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Diversity and complexity complement apparent competition: Nematode assemblages in banana plantations

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ABSTRACT

The structure of communities of soil organisms, and, therefore, their ecosystem functions, respond to spatial and temporal changes in plant diversity and to subsidies of organic matter. We introduce the concept of amplifiable and target prey in directing the impact of shared predators on pest organisms. In soil nematode assemblages, rather than overt apparent competition between the two prey categories, the effects were more subtle and expressed as increased predation pressure on the target prey when resources for the amplifiable prey were greater. We conclude that the connectance complexity of the food web subverts resource flow through a sequential chain of trophic interactions so that interaction strength decreases at successive trophic exchange. However, the effect of resource diversion is that the net regulatory pressure on the target prey is potentially enhanced by the increase in alternate predators of each prey category. The system requires that certain criteria are met, including that predator populations are resource limited, that conditions are conducive for predator survival and increase, and that predators, amplifiable and target prey are co-located in a majority of patches associated with resource subsidy, favorable conditions or migration patterns.

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1. Introduction

Apparent competition is an interaction between populations in which, when one species increases in abundance, there is a decrease in abundance of another species, even though there is no conceivable basis for competition for resources between the two populations (Holt, 1977). The mediating force of apparent competition is usually the sharing of a predator. Increase in abundance of one prey population provides resources for the predator, resulting in an increase in predator abundance and, consequently, greater predation pressure on another prey population. The phenomenon requires that the predator abundance is resource limited and that

environmental conditions do not constrain increase of the predator population.

The structure of communities of soil organisms is affected by spatial and temporal changes in plant diversity and production, and by subsidies of organic matter (Ferris et al., 2004; Sánchez-Moreno et al., 2009). Our overarching apparent competition hypothesis is that resource subsidy in soil will result in increase of the many species of bacteria, fungi and their predators, including protozoa, rotifers, nematodes, microarthropods, and other organisms with similar functional roles. We define such organisms as *Amplifiable Prey* (AP). The additional prey provide resources for generalist and specialist predators in the system and their greater abundance will increase top-down pressure on their other potential prey, the functional guilds of plant-damaging, root-feeding organisms resident in the soil which we term the *Target Prey* (TP).

Most studies on apparent competition have focused on the impact of the predator on the prey (e.g., Gallet et al., 2007; Jones

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et al., 2009; Van Veen et al., 2008). In the current study, we focus on the impact of resources on one or more AP guilds and the consequent effects on the predators and TP guild; in essence, we are seeking opportunities for managed apparent competition. Effects of resources on the structure and function of the system could be tested either by experimentally subsidizing available C or by deriving insights from whole systems that differ in levels of C. The former approach requires considerable time to stabilize to an equilibrium state across trophic levels of soil organisms (Poudelet et al., 2001); we used the latter approach, facilitated by our access to a large dataset derived from a study on soil health (Rosales et al., 2008).

1.1. The model

Functional guilds of bacterivore and fungivore nematodes, the AP for this study, participate in organic matter decomposition pathways in the soil. Several species, often differing in ecological amplitude, may be present at the same time, each contributing to complementarity and continuity of their integral ecological function (Bongers and Ferris, 1999; Ferris, 2010; Ferris and Bongers, 2006; Ferris et al., 1996, 2001; Loreau, 2004). The bacterial and fungal prey of these nematodes derives resources from the sugars and amino acids of root exudates and from more complex detritus. The AP share predators with the TP (plant-feeding nematodes) that compromise plant growth (Fig. 1). The shared predators include nematodes, which may be specialist or generalist in their prey selection (Khan and Kim, 2007; Linford and Oliveira, 1937; Yeates et al., 1993). Specialist predators have oral characteristics adapted for ingesting nematode prey and although they may, as juveniles, feed on bacteria (Yeates, 1987) they feed predominantly on other nematodes (Yeates et al., 1993). Generalist predators (often termed omnivores) are equipped with a protrusible hollow stylet for ingesting substrate from a range of prey, including nematodes, microarthropods, annelids, tardigrades and fungi (Yeates et al., 1993). Specialist and generalist predators have larger bodies, lower turnover, and lower fecundity than their prey (Bongers and Bongers, 1998; Bongers and Ferris, 1999; Ferris et al., 2001).

1.2. Hypotheses

We use composition of the soil nematode assemblage, which has convenient trophic diversity, as a model system for testing the following hypotheses:

1. The abundance of the AP of predator nematodes (Pr) increases with available soil organic matter (SOM), microbial biomass carbon (MBC) or other proxies of resource availability;
2. The abundance of Pr increases with the abundance of AP;
3. The abundance of AP is an indicator of the predator pressure on the TP;
4. Abundance of root-feeding TP will increase in relation to available root tissue measured as root weight (RW);
5. Abundance of TP will decline as abundance of predators per AP increases, mediated through Pr shared in common by AP and TP.

2. Methods

2.1. Data sources

The data resulted from a multinational study of soil and root health parameters in banana plantations. Teams of horticultural experts selected farms in Costa Rica, Dominican Republic, Panama and Venezuela based on range of plant vigor and historical productivity, and on soil conditions. Data on 72 parameters selected as potential indicators of soil health and productivity, were collected from 38 farms in the four countries (Rosales et al., 2008). The farms included banana production systems managed intensively for export (EP) and less intensively for local (LP) markets; they represented both conventional and organic practices.

Soil samples from high and low vigor and productivity levels of each farm were analyzed for chemical and physical characteristics, RW, MBC, microbial respiration (MR), colony-forming-units of bacteria, fungi and actinomycetes (cfus) and nematode assemblages. Four sets of samples from high and low vigor areas of each farm were processed within three days of the sampling date.

Soil sampling sites were standardized by selecting recently-flowered banana mother plants which had daughter shoots between 1.2 and 1.8 m high. A cube of soil, 15 × 15 cm square by 30 cm deep, was removed 10 cm from the base of the daughter shoot. Each sample representative of a productivity level was a composite of soil from five plants. Roots were hand-picked from the sampled soil, washed, weighed, and used for determination of endoparasitic nematode levels; the soil was used for determination of both plant-parasitic and free-living nematodes and for microbiological and chemical analyses.

Endoparasitic nematodes were assessed by macerating 25 g roots in 250 ml water in a blender for 10 s at low speed and 5 s at high speed. The resulting suspension was poured through a stack consisting of sieves with 250, 106 and 25 μm apertures and flushed with water for 2 min. Nematodes were collected from the 25 μm sieve, suspended in 200 ml water, and counted and identified in 2 ml aliquot samples (Araya, 2002; Rosales et al., 2008). Soil samples were passed through a 4 mm sieve to remove stones and large roots and nematodes were extracted from 250 g soil by placing the soil on a paper towel supported by a 15-cm diam screen suspended in a pan of water (the Baermann tray method). After 48 h, nematodes from the water in the pan were concentrated using a 25 μm sieve, counted and identified (Rosales et al., 2008).

The standard methods used for the soil chemistry and microbiology analyses are detailed in Rosales et al. (2008) and are summarized herein. Percent SOM was measured by the Walkley-Black method; a 0.5 g sample of oven-dried soil was agitated for

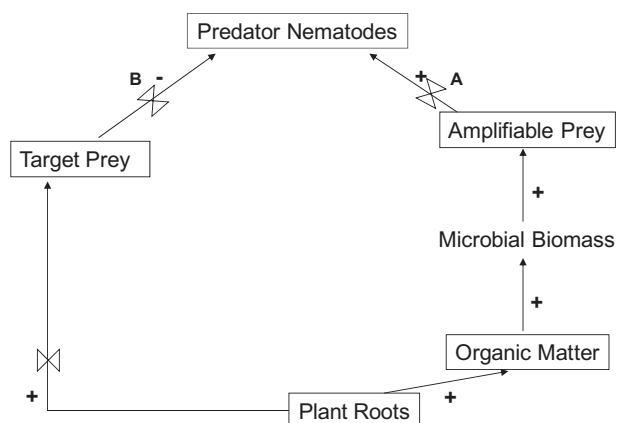


Fig. 1. Model of the cascading system of amplification of predaceous nematodes leading to the regulation of target prey through apparent competition. Regulation of target prey becomes suppression when the rate of flow from target prey to predators (a function of predator abundance and consumption rates) must exceed the rate of increase in target prey biomass (a function of target prey abundance, growth rates and resource availability). Impact regulators marked A indicate the need for favorable conditions for sensitive predator species; those marked B indicate the need for co-location of predators and prey.

