within trophic groups and total nematode community) and abiotic measures as the ecosystem shifted from the influence of the native vegetation to *M. quinquenervia* at individual sites in both sampling years. Only measures that showed statistically significant ($P \leq 0.05$) responses are presented. (+) or (–) next to the measure (e.g., *Acrobeles* (+) or *Alaimus* (–)) indicates an overall trend as determined by statistical significance ($P \leq 0.05$) of ANOVA across all sites and years.

Variable	C 2004	C 2006	CS 2004	CS 2006	HP 2004	HP 2006	LW 2004	LW 2006	FM 2004	FM 2006	PP 2004	PP 2006
Biotic measures												
Genus												
Acrobeles (+)	–		+							+	+	+
Alaimus (–)	–			+	–	–		–		–		
Chronogaster (–)			–		–			–		+		
Cryptonchus (–)			–		–			–				
Panagrobellus (–)			+						–	–	–	
Zeldia (–)	–		–	+							–	–
Diphtherophora (–)	–	–	–				–		–	–		–
Leptonchus (–)	–		–	–			–	+	+	+		
Tylencholaimus (–)	–	–				+	+					
Helicotylenchus (–)	–	–		+			+	–		–	–	–
Hemicriconemoides (–)			–	+	–		+		–		–	
Hemicycliophora (–)	–		–		–		–	–	+	+		–
Heterodera (–)				–		–	–					
Mesocriconema (–)	–	–			–	–	–	–				
Nothotylenchus (–)	–	–			–			+	+		–	
Tylenchidae (–)	–	–	–	+			–				–	
Rare plant parasites (–)	–	–	–		–	–	–			+	–	
Dorylaimellus (+)	–	–	+	–		+	+	+	+		+	
Rare Mononchida (–)	–	–	–	–			–	–		+		–
Trophic												
Fungivores (–)	–	–				+	–			–		
Plant parasites (–)	–	–	–	+			+		+		–	
Total (–)	–	–	–			+	+				–	
% Bacterivores (+)	+	+	+								+	
% Plant parasites (–)	–	–	–	+					+		–	
% Predators (+)		+	+	–	+	+			+	+		
Richness												
Bacterivores (–)	–				–		+				–	–
Fungivores (–)	–				–	+	–			–		
Plant parasites (–)	–	–	–		–						–	
Total (–)	–	–	–								–	
Abiotic measures												
%H₂O (+)	+	+		+			+			–	–	
P (ppm) (–)	–	–	–		–	+			–	–		
K (ppm) (–)	–	–						–		–		
Ca (ppm) (–)	–	–		+			+		–			
Mg (ppm) (–)	–				+	–	+		–	–		
Ca (%) (+)		–	+	+			+	+	–		+	
Mg (%) (+)	+	+			+	–	–			+	+	
CEC (–)	–	–					–	+		–		
% clay (+)		+				+						–
% N (+)	+	+						–		–		
% C (+)	+	+								–		

32.5) being more than twice as abundant under native plants as under *M. quinquenervia* (Fig. 2). Moreover, the nematode communities shifted away from plant parasite-dominated (an average of 44% of plant parasites, 30% bacterivores) under native plants to bacterivore-dominated under *M. quinquenervia* (an average of 30% of plant parasites, 40% of bacterivores). In addition to changes in nematode densities, the diversity of nematodes was also affected. Significantly fewer nematode genera were observed among bacterial feeders (10%, $F_{1,71} = 6.2$), fungal feeders (30%, $F_{1,71} = 13.8$), and plant parasites (36%, $F_{1,71} = 66.3$), resulting in overall poorer nematode communities under *M. quinquenervia* by an average of 20% ($F_{1,71} = 30.9$) (Fig. 3). Surprisingly, changes observed for abundance and richness were not reflected in Simpson's and Shannon diversity indices either at the generic (overall averages 7.8 and 2.4, respectively) or trophic level (overall averages 2.7 and 1.1, respectively). Plant richness along the transects was not different between the two vegetation types and averaged 6 plant species/transect. Some of the encountered plants within the invasive but also the native plots
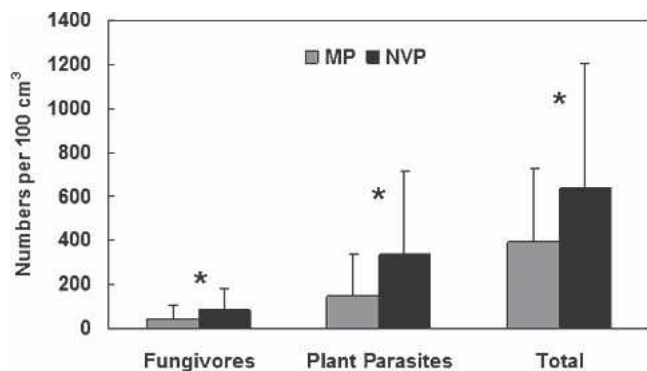
FIG. 2. Abundance of fungivorous, plant-parasitic and total nematodes under native vegetation (NVP) vs. *M. quinquenervia* (MP). Bars indicate means ± 1 SD (standard deviation) across all sites and years. Statistical differences were assessed on log(x+1) transformed data, but figure shows untransformed numbers. * indicates statistically significant ($P \leq 0.05$) differences.

included other exotics such as *Schinus, Casuarina* or *Lygodium* spp., but at sampling they were minimal components of the ecosystems.

As mentioned above, although general patterns could be discerned, they often depended on the specific characteristics of the sites. Consistent negative (decrease of abundance and/or richness) nematode responses to *M. quinquenervia* were observed only at two of the six sites (C and PP). At one location (FM), nematodes exhibited a positive response (increase of abundance and/or richness). At other sites, negative effects were more common, but positive responses were also present.

Abiotic measures: Almost all measures of the abiotic soil characteristic were significantly influenced by the origin of vegetation with site and year of sampling interaction (data not shown, available upon request). In contrast to the nematode measures, positive and negative effects were equally common. While positive effects to *M. quinquenervia* were observed for soil moisture, percentage of Ca and Mg, the contribution of clay par-
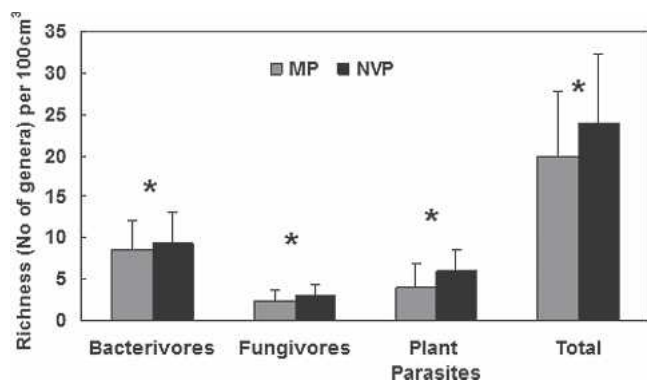

FIG. 3. Number of genera of bacterivorous, fungivorous, plant-parasitic and total nematodes under native vegetation (NVP) vs. *M. quinquenervia* (MP). Bars indicate means ± 1 SD (standard deviation) across all sites and years. Statistical differences were assessed on log(x+1) transformed data, but figure shows untransformed numbers. * indicates statistically significant (P ≤ 0.05) differences.

ticles, and total soil C and N, the overall plant-available concentrations of P, K, Ca and Mg as well as CEC were significantly reduced (Table 2). One of the most consistent responses across sites and years was significantly elevated soil moisture under *M. quinquenervia* ($F_{1,71}$ = 29.2). Although the average (across sites and years) soil moisture jumped only from 25% to 35% from plots under the native vegetation to *M. quinquenervia*, doubling (at CS), tripling (at C) or even quadrupling (at LW) of soil water content was common. The concentration of P ($F_{1,69}$ = 6.9) and K ($F_{1,69}$ = 101.2) was significantly suppressed under the influence of *M. quinquenervia* (average 7.3 ppm and 29.4 ppm, respectively), with their values under the native vegetation already at extremely low levels (average 8.8 ppm and 46.5 ppm, respectively). While CEC under *M. quinquenervia* (average 14.4) was almost half of that under the native vegetation (average 21.1) ($F_{1,69}$ = 20.6), the C ($F_{1,71}$ = 13.8) and N ($F_{1,71}$ = 10.3) content of soil almost doubled as a result of *M. quinquenervia* presence (C average 8.4%, N average 0.6%). Soil pH varied among sites ranging from acidic (~5 at CS) to slightly basic (~7.5 at C and HP), but there was no relationship between pH and vegetation cover. Soil organic matter content (OM) was generally low (2.5–5.5%) across all the sites, but the plant cover type had no effect on its value. All sites were dominated by sand (75–95%), with only C and HP having considerably greater levels of clay (~20%) than other sites (~5%). Clay content was found to be slightly higher under *M. quinquenervia* cover.

