

# Saprotrophic mycelial cord abundance, length and survivorship are reduced in the conversion of tropical cloud forest to shaded coffee plantation

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Received 9 July 2004; accepted 24 March 2005

Available online 11 May 2005

## Abstract

One of the most conspicuous soil elements of the tropical cloud forest in central Veracruz, mycelial cord-forming fungi, is strongly affected by the conversion of forest into shaded coffee plantations. Mycelial cord-forming fungi are less abundant, smaller and have a sharper mortality rate in shaded coffee plantations than in relatively conserved forest sites. I present evidence that suggests that changes in soil microenvironmental conditions affect the abundance of mycelial cord forming fungi. These results lend further support to growing evidence that the biodiversity of the understorey and soil are not being conserved within shaded coffee plantations. This contrasts markedly with other studies that suggest that over storey biota is effectively conserved by this conversion.

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*Keywords:* Evergreen cloud forest; Fungal ecology; Mycelial life form; Rustic coffee; Saprotrophic fungi; Soil biodiversity

## 1. Introduction

There is no doubt that shaded coffee agro-ecosystems are valuable refuges for conserving part of the local biological diversity in coffee-producing regions. This is supported by many studies accumulated over the past 20 years, showing that shaded coffee plantations support similar species richness of focal taxa (or groups) to that found in relatively undisturbed local forests (see Perfecto and Armbrecht, 2002). Furthermore, some studies show that shaded coffee plantations preserve other qualities of forest ecosystems such as a low soil erosion rate (Rice, 1990) and high carbon sequestration (De Jong et al., 1995). In the construction of a traditional shaded coffee plantation, coffee bushes replace the forest understorey plant species, but trees tend to be conserved (Moguel and Toledo, 1999). Therefore, beyond the sudden loss of

plant species from the understorey, there could be stronger negative effects on the biodiversity from the understorey to the soil stratum (the same degree of simplification observed in the understorey level occurs underground) than in the arboreal stratum, since the understorey is largely simplified but at least part of the tree diversity is conserved.

Nevertheless, most studies showing that shaded coffee plantations serve as refuges for biodiversity have looked at the species richness of particular groups or taxa that are mainly of arboreal habits, such as birds (e.g. Aguilar-Ortiz, 1982; Corredor, 1989; Greenberg et al., 1997; Wunderle and Latta, 1998; Petit et al., 1999; Wunