



# Management impacts on the trophic diversity of nematode communities in an indigenous agroforestry system of Chiapas, Mexico

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## Summary

The Lacandon Maya of Chiapas, Mexico practice a system of agroforestry that mimics the surrounding ecosystem and its successional stages. Their fields rotate through grass (milpa), and shrub (acahual) and forest fallow stages that regenerate soil, nutrients, and seed banks. Each successional stage, including the fallow stages, produces over 25 types of crops, raw materials, and medicines. Lacandon traditionally do not use fertilizers, pesticides, or herbicides. Nematodes were chosen to analyze soil ecology in the Lacandon system because they have been shown to be dynamic indicators of environmental conditions. Nematodes were classified by trophic level as plant parasite, fungivore, bacterivore, and omnivore-predator, and were found to be a function of management practice. In milpas where weeds were removed and applied to the field, plant parasites were reduced by 44% and fungivorous nematode concentrations were reduced by 50%. In these same fields, percentage of bacterivorous nematodes was positively related to soil organic matter concentration ( $R^2 = 0.61$ ,  $P < 0.001$ ). These results indicate that management practices reduced concentrations of plant parasites and delayed the nematode successional pathway from bacterivorous to fungivorous. This study demonstrates the potential for Lacandon Maya techniques to sustainably manage pests and maintain soil fertility in other tropical agroecosystems.

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## Introduction

The Lacandon rainforest of Chiapas, Mexico is losing over 7% of the remaining forest each year. Erosion has moderately degraded 10–25% of the arable soil and severely degraded 5% of the arable soil in the lowlands of Chiapas (Howard and Homer-Dixon, 1996). Such problems are endemic throughout the tropics, as increasing human population densities stress the environment through demands on agricultural land (Lal, 1995; Alvarez and Naughton-Treves, 2003). These demands commonly result in diminished fallow time, which leads to deforestation and soil erosion (Drechsel et al., 2001).

The Lacandon Maya are an indigenous group that has supported itself for centuries through effective use of their environment. They practice a unique method of agroforestry in which they manage the fallow period for production and soil regeneration (Nations and Nigh, 1980; Levy, 2000; McGee, 2002). They live in three villages, Naja, Lacanja Chansayab, and Metzobok, in the Lacandon rainforest within the southern-most Mexican state of Chiapas. Components of their agroforestry could serve as a model to be applied by farmers in Chiapas and in similar ecological regions throughout the tropics. Population is increasing at the greatest rates in the humid tropics, so the discovery of new tools for sustainable natural resource management there is particularly vital (Ram, 1997). Because our current understanding of the ecology of the Lacandon agroforestry is incomplete, and the oral tradition that preserves the system is dying out, it is of vital importance to record and understand sustainable elements of this system.

Traditional Lacandon agroforestry systems cycle through three field stages starting with the milpa, progressing to the acahual, and then to the secondary forest, before returning to the milpa. The duration of each stage differs, and often a field reverts to milpa from acahual before reaching the secondary forest stage. Ecological succession drives the conversion between field stages (Nations and Nigh, 1980; Levy, 2000). From the viewpoint of ecological succession, the milpa represents early successional grasses, the acahual represents the shrub or early woody stage, and the forest is the climax stage.

Previous research qualitatively explored Lacandon agroecosystems (Nations and Nigh, 1980). Current work focuses on quantitative examinations of their ecological processes and management techniques (Nair, 1998). Nematodes have been shown to be dynamic indicators of environmental

conditions in both natural successional systems and managed agroecosystems (Bongers and Ferris, 1999; Schloter et al., 2003). Trophic level identification is straightforward and can be carried out using a stereomicroscope at low magnification (Ritz and Trudgill, 1999). As nematodes have been shown to respond rapidly to changes in the food supply, much useful information can be gained from nematode analysis to trophic level. For example, an increase in microbial activity associated with decomposition of barley roots resulted in a rapid increase in bacterivore nematode concentrations (Christensen et al., 1992). Matlack (2001) found that plant parasite nematodes increased in number as a function of plant cover and that fungivore concentrations increased as soil organic matter increased. Ferris and Matute (2003) concluded that nematode assemblage succession from bacterivore to fungivore was suppressed by the addition of organic material to a fallow field in California. Nematode communities have been shown to increase in number and diversity as systems develop through successional stages (Sohlenius, 2002; Thornton and Matlack, 2002; Hanel, 2003). In other successional swidden systems, similar to the Lacandon system, fallow length appeared to increase both the abundance and diversity of nematode species (Pate et al., 2000; Villenave et al., 2001). These changes were a function of the changing plant community that in turn affected soil organic matter, bacterial and fungal communities (Thornton and Matlack, 2002).