DISCUSSION

Differences in nematode community composition: Recent studies suggest that invading plant species could benefit from soil biotic communities by modifying their abundance, composition and structure so that the net effect of soil biota on the exotic plant growth is positive (Klironomos, 2002; Reinhart et al., 2003; Van der Putten et al., 2005). This is different from native plant species that are thought to be regulated by negative feedback (limited growth rate) driven by root herbivores and soil pathogens (Bever, 2003). The ability of exotic plants to change the direction of feedback from negative to more positive may result from an escape from their natural herbivores and pathogens (Callaway and Aschehoug, 2000; Klironomos, 2002). Our study indicates that *M. quinquenervia* influenced the development of depauperate nematode communities with reduction of both abundance and richness across nearly all nematode trophic levels. The most prominent reductions among plant parasites and fungivores could be indicative of reduced root parasite pressure and thus of a shift from more negative towards more positive feedbacks.

Ecological attributes of *M. quinquenervia* differ between its native and adventive range. In Australia, *M.*

quinquenervia is non-invasive, and its habitats are paradoxically considered threatened (Turner et al., 1998), while in South Florida the species has become an aggressive weed. A similar pattern was observed for *Prunus serotina* (Reinhart et al., 2003) where low densities of the tree in its native range (North America) were attributed to negative feedback from the soil community, while a high aggregation of trees in invaded regions of north-western Europe corresponded with positive feedback. Our preliminary data on nematode communities of the native range of *M. quinquenervia* agree with the above results, with total nematode abundances even larger than under South Florida native plants and plant parasites reaching as high as 90% composition. It is conceivable that belowground negative feedback in the home range of *M. quinquenervia* along with aboveground herbivores and pathogens (over 400 species of arthropods, 15 species of fungi) (Balciunas et al., 1994, 1995; Goolsby et al., 1999) limit tree success, while a release from negative feedback through an escape from pathogens and parasites plays a role in its invasiveness in the Florida Everglades. However, what exactly influences the nature of the feedback?

Composition and density of the soil community can vary with the plant species (Bardgett et al., 1998; Wardle et al., 1999; Klironomos, 2003; Porazinska et al., 2003) and with the quality and quantity of plant material that enter the soil (Wardle and Lavelle, 1997). The observed negative effects on soil nematodes in our study do not appear to result from low resource quality of *M. quinquenervia* (N = 0.7%, C:N = 74), as many native plants included in this study offer even lower tissue quality (e.g., pine or sawgrass with N of 0.4% and 0.55% and C:N of 130 and 82, respectively) (Van and Rayamajhi, personal communication). In addition, resource quantity does not explain the negative effects, as *M. quinquenervia* produces root densities at all depths several fold higher than those of many native plant species (e.g., bluestem or pine) (Lopez-Zamora et al., 2004). Additionally, litter inputs of *M. quinquenervia* are at least comparable to other Florida forests or to *M. quinquenervia* forests in its native region (Van et al., 2002). Clearly, factors other than plant resource quality and quantity must be responsible for reduced abundances and richness of the nematode communities.

Melaleuca quinquenervia is characterized by high concentrations of terpenoids (sesquiterpenes) and other essential oils of highly allelochemical nature (Brophy and Doran, 1996). Allelochemicals present in roots and in aqueous soil extract from root exudates and decomposing leaf litter (Wardle et al., 1998; Hierro and Callaway, 2003; Walker et al., 2003; Wolfe and Klironomos, 2005) can have a detrimental effect on the soil biota. Allelochemicals have been demonstrated to alter composition and function of the microbial community in soils that have been invaded, e.g., by *Centaurea diffusa* (Callaway et al., 2004), *Carduus nutans* or *Empetrum her-*

maphroditum (Wardle et al., 1998). Invasion by highly allelopathic *E. hermaphroditum* also has been shown to have strong negative effects on macrofauna and, similar to *M. quinquenervia*, results in thick litter accumulation (Wardle and Lavelle, 1997). Plant-parasitic nematodes, nematodes most closely associated with the plant and therefore potentially most sensitive to allelochemicals, were significantly more affected by *M. quinquenervia* than other nematode trophic groups, suggesting that less negative plant-soil feedbacks under *M. quinquenervia* may result from its allelochemical nature. Furthermore, since South Florida ecosystems lack native plant species related to *M. quinquenervia*, sesquiterpenes are novel to the soil biotic community, and so their effects may be exaggerated in the adventive range in comparison to the effects they can exert at their place of origin. Preliminary data for plant parasites under *M. quinquenervia* in its native range of Australia show considerable abundance and dominance exceeding by several folds those of South Florida. Most plant-parasitic genera were common to both regions (e.g., *Pratylenchus, Paratylenchus* and *Tylenchorhynchus*), but some were never observed in our study (e.g., *Cryophodera, Morulaimus*). It should be noted, however, that the magnitude of the effect on plant parasites was not equally negative. From the total of 13 identified genera of plant parasites in Florida, only seven were affected by the origin of vegetation. The group of genera unresponsive to *M. quinquenervia* included both ectoparasites and endoparasites, a distinct difference than that seen by Van der Putten et al. (2005). From the nematode genera that were negatively affected by *M. quinquenervia*, only two showed a consistent response, and these included both types, an endoparasitic specialist (*Heterodera*) and an ectoparasitic generalist (*Mesocriconema*). Although the other five nematode genera were, for the most part, suppressed by *M. quinquenervia*, the response was occasionally reversed. It is possible that *M. quinquenervia* always induces a negative effect on plant parasites (through allelochemicals) but the presence of other plant species in the system provides pockets of temporary refugia for these nematodes.

The scant literature on nematode communities in relation to plant invasions demonstrates variability of responses to an invader, ranging from no change of feedback (Belnap and Phillips, 2001) to a change towards more positive feedback (Van der Putten et al., 2005) to species- and site-specific responses with no overall general trends (Yeates and Williams, 2001). This wide array of responses was also illustrated by a series of studies on only one plant species, *Ammophila arenaria*, whose successional displacement in its native range has been attributed to negative feedback exerted by pathogenic fungi and parasitic nematodes (Van der Putten et al., 1993). The magnitude and the strength of the feedback was shown to vary with the invaded geographic regions, identity of the co-occurring native plant spe-

cies and characteristics of the experimental conditions (Beckstead and Parker, 2003; Knevel et al., 2004; Van der Putten et al., 2005). Our study suggests that spatial and temporal variations can also reflect on the nature of the plant–soil feedback. For instance, from the six sites across South Florida, potential switch to exclusively less negative feedbacks occurred only at two sites (C and PP). It is difficult to explain what contributes to this spatial and temporal variation of nematode responses. All investigated sites were under *M. quinquenervia* encroachment spanning between 20 and 50 years, and thus the observed shifts in nematode communities should be reflective of long-term effects only. Local climatic conditions did not seem to explain the response, nor did the soil type, amount of organic matter, pH, water content, or type of native vegetation. Regardless of the mechanisms, it is very clear that, in order to define any generalizations on the plant–soil biota feedback associated with plant invasions, more field experiments that include large spatial and temporal components are necessary.

Differences in soil abiotic measures: Plant invasions have been shown to alter chemical aspects of soil environments, such as soil carbon and nitrogen, moisture, pH and levels of phosphorus and other soil nutrients; however, the direction of the change in comparison to the native sites proved to be variable and included increases as well as decreases in any of the soil chemical variables (Ehrenfeld, 2003). In our study, very few of the measured chemical variables were unaffected by the invasive plant, but the direction of responses was specific to the measured variable.

Melaleuca quinquenervia is considered to reduce the water level tables and to increase the distance to the water table via high rates of evapotranspiration (Serbesoff-King, 2003), so levels of soil moisture higher under *M. quinquenervia* than native plants are surprising. It is possible that a thick litter layer accumulating under *M. quinquenervia* prevents soil drying in the top horizon of the soil profile. Although an opposite pattern was observed at FM, this site experienced continuous mowing and thus no litter layer accumulation. In addition, dense *M. quinquenervia* trees provide significant shade, so the higher soil moisture retention might result from a combination of soil surface shading and litter accrual.

Higher soil C and N levels under *M. quinquenervia* could also be related to litter accumulation. Although C and N buildup is a slow process, and detecting even slight changes can be difficult (Baer et al., 2002), the residence time of *M. quinquenervia* seems sufficient to account for elevated total soil C and N.

Exotic plants most commonly affect net primary productivity with faster growth rates and much greater biomass (Ehrenfeld, 2003). The general trend of decreasing concentrations of soil nutrients such as P, K, Ca and Mg might stem from higher-than-natives' net productivity and lower-than-natives' decomposition rates. Temporary variations could be associated with year-to-year differences in rainfall, levels of flooding and nutrient leaching.

Overall, our study indicates that invasions by *M. quinquenervia* affected the structure and composition of nematode communities and the chemical characteristics of the soil. Although many effects were site- and time-dependent, general trends of the changes in soil biota and soil chemistry could still be discerned. Suppressive influence of *M. quinquenervia* on the abundance and diversity of nematodes, particularly plant parasites and fungivores, suggests that the invasion may involve less negative feedbacks resulting from lower root parasite pressure and/or allelochemical nature of *M. quinquenervia*. Combination of changes in the biotic and abiotic characteristics of the soil may promote the success of the exotic and at the same time undermine the native plant species. To support observational data, direct experiments testing the direction and magnitude of the feedback and allelochemistry across spatial and temporal scales are needed to advance our understanding of *M. quinquenervia* invasion.

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