2 h in a mixture of 10 ml of 0.167 M $K_2Cr_2O_7$ and 10 ml concentrated H_2SO_4 and the remaining chromate determined colorimetrically (Nelson and Sommers, 1982). Colony-forming-units of soil microorganisms were determined by dilution plating. Soil (10 g) was shaken in 90 ml water, followed by repeated concentration and dilution. At each dilution, the concentrate was plated on both nutrient agar (for bacteria and actinomycetes) and potato dextrose agar (for fungi) and the number of colonies determined after 3 and 5 days (Seeley et al., 1991). Microbial biomass carbon was determined by comparison of C, extracted in 0.5 M K_2SO_4 solution, from chloroform fumigated and unfumigated soil samples. The difference represents the C released by lysis of cell membranes of soil microbes (Vance et al., 1987). Basal microbial respiration was assessed by CO_2 evolution during 10 days of incubation of soil at 25 °C; CO_2 evolved was absorbed in 0.05 M NaOH solution and, after adding $BaCl_2$ to precipitate the CO_2 as Ba_2CO_3 , quantified by titration with 0.1 M HCl (Anderson, 1982).

2.2. Data reduction

We tested our hypotheses using a dataset that exhibited the widest possible range of the independent variables and in which the data were not confounded by farm management practices that might mask relationships of interest. Prevalence and abundance of nematode species and trophic groups varied among national datasets and between EP and LP systems. In the EP systems, consistent with frequent chemical perturbation of the soil environment, soil nematodes, both plant-feeding and other trophic groups, were generally less abundant than in LP systems. Based on testimony of field experts, and examination of the data, the majority of farms in the Costa Rica component of the dataset were in the EP category, receiving up to 50 applications of fertilizers or pesticides per year. The data from EP systems in Venezuela were deemed similarly constrained. Consequently, data from Costa Rica plantations and Venezuela EP plantations were excluded from the analyses of food web interactions. To achieve the desired widest possible range of the independent variables, we tested hypotheses using the 172 soil samples taken across all vigor/productivity levels of the 24 plantations in which food web interactions were not compromised by intensive management.

2.3. Statistical analyses

All analyses of the composite dataset of samples from the Dominican Republic, Panama and Venezuela were conducted with the General Regression Models (GRM) component of the Advanced Linear/Nonlinear Models package of Statistica 8 (StatSoft, 2004).

3. Results and discussion

Our hypotheses were based on a simple model of carbon and energy flow (Fig. 1). The progression of analyses and observations

described herein revealed the inadequacies of that model. Subsequently we present a more complex model of system interactions and discuss its application.

3.1. Relationships among model components

We tested each link of the simple model (Fig. 1) with the multinational dataset using “country” as a categorical variable and the relevant independent variable of each component of the model as continuous. We examined relationships among the abundance of organisms of each functional guild and the abundances of their hypothesized principal prey and predators. As expected from biogeographic, laboratory, and personnel differences, there was a significant effect of country in each relationship. In most cases where the R^2 of the whole model (country and independent variable) was significantly high, there is a significant contribution of the independent variable in explanation of the relationship (Table 1).

As hypothesized, and as depicted in the simple model (Fig. 1), there is a positive relationship in the multinational dataset between the abundance of TP and Root Weight (RW) (Table 1). The RW effect on TP creates a second conduit of C and energy into the food web. We were unable to detect a clear and direct relationship in the multinational dataset between RW and either SOM or MBC (as a proxy for labile C) (data not shown). Studies in East Africa, however, suggest a relationship between RW and organic mulching in bananas (Gaidashova et al., 2009).

The abundance of AP increases with MBC (Table 1) per hypothesis, but there is no relationship in the multinational dataset between SOM and MBC. In an organic vegetable production system in California, USA, there was a strong relationship between biomass of bacterial- and fungal-feeding nematodes two months after incorporation of organic sources but the relationship was no longer detectable after six months (Ferris et al., submitted for publication). The SOM in the current study included all organic sources, labile and recalcitrant. Unfortunately, labile C and potentially mineralizable nitrogen (PMN), both measures of immediate resource availability to soil organisms, were not determined in the original study (Rosales et al., 2008). Some recalcitrant components of SOM may represent years of accumulation rather than currently utilizable resource levels. Resources available to AP may be quite ephemeral; they are patchy around concentrations of organic matter or auto-trophic activity and can change rapidly. Soil microbes respond most rapidly to labile carbon, which is often in the range of 1–2% of total SOM (e.g., Zou et al., 2005). Usually there is a spike of MBC as labile organic sources are provided through incorporation of organic matter into field soil. However, the elevated levels dissipate quite rapidly as available resources decrease (Ferris et al., 1996; Gunapala et al., 1998; Semenov et al., 2002). Bacterial-feeding nematodes with various colonization characteristics increase and either disappear or persist at different rates after the initial flush of bacteria and MBC (Ferris et al., 1996). Consequently, the detection of relationships between AP and their food resources requires

Table 1

Parameterization of the trophic cascade model relating target prey abundance and organic resources. Data from banana plantations in the Dominican Republic, Panama and Venezuela.

Relationship	Whole model R^2	Intercept	Independent variable coefficient	Independent variable effect (P)	Country effect (P)	df
Amplifiable prey > Predators	0.39	19.00	0.08	<0.0001	0.0003	163
Predators > Target prey	0.22	65.06	1.93	<0.0001	0.0004	163
Amplifiable prey > Target prey	0.19	60.64	0.42	<0.0001	0.0003	168
MBC > Amplifiable prey	0.42	125.2	2.62	0.026	<0.0001	168
Root weight > Target prey	0.08	59.67	0.74	0.03	0.002	168
OM > MBC	0.40			ns	<0.0001	168

intensive time course study and controlled microcosm observations with appropriate measure of the nature of the organic resources (e.g., Fu et al., 2005; Jaffee, 1996).

Several proxies provide alternative measures of resource availability in our multinational dataset. In some cases, the proxies allow bypassing a component step of the model with the rationale that resources at a particular level may be too ephemeral or difficult to measure to allow appropriate resolution in the analysis. The only significant relationships in our series of exploratory analyses of proxies were those between Pr abundances and MBC and between TP abundances and MBC (Table 2). We are unable to support the hypothesis that the relationship between MBC and TP abundance was mediated by an effect of MBC or microbial activity on RW. The lack of apparent relationships among its links suggests need for revision of the simple model.

3.2. Model revision: diversion of the carbon cascade and the power of diversity

Organism diversity in the soil is likened to that of a tropical rainforest (Giller, 1996). The myriad interactions in a small volume of soil provide a model for those of an aboveground landscape. Clearly, our initial simple model (Fig. 1) is inadequate for explaining interactions among the selected variables; many others should be considered. Revisions to the model (Fig. 2) emerge from interpretation of these results and of interactions reported in the literature but outside the scope of the current study. As hypothesized, the relationship between Pr abundance and AP abundance is positive (Table 1). In highly disturbed intensive organic vegetable production systems, there was a similar significant positive relationship between abundances of Pr and AP (Ferris et al., submitted for publication). In the banana system there is also a positive relationship between Pr abundance and TP abundance and the abundances of AP and TP are positively related (Table 1) which is the antithesis of the classical apparent competition pattern. However, the ratio of Pr to TP increases with levels of AP. We interpret this as a cryptic form of apparent competition expressed through greater predator pressure on the TP (Table 3). Interestingly, the abundance of Pr per AP is negatively related to AP abundance (Table 3). We suggest that there is a diversion of resources to other predators of AP, including tardigrades and microarthropods (Imbriani and Mankau, 1983; Sánchez-Moreno et al., 2008a; Walter et al., 1986), and the need for expansion E1 of the simple model (Fig. 2). Those other predators of nematodes would also exert pressure on the TP.

Inconsistent with the predator-prey relationships in Table 3, the ratio of Pr to TP did not increase with MBC (Table 2), supporting the hypothesis of resource flow inefficiencies in the path through AP and MBC via diversion to other consumers at those trophic levels. The siphoning of resources from the simple cascade of Fig. 1 prompts model expansion suite E2, which recognizes that there are other consumers of MBC, including protozoa. Some protozoa

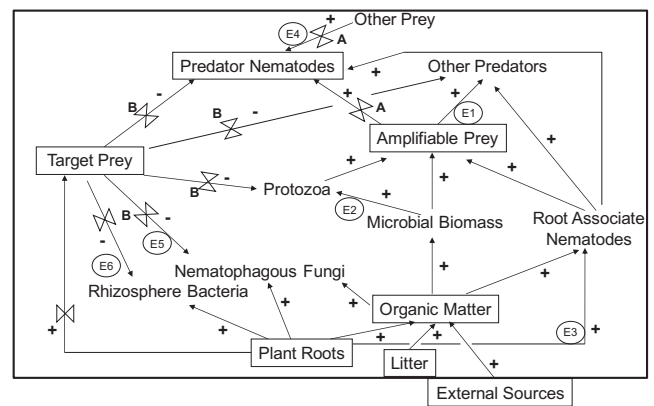


Fig. 2. An expanded model to reflect the importance of cascade diversion in a food web system that leads to regulation of target prey through subtle apparent competition and functional complementarity. Impact regulators marked A indicate the need for favorable conditions for sensitive predator species; those marked B indicate the need for co-location of predators and prey. Expansions of the simple model (Fig. 1) are: E1-resource diversion to other predators of the amplifiable prey which may also consume target prey; E2-resource diversion to other consumers of amplifiable prey, including protozoa of which some may consume target prey and some become resources for amplifiable prey; E3-root associate nematodes are stimulated by roots and organic matter; they contribute to the amplifiable prey and function as resources for predators; E4-access of generalist predators to other resources besides amplifiable prey; E5-nematophagous fungi are stimulated by roots and organic matter and are generalist predators of both target prey and amplifiable prey; E6-rhizosphere bacteria stimulated by roots may have antibiotic and other effects on target prey.

are also predators of nematodes (Clarholm, 1989; Yeates and Foissner, 1995), while some nematodes in the AP group are predators of protozoa (Hunt et al., 1987; Nelmes, 1974) (Fig. 2).

Nematodes in the family Tylenchidae, collectively referred to as root associates (Yeates et al., 1993) although some are fungivores (Okada et al., 2005), generally do not negatively impact plant growth and respond to increases in OM and RW (E3) (McSorley and Frederick, 1999; Wallace et al., 1993). Such nematodes contribute to the AP pool. Besides providing resources for predator nematodes, they are also prey for microinvertebrate predators of nematodes which, in turn, increases predation pressure on TP (Fig. 2).

To illustrate the *cryptic apparent competition* evident in the multinational dataset, we use the linear relationships between variables at each component step of the simple model (Fig. 1) for the Panama (Pan) (Fig. 3A–C) and Dominican Republic (DR) datasets (Fig. 3D–F). To reduce scatter and enhance visual presentation, the data are log transformed. The abundance of Pr is positively related to the abundance of AP in both Pan and DR ($p < 0.0001$, Fig. 3A,D) but the relationships between Pr and TP are not consistent, weakly negative in Pan and positive in DR (Fig. 3B,E). The inconsistency in the two datasets, and weakness of the Pan relationship between Pr and TP, support the need for model expansion E4 (Fig. 2) which recognizes that generalist predators may have

Table 2
Tests of proxies of model components for higher resolution of descriptive analyses.

Relationship	Whole model R^2	Intercept	Independent variable coefficient	Independent variable effect (P)	Country effect (P)	df
Total cfu > Amplifiable prey	0.41			ns	<0.0001	168
Total cfu > Predators	0.30			ns	<0.0001	163
OM > Amplifiable prey	0.41			ns	<0.0001	168
OM > Predators	0.30			ns	<0.0001	163
OM > Target prey	0.06			ns	ns	168
MBC > Predators	0.32	25.18	0.57	<0.01	<0.0001	163
MBC > Target prey	0.09	94.68	3.51	<0.01	0.0003	168
MBC > Predators/target prey	0.25			ns	<0.0001	163

Table 3

Predator-prey ratios linking potential predator pressure on target prey and amplifiable prey abundance. Data from banana plantations in the Dominican Republic, Panama and Venezuela.

Relationship	Whole model R^2	Intercept	Independent variable coefficient	Independent variable effect (P)	Country effect (P)	df
Amplifiable prey > Predators/target prey	0.35	0.176	0.0007	<0.0001	0.002	163
Amplifiable prey > Predators/amplifiable prey	0.36	0.58	-0.0015	<0.0001	<0.0001	163

access to other resources besides the TP (Thorne, 1930; Yeates et al., 1993). TP, like the AP, are subject to other predators besides nematodes (E1, Fig. 2), which contributes to the ambivalent relationship between nematode Pr and TP but complements the apparent competition effect.

In initiating resource input into the model through organic material, produced either endogenously or through allochthonous introduction, we recognize the potential for enhancing fungal predation of nematodes (E5, Fig. 2). While some nematophagous fungi are obligate parasites of microinvertebrates, many are facultatively-parasitic saprophytes. Experience varies on the degree to which the predaceous activities of these fungi respond to increases in organic matter (Jaffee, 2006; Linford, 1937) but they constitute a potential channel for exerting regulatory effects on the TP. They may also negatively affect AP. Additionally, rhizosphere bacteria, supported and stimulated by roots, may have antibiotic and other effects on TP (E6, Fig. 2).

The ratio of Pr per AP decreases slightly with AP abundance (y1, Fig. 3C) in Pan and exhibits a non-significant trend in DR (y1, Fig. 3F). Different effects on numerators and denominators of the predator-prey ratios are consistent with the notion that there are other predators of the AP (E1) and other resources for the generalist predators (E4) (Fig. 2). As in the multinational dataset, the ratio of Pr per TP to AP was strongly positive in Pan (y2, Fig. 3C) and had a positive trend in DR (y2, Fig. 3F), supporting the emergent conclusion of the study that the apparent competition effect is complemented and enhanced by other sources of predation (E5, E6) and by other resources for the nematode and non-nematode predators (E1, E2, E4) (Fig. 2).

The revised and expanded model (Fig. 2) reflects multiple diversions of the cascade of carbon and energy envisioned in the simple model (Fig. 1) to other components of the functional guilds at each trophic level. Cascade diversion, as reflected in weak resolution of relationships at each component step of the simple model

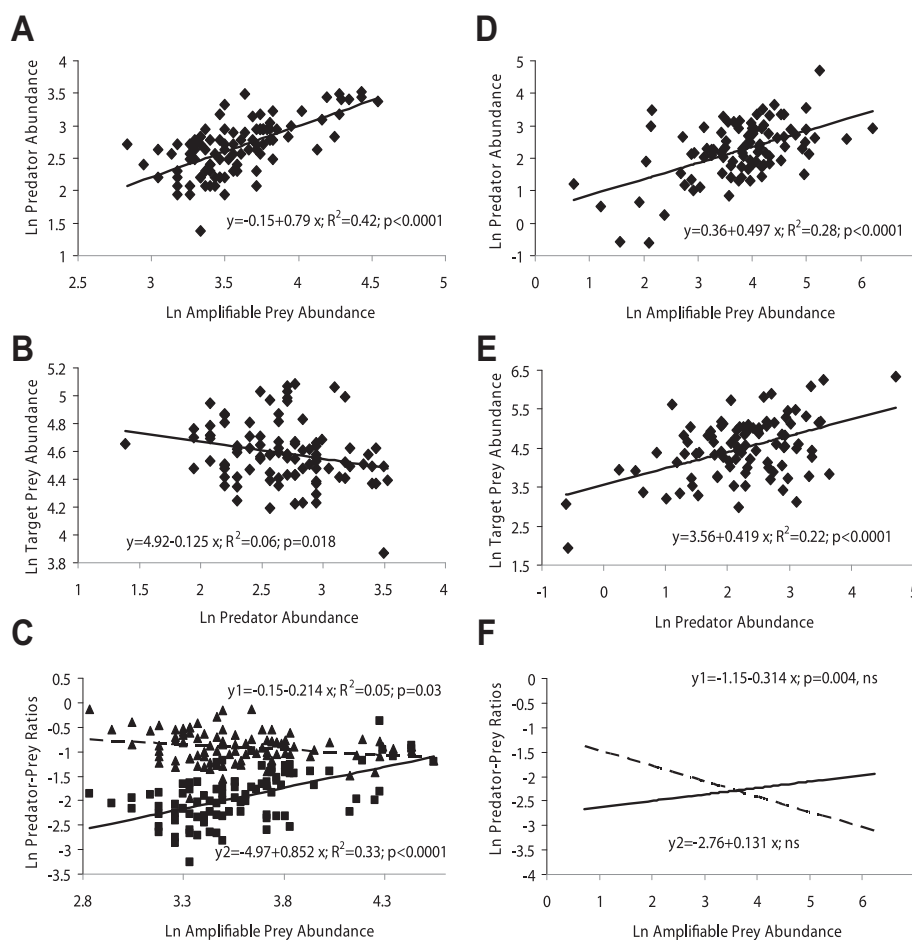


Fig. 3. Relationships between (A,D) predator abundance and amplifiable prey abundance, (B,E) target prey abundance and predator abundance, and (C,F) predators-prey ratios for amplifiable prey (y1) and target prey (y2) for Panama (A–C) and Dominican Republic (D–F) datasets.

in the Pan and DR datasets (Fig. 3), is both an indicator and a consequence of food web connectance (*sensu* Cohen, 1989; Martinez, 1992). Connectance, a measure of the realized proportion of potential trophic linkages among organisms, is an important indicator of functional redundancy and complementarity (Loreau, 2004) in the food web. Functional redundancy, in turn, is an indicator of functional continuity, that is, the continuation of the function on a seasonal basis, resources permitting, by components of the functional guild adapted to differences in environmental conditions and quality of the diminishing resources (e.g., Ferris et al., 1996, 2004).

One might argue that, in a strictly linear and microcosmic sense, increase in AP biomass as depicted in the simple model (Fig. 1) would engender a concomitant increase in predator biomass without altering predator-prey ratios. However, predator population levels usually lag behind those of their prey and predator-prey ratios oscillate accordingly. Increased predator pressure may result in decimation of prey populations and cause predators to seek alternate prey sources. Spatial, temporal and organismal diversity of food webs may be critical to the stability of their function (Fig. 2). An underpinning for the stability of predator-prey systems in the soil is their patchiness (Gallet et al., 2007). Patchy distribution of prey around food sources, for example root tips or bacterial colonies, may differ from, and be asynchronous with, predator prevalence and dynamics.

3.3. Experimental and analytical approach revisited

Community interaction hypotheses may be tested in highly controlled microcosms and inferences extrapolated to the field scale (Jaffee, 1996). Often relationships observed in microcosms differ at the field scale due to interactions excluded in the microcosm experimental design. In contrast, studies at the field scale may measure a wide range of variables and then attempt to extract relationships through sophisticated multivariate analyses. Often, strong and intriguing correlations are revealed among variables but, in many cases, the correlations defy explanatory interpretation. We have taken an alternative approach. We have considered the biological interactions from the standpoint of enhancing less chemically-intensive and, arguably, more sustainable management of pest nematode populations in banana plantations. In our approach, we have stated hypotheses that seem mechanistically and functionally plausible. We have tested those hypotheses with selected data from large datasets and have accepted their central theme that the managed amplification of bacterial- fungal- and non-damaging plant-feeding nematodes promotes important and useful population interactions in regulation of target species. Rather than overt apparent competition, which we initially expected, this study suggests a web of interactions in which increase in abundance of one organism group potentially affects the regulatory contributions of other groups that have predators in common but not resources in common.

3.4. Transition of community structure in response to biointensive management

In their quest for carbon, populations are shaped by bottom-up forces of resource availability and competition, top-down pressures of predation and disease, and their tolerance of environmental perturbation. The forces invoke differential taxon-specific responses in all functional guilds of communities and at all trophic levels of carbon and energy transfer. Populations of individual taxa may be stimulated, regulated or suppressed by the individual or combined effects of the various influences (Hunter and Price, 1992; Power, 1992; Sousa, 1984; Wardle and Yeates,

1993). Rather than an individual taxon approach, we advocate systems level regulation of soil pest species by providing resources to predators through a trophic web of carbon and energy exchanges. There are two fundamental components to the strategy of managed apparent competition for regulation or suppression of TP. One is to increase and sustain the carbon and energy supply to soil organisms, the other is to remove chemical and physical constraints to the survival and increase of the AP and their generalist and specialist predators.

Microhabitats for soil-inhabiting root-feeding nematodes, the TP in this study, are determined by the distribution of plant roots. Generalist and specialist predators of nematodes are sensitive to environmental disturbance and exposure to pesticides and mineral fertilizers (Gruzdeva et al., 2007; Tenuta and Ferris, 2004). Unless the tips of feeder roots are located near the soil surface, plant-feeding nematodes attracted to root tips for feeding or root penetration will be less accessible to generalist and specialist predators increased by amplification of their prey through subsidy of material at the soil surface. Co-location of root distribution with surface organic matter is more likely in the absence of herbicides and soil disturbance of low-input systems than in high input systems. Distribution of roots in the same region of the soil profile inhabited by both the AP and their predators will be important for realization of the effects of apparent competition on the TP constituted by soil-inhabiting, root-feeding nematodes (Fig. 2).

To develop and maintain an abundance of predators requires that a consistent supply of food reaches that trophic level or that the predators be long-lived with slow metabolism and slow turnover rate. In a one-year study by Wardle and Yeates (1993), predator nematodes were sometimes strongly related to microbial levels but not to abundance of the intermediate levels of bacterial and fungal-feeding nematodes feeding on the microbes. They suggested that the bacterial and fungal-feeding nematodes simply served as a conduit by which resources pass from the bottom to top trophic levels. There are two other possible explanations for such observations. One is that differences in turnover rates and life course time scales at each trophic level result in abundances that are not numerically related at one point in time. The other is that generalist predators may be accessing other prey taxa and so increasing despite the lack of relationship with abundance of prey nematodes.

The supply of carbon and energy to the organisms that provide resources for the AP (mainly bacteria and fungi) may be achieved by frequent application of organic matter and compost to the soil surface. Where the strategy is designed to achieve co-location of target nematodes and their predators, physical incorporation of the organic matter may be counter-productive to the goal of enhancing feeder-root distribution at the soil surface. Such organic matter import strategies may only be feasible where there are abundant sources in close proximity. Some examples in tropical systems include sugarcane residues and bagasse, which might otherwise be burned, and oil palm residues (e.g., Linford et al., 1938). An alternative approach to importation of organic material is to grow it in the plantation as natural understorey vegetation, a cover crop, or a cover crop mixture designed to provide specific ecosystem services. The services might include N-fixation, soil stabilization, soil porosity, and rhizodeposition to support the soil food web.

The other necessary component of the AP enhancement strategy is to minimize inputs that disrupt or constrain the establishment and increase of generalist and specialist predators. Such constraints include herbicides, mineral fertilizers, and soil disturbance (Berkelmans et al., 2003; Fiscus and Neher, 2002; Gruzdeva et al., 2007; Tenuta and Ferris, 2004). Implementation of practices to enhance soil food web activity for regulation of TP face the challenge of co-locating predators and TP by designing systems that



Fig. 4. Root distribution in an organic banana plantation. Roots of various plant species inter-layered and interacting at the soil surface.

promote root development in the areas of carbon subsidy or subsidizing carbon around roots (Fig. 4).

Finally, a caveat. Management practices promoting above-ground biodiversity, low-disturbance, higher resource availability, and more complex soil food webs are expected to result in greater biodiversity of the belowground organisms mediating multiple soil ecosystem functions (Brussaard et al., 2007; Ferris et al., 2004). However, the transition from intensive production practices to more sustainable, less input-intensive systems is challenging. A limited number of transition studies in annual crop systems suggest that a period of 5–7 years may be required for the new system to evolve and stabilize (Kerry, 1987; Scow et al., 1994; Sánchez-Moreno et al., 2008b). That period is necessary for resources to accumulate in the soil, previous constraints on organisms at different trophic levels to dissipate, and for stable equilibria to evolve among predators and prey within the community aggregates that constitute the soil metacommunity.

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