This paper describes an analysis of the soil nematode community in Lacandon Maya agroforestry as it is practiced in Lacanja Chansayab, Chiapas, Mexico. The nematode community was examined in three successional stages of the Lacandon system: milpa, acahual and secondary forest, and in the surrounding primary forest. The first goal was to determine what patterns exist between field stages in terms of nematode communities as defined by nematode trophic level. The second goal was to determine patterns of differences in nematode communities in traditional Lacandon agroforestry systems and in systems where traditional practices are no longer being practiced (non-traditional). The third goal was to use these results to examine differences in soil ecology between traditional and non-traditional Lacandon agroforestry systems.

We hypothesized that as the Lacandon agroforestry system progressed through successional stages, the following changes would take place: the abundance of all nematode trophic groups would increase as a function of increasing plant cover; the decomposition pathway would become

increasingly fungal-based, which would increase the relative abundance of fungivores compared to bacterivores; these changes would occur more slowly in traditional systems.

## Materials and methods

Lacanja Chansayab is located at 16° 56' 60N and 91° 16' 60W and at an elevation of 500 m. Soil type is Luvisol (INEGI, 1982), texture is clayey, and soil pH is neutral.

### Agroecosystems of the Lacandon Maya

The milpa is a polyculture field, dominated by *Zea mays*, that includes 20–30 additional plant species (Nations and Nigh, 1980). Some of these species are planted, while others are allowed to regenerate from the soil seed bank (Quintana-Ascencio et al., 1996). The milpa stage is farmed for up to 5 years in continual production. Farmers following traditional practices weed the milpa daily and do not apply pesticides, herbicides or fertilizer. In non-traditional systems weeding occurs less often, perhaps once per month, and the cultivated species are less diverse. No farmers included in this study used pesticides or herbicides during the study. After approximately 5 years, weeds in both traditional and non-traditional systems become more prevalent, and the farmer will allow the field to move into the next successional stage, the acahual (Levy, 2000; McGee, 2002). The acahual stage includes a range of 60 species of shrubs and bushes from which the Lacandon extract useful plants and fungi (Nations and Nigh, 1980). Dominant plant species include *Piper aduncum*, *Calophyllum brasiliense*, *Ananas comosus*, and *Cecropia obtusifolia*. The acahual is managed for approximately 7 years, at which time the Lacandon can cut, dry and burn the acahual, returning it to milpa, or allow the acahual to develop to the secondary forest stage. Once again, non-traditional acahuales are less managed than traditional. Herbaceous weedy species are more prevalent in non-traditional systems, and fewer cultivars are planted. The Lacandon rely on burning to return nutrients to the forest floor and activate the seed bank of early successional species (Quintana-Ascencio et al., 1996). The next successional stage is the secondary forest. The Lacandon extract many products from the forest including wood, fruit, fungi and animals (Nations and Nigh, 1980). Dominant plant species include *Eupatorium nubi-genum*, *Cecropia obtusifolia*, *Swietenia macrophyl-*

*la*, and *Spondias mombin*. After approximately 20 years the forest may be cleared, dried, and burned again and returned to milpa (Nations and Nigh, 1980). The Lacandon preserve areas of primary forests to insure a rich source of biodiversity to drive the conversion of the fields between these stages (Quintana-Ascencio et al., 1996; Levy, 2000). By directing natural succession using control of seed banks and plantings, and utilizing resources from all stages during this process, the Lacandon are able to sustainably manage their fields without supplements of seeds, fertilizer, herbicides, and pesticide (Nations and Nigh, 1980; Levy, 2000).

### Data collection

Sampling was conducted during July and August 2003 in six Lacandon Maya agroforestry systems in Lacanja Chansayab, Mexico. Soil and plant community sampling was performed in each successional stage from each system. Three traditional Lacandon systems and three non-traditional agroforestry systems were sampled, except that only one non-traditional acahual was sampled. A primary forest was also sampled.

Sampling locations in each field stage were determined using a transect method, with 10 samples collected at intersections of a 20 m grid. Within a circular 1-m<sup>2</sup> area at each sampling location, the detrital layer was removed and 8 replicate 2.5 cm diameter cores taken from 0 to 20 cm soil depth and pooled. We sampled 10 locations within each field stage. Each soil sample was analyzed for organic matter (Walkley and Black, 1934), and nematodes were extracted from 20 g soil for analysis. Soil samples for nematode extraction were kept cool and extracted over 72 h using the Baermann wet funnel technique (McSorley and Welter, 1991). Nematodes were heat fixed. Extract was stored in 2% formaldehyde, and all nematodes in bottom 10 mL of extract were identified to trophic level at 90× magnification (Parmelee and Alston, 1986; Edwards et al., 1991; Dominguez et al., 2003; Arancon et al., 2003). Nematodes were allocated to plant parasite, fungivore, bacterivore, and omnivore-predator trophic groups according to Parmelee and Alston (1986).

Plant cover was assessed at each sampling location. In the milpa, all plants in the 1 m<sup>2</sup> sampling area above 2-cm in height were recorded based on percent cover. In the acahuales, secondary and primary forests, plants with a stem or trunk diameter greater than 1-cm were counted in the 1 m<sup>2</sup> sampling area, and all plants with a basal

diameter greater than 5-cm were counted within a 20m<sup>2</sup> circular area that contained the sampling location as its center point.

To evaluate gross differences in soil texture, moisture, and pH according to field stage and management, an additional sampling event was conducted November 2004. Soil was collected in the manner specified above at three sampling locations along one transect in each field stage of the systems utilized in the first sampling event, and were analyzed for texture (Bouyoucos, 1951). Soil moisture and pH were evaluated in the field at the same sampling locations using a Kelway soil acidity and moisture meter.

## Analysis

Statistical analysis was conducted using Systat 10.2 and SPSS 12.0, with data being log-transformed as required for normality. Sampling locations were pooled to document patterns consistent with our hypotheses. Regression, ANOVA, and Independent Samples *T*-test were used to test significance of results. For ANOVA tests, Fischer's LSD was used to determine the significance of multiway comparisons.

## Results

When the data from traditional and non-traditional systems was pooled, the concentrations of plant parasites, bacterivorous, and total nematodes differed by successional stage (Table 1). Plant parasitic nematodes concentrations were 1.6 times greater in the secondary forests compared to the milpa. Bacterivorous nematode concentrations were 1.3 times greater in secondary forest stage compared to the milpa, and were 1.7 times greater in the secondary forest compared to the primary forest stage. Mean concentration of plant parasites and bacterivores showed an increasing trend with successional stage (Table 1), although the acahual was not statistically different from other successional stages. Total nematode concentration increased with field stage, as indicated by a 30% increase in the secondary forest compared to the milpa. The ratio of fungivorous to bacterivorous nematodes (*f/b*) in the primary forest was twice that of the acahual and secondary forest. Although a number of parameters were affected by stage of development, regression analysis of all nematode concentrations and ratios as a function of age (time since last fire disturbance) did not result in *R*<sup>2</sup> values above 0.1, indicating a weak relationship

between age and nematode concentrations and ratios. Soil organic matter concentration increased with each field stage from 11% in the milpa, to 12% in the acahual, 14% in the secondary forest, and 18% in the primary forest (*P* < 0.05). Soil moisture and pH did not change with field stage. Soil texture differed in different field stages (*P* < 0.01): milpa (sand:silt:clay, 29:17:54), acahual (25:21:54), secondary forest (34:23:43), primary forest (40:11:49).

Comparing the data from traditional and non-traditional systems indicated a pattern of management practices associated with differences in the nematode community by successional stage (Table 1). Whereas non-traditional systems did not exhibit any change in plant parasite and fungivore concentrations with successional stage, traditional systems showed an overall increase in plant parasite and fungivore community with successional stage. In the traditional systems nearly three times as many plant parasites were discovered in the secondary forest as compared to the milpa. Fungivores were twice as abundant in the secondary forest compared to the milpa and were 2.5 times more abundant in the primary forest compared to the milpa. In contrast, non-traditional systems exhibited changes in bacterivore concentrations that were not found in traditional systems. Bacterivore concentration was 50% greater in the secondary forest of the non-traditional systems compared to the milpa and acahual, and were nearly double that of the primary forest. These differences affected nematode ratios, in particular the ratio of fungivore to bacterivore (*f/b*). The *f/b* ratio increased from milpa and acahual to secondary forest in traditional systems, but decreased in non-traditional systems. At a level slightly outside significance (at an alpha of 0.05), the *f/b* ratio in the non-traditional secondary forest was half that of the milpa (Table 1). Whereas, the *f/b* ratio in the secondary forest of the traditional systems was 50% higher than the milpa (Table 1).

The concentration of nematode trophic levels, *f/b* ratios, and the ratios of plant parasites to free (fungivore, bacterivore, and omnivore-predator) nematodes (*pp/free*) were compared between non-traditional and traditional systems (Table 2). In the milpa stage, non-traditional systems were found to have higher concentrations of plant parasites, fungivores and total nematodes (Table 2). Concentrations of plant parasites and fungivores in non-traditional milpas were twice as great as in traditional milpas (Tables 1 and 2). Similar differences were found in the acahual, where plant parasites and fungivores were twice as abundant in the non-traditional compared to traditional systems, and the ratio *pp/free* in the nontraditional

**Table 1.** Mean concentration (#/20 g soil sample  $\pm$  1 SD) of each nematode trophic level in successional stages of non-traditionally managed, traditionally managed, and all Lacandon Maya agroforestry systems. Also shown are the ratios of plant parasite to free nematode (bacterivore, fungivore, and omnivore-predator) concentrations (pp/free) and fungivores to bacterivores (f/b). Age (years  $\pm$  1SD) denotes time since last fire disturbance. Different letters after concentrations and ratios indicate a statistically significant difference ( $\alpha = 0.05$ ) within non-traditional, traditional, and all system for each trophic level and ratio. If different letters are in italics, the difference was just outside this significance level ( $\alpha = 0.075$ ). Log values were used for comparisons when the variances were determined to differ significantly

	Age	Plant parasite	Fungivore	Bacterivore	Omnivore-predator	Total	pp/free	f/b
Non-traditional								
Milpa ( $n = 27$ )	3.4 $\pm$ 1.3	4.4 $\pm$ 3.9 a	6.0 $\pm$ 4.1 a	11.0 $\pm$ 6.4 a	4.7 $\pm$ 2.2 a	26.0 $\pm$ 9.2 a	0.22 $\pm$ 0.16 a	0.94 $\pm$ 0.97 a
Acahual ( $n = 9$ )	9.0	7.2 $\pm$ 5.8 a	8.2 $\pm$ 6.0 a	10.3 $\pm$ 4.4 a	6.1 $\pm$ 4.1 a	31.9 $\pm$ 14.7 a	0.30 $\pm$ 0.18 a	0.76 $\pm$ 0.52 ab
Secondary forest ( $n = 20$ )	18.7 $\pm$ 5.0	5.5 $\pm$ 6.0 a	5.7 $\pm$ 4.6 a	15.5 $\pm$ 8.5 b	4.4 $\pm$ 2.7 a	31.0 $\pm$ 12.7 a	0.22 $\pm$ 0.22 a	0.54 $\pm$ 0.57 b
Primary forest ( $n = 10$ )	undisturbed	4.8 $\pm$ 4.9 a	7.8 $\pm$ 6.0 a	7.7 $\pm$ 4.4 a	5.4 $\pm$ 3.5 a	25.7 $\pm$ 14.5 a	0.19 $\pm$ 0.12 a	1.18 $\pm$ 0.79 ac
Traditional								
Milpa ( $n = 23$ )	1.9 $\pm$ 0.8	2.2 $\pm$ 2.6 a	3.1 $\pm$ 2.9 a	7.9 $\pm$ 4.1 a	5.2 $\pm$ 4.3 a	18.4 $\pm$ 8.1 a	0.14 $\pm$ 0.14 a	0.57 $\pm$ 0.62 a
Acahual ( $n = 26$ )	7.8 $\pm$ 2.6	3.2 $\pm$ 3.0 ab	4.8 $\pm$ 3.3 b	10.7 $\pm$ 5.4 a	6.3 $\pm$ 3.3 a	25.0 $\pm$ 10.4 b	0.16 $\pm$ 0.14 ab	0.49 $\pm$ 0.37 a
Secondary forest ( $n = 22$ )	26.1 $\pm$ 6.5	6.0 $\pm$ 5.6 c	6.5 $\pm$ 4.1 b	9.8 $\pm$ 5.7 a	5.5 $\pm$ 3.0 a	27.8 $\pm$ 12.9 b	0.29 $\pm$ 0.20 c	0.72 $\pm$ 0.36 b
Primary forest ( $n = 10$ )	undisturbed	4.8 $\pm$ 4.9 ac	7.8 $\pm$ 6.0 b	7.7 $\pm$ 4.4 a	5.4 $\pm$ 3.5 a	25.7 $\pm$ 14.5 ab	0.19 $\pm$ 0.12 ac	1.18 $\pm$ 0.79 ab
All systems								
Milpa ( $n = 50$ )	2.7 $\pm$ 1.3	3.4 $\pm$ 3.5 a	4.7 $\pm$ 3.8 a	9.6 $\pm$ 5.6 a	4.9 $\pm$ 3.3 a	22.5 $\pm$ 9.5 a	0.18 $\pm$ 0.16 a	0.77 $\pm$ 0.84 a
Acahual ( $n = 35$ )	8.1 $\pm$ 2.3	4.2 $\pm$ 4.2 ab	5.7 $\pm$ 4.4 a	10.6 $\pm$ 5.1 ab	6.3 $\pm$ 3.5 b	26.7 $\pm$ 11.8 ab	0.19 $\pm$ 0.16 ab	0.56 $\pm$ 0.42 a
Secondary forest ( $n = 44$ )	22.2 $\pm$ 6.9	5.7 $\pm$ 5.7 b	6.1 $\pm$ 4.4 a	12.8 $\pm$ 7.7 b	4.9 $\pm$ 2.9 ab	29.5 $\pm$ 12.8 b	0.25 $\pm$ 0.21 b	0.62 $\pm$ 0.48 a
Primary forest ( $n = 10$ )	undisturbed	4.8 $\pm$ 4.9 ab	7.8 $\pm$ 6.0 a	7.7 $\pm$ 4.4 ab	5.4 $\pm$ 3.5 ab	25.7 $\pm$ 14.5 ab	0.19 $\pm$ 0.12 ab	1.18 $\pm$ 0.79 b



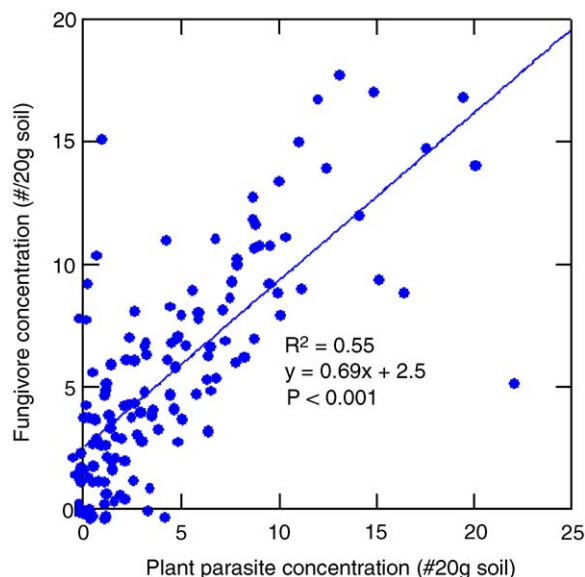
**Table 2.** *P* values of comparisons by trophic level of non-traditional and traditional Lacandon agroforestry systems at three successional stages: milpa, acahual, and secondary forest. Also shown are ratios of plant parasite concentrations to free nematode (bacterivore, fungivore, and omnivore-predator) concentrations (pp/free) and fungivores to bacterivores (f/b). The higher value is demarked by "nt" if it is non-traditional and "t" if it is traditional if differences were significant ( $\alpha = 0.05$ )

Successional stage	Plant parasite	Fungivore	Bacterivore	Omnivore-predator	Total	pp/free	f/b
Milpa	0.026 nt	0.007 nt	0.055	0.636	0.003 nt	0.076	0.122
Acahual	0.010 nt	0.038 nt	0.873	0.864	0.132	0.024 nt	0.111
Secondary forest	0.826	0.692	0.034 nt	0.528	0.298	0.546	0.381
All stages	0.071	0.056	0.006 nt	0.110	0.010 nt	0.259	0.160

system was double that in the traditional systems (Tables 1 and 2). These differences did not continue into the next successional stage, the secondary forest, although bacterivores were 60% more abundant in non-traditional than traditional systems. When the data from all stages was combined, non-traditional systems had greater concentrations of bacterivores and total nematodes compared to traditional systems (Table 2).

Soil organic matter, plant coverage, and soil texture were also found to differ between non-traditional and traditional systems. Soil organic matter averaged 15% in the non-traditional acahuals compared to 11% in the traditional acahuals ( $P < 0.001$ ). Soil organic matter in non-traditional and traditional milpas and secondary forests were not significantly different. Across all stages non-traditional soil organic matter and traditional soil organic matter were similar, 13% compared to 12%, respectively, but did differ significantly ( $P < 0.05$ ). The coverage of herbaceous species differed significantly ( $P < 0.001$ ), and coverage was 41% in non-traditional and 2% in traditional milpas. Non-traditional milpas were found to have higher concentration of silt, 19%, compared to 15% in traditional systems ( $P < 0.05$ ), and lower concentrations of clay, 50%, compared to 58% in traditional systems ( $P < 0.05$ ). No differences in soil moisture and pH were exhibited between the systems.

Relationships were found between nematode trophic groups, and between nematodes and soil organic matter. In order to evaluate relationships between nematode trophic groups, data from traditional and non-traditional systems and all field stages was pooled. The only strong relationship regarding nematode concentrations was a positive relationship between fungivores and plant parasites (Fig. 1). In contrast to nematode concentrations, the percent that each trophic group contributed to total nematode abundance revealed several relationships. The percentage of fungivores was inversely related to the percentage of bacterivores (Fig. 2). In contrast, the percentage of

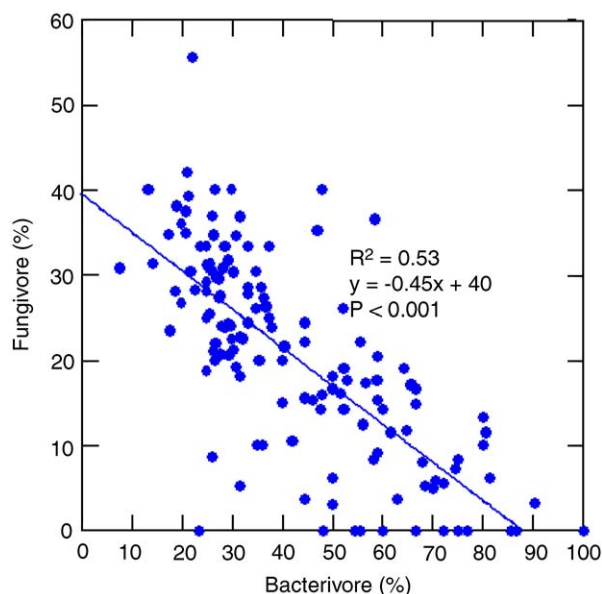


**Figure 1.** Fungivore concentration (number in 20 g soil sample) as a function of plant parasite concentration (number in 20 g soil sample) in all fields and field stages.

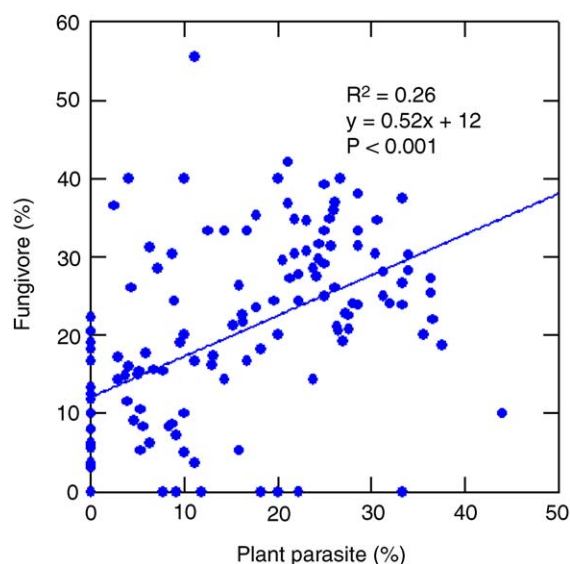
fungivores was positively related to the percentage of plant parasites (Fig. 3). The percentage of plant parasites was also inversely related to the percentage of bacterivores ( $R^2 = 0.51$ ,  $P < 0.001$ ,  $\text{coeff.} = -1.2$ ). Soil organic matter did not exhibit a relationship to nematode concentrations or percentages. However, in the traditional milpas, soil organic matter was correlated with bacterivores and fungivores. The percent of bacterivores was directly related to soil organic matter concentration in the traditional milpas (Fig. 4). Percent of fungivores was inversely related to soil organic matter concentration ( $R^2 = 0.39$ ,  $P < 0.005$ ,  $\text{coeff.} = -3.6$ ).

## Discussion

The Lacandon system of agroforestry has three successional field stages, milpa, acahual, and

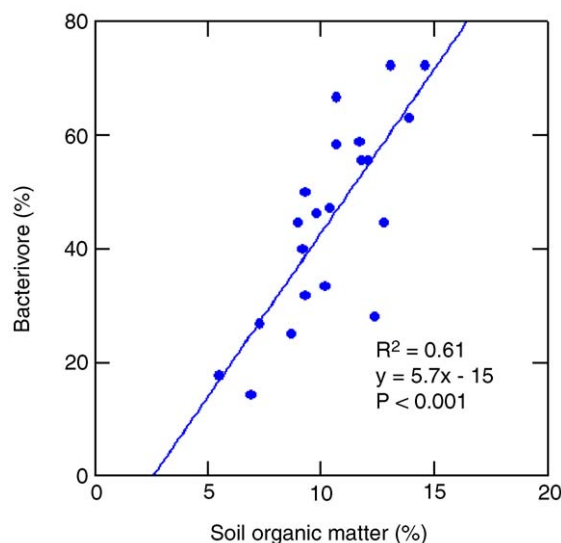


**Figure 2.** Fungivores (% of total nematodes) as a function of bacterivores (% of total nematodes) in all fields and field stages.



**Figure 3.** Fungivores (% of total nematodes) as a function of plant parasites (% of total nematodes) in all fields and field stages.

secondary forest with distinct management techniques, and requires protection of the surrounding primary forest. The nematode community exhibited significant differences between these field stages, which would be expected based on previous work by Villenave et al. (2001), Ferris and Matute (2003), and Hanel (2003), who have documented successional changes in nematode concentrations



**Figure 4.** Bacterivores (% of total nematodes) as a function of soil organic matter (% of total nematodes) in all traditional milpas.

as a function of time since disturbance. Recovery of nematode concentrations after disturbance in the Lacandon system occurred more quickly than the recovery observed by Thornton and Matlack (2002) and Pate et al. (2000). Thornton and Matlack (2002) found that recovery to undisturbed concentrations of nematodes required as much as 50 years. In contrast, nematode concentration recovery in the Lacandon system required as little as 8 years (Table 1). Concentrations of plant parasites, bacterivores, omnivore-predators, and total nematodes reached concentrations found in the undisturbed primary forest stage by the acahual stage. Two possible reasons for this difference in recovery time are biomass clearing during disturbance and the environmental differences of the two study sites. Thornton and Matlack (2002) were reporting on commercial logging operations. The Lacandon selectively remove biomass for construction material for their houses, but on a much smaller scale than commercial logging. Also, Thornton and Matlack (2002) were working in southern Mississippi and hypothesized that the establishment of the nematode community was a function of the above-ground vegetation. Pate et al. (2000) working in semi-arid tropical Senegal, found nematode community recovery to primary forest concentrations after 20 years of fallow had passed. Conditions favorable to vegetative growth and decay, including increased rainfall, likely led to more rapid nematode recovery in the Lacandon system compared to the semi-arid environment.

The absence of a strong correlation between time since fire disturbance and nematode community indices demonstrates that changes in the nematode community were not a function of time in the Lacandon system, but instead a function of the management stages. Thus, the Lacandon management techniques appeared to alter nematode diversity by successional stage, so density changes were not linear but instead followed a step-wise process (Tables 1 and 2). Pate et al. (2000) also found that nematode community change was related to field stages in similar tropical agricultural systems. In a Swedish forest the nematode community was lowest in areas with decreased amounts of vegetative cover, and greatest in areas with more abundant vegetative cover (Sohlenius, 2002). The milpa, acahual, and forest are all managed to maintain distinct types of plant community, and above-ground biomass of the milpa and acahual are relatively static compared to the secondary forest. These system characteristics coupled with the findings of Sohlenius (2002) indicate why nematode changes were related to the management stages.

Comparing the traditionally and non-traditionally managed systems revealed differences between nematode trophic group concentrations related to field stages. In the non-traditional systems, all successional stages had similar concentrations of plant parasites. In contrast, in traditional systems plant parasites were highly suppressed in the milpa compared to other field stages. Following the traditional milpa stage, the abundance of plant parasites increased by 50% in the acahual, and by 200% in the secondary forest. Concentrations of plant parasitic nematodes were greater in the nontraditional milpas and acahuals compared to the traditional milpas and acahuals. However, no difference was found when comparing plant parasitic nematodes between traditional and non-traditional secondary forest stages. These results demonstrate that traditional management practices in the milpa and acahual appear to decrease the amount of plant parasites. Past research supports a link between greater coverage of herbaceous species in the non-traditional milpa compared to the traditional milpa and greater concentration of plants parasites (Yeates, 1999). Thornton and Matlack (2002) found that plant parasites increased with plant cover in Mississippi woodlands. The cause of the difference in plant parasite concentration in the non-traditional and traditional acahuals is less evident because no difference in plant cover was detected between the traditional and non-traditional acahuals. However, in the acahual, plant cover was only recorded

for plants with a diameter greater than 1-cm. This arbitrary cutoff may have resulted in underestimating herbaceous species in the acahual. The 36% greater soil organic matter concentration in the non-traditional acahual compared to the traditional acahual was evidence that the non-traditional acahual may have had a greater cover of herbaceous species.

Higher concentrations of fungivores in the non-traditional systems may also have been related to herbaceous cover. The collection and reapplication of weeds in traditional milpas, decreased the coverage of herbaceous species compared to non-traditional milpas. This application of dried weeds occurs more often in traditional systems (pers. obs.). Ferris and Matute (2003) discovered that without continual amendments of organic matter, a field will progress from bacterivore to fungivore. The lack of organic amendment from weeds in the non-traditional systems likely caused the degradation pathway to progress from bacterial to fungal, whereas in the traditional systems, due to dried weed amendment, this conversion occurred more slowly. As evidence to this, in the traditional milpas, bacterivorous nematode abundance increased with soil organic matter concentration (Fig. 4), and fungivorous nematodes decreased in relative abundance with an increase in soil organic matter ( $P < 0.05$ ). Arancon et al. (2003) also found bacterivores to be positively related to organic material amendment.

The relationship between nematodes and soil organic matter in the traditional milpas, described above, were not observed when data from all field stages and traditional and non-traditional were pooled. Although fungivore and plant parasite percentage increases were matched by decreases in bacterivore percentages, the changes were not a function of soil organic matter. In other field stages the Lacandon were not amending the soil with dried weeds. These results indicate that the nematode community did not change with total soil organic matter concentration, which increased through the field stages, but instead, was impacted by the relative amounts of labile and recalcitrant soil organic matter.

Soil moisture, texture, and pH were not investigated as part of the same sampling event used to investigate nematodes, soil organic matter, and plant community. To address this limitation a second sampling event was conducted. pH and soil moisture did not significantly vary due to successional stage or management technique. Texture did vary with successional stage and differed between traditional and non-traditional milpas, and could have affected the nematode



community (Cadet and Thioulouse, 1998; McSorley and Frederick, 2002). Nonetheless, although texture differences were significant, they were relatively small (variation of sand, silt, and clay was less than 12%), and soil in all systems and field stages was classified as clayey.

The nematode community was used to investigate patterns of Lacandon agroforestry as practiced by six farmers. Compared to other nematode successional studies, the nematode community quickly recovered after fire disturbance in Lacandon agroforestry. The nematode community exhibited trends that appeared to be a function of successional stage and management practices rather than time since fire disturbance. Traditional Lacandon farmers managed their fields through weeding and application of dried weeds. Weeding appeared to decrease the population of plant parasites in the traditional fields. The application of dried weeds to the fields is hypothesized to increase labile soil organic matter concentrations and delay the succession of the nematode community from bacterivore to fungivore. The secondary forest stage was less managed than the first two successional stages. Little difference existed between traditional and non-traditional systems in this stage. These trends indicate that by the secondary forest stage, the degradation pathway in both traditional and non-traditional systems had become more fungal. Lacandon agroforestry is instructive on how to successfully manage pests and amend the soil in a tropical swidden system. The control of plant parasites through effective weeding and the possible suppression of the conversion of the field from bacterivorous nematode dominance to fungivorous dominance through application of dried weeds in the fields may be of fundamental importance to sustainable agroforestry practice. These results offer a partial explanation of the success of the Lacandon Maya in producing food and other material from their fields without degrading field fertility (Nations and Nigh 1980, McGee 2002).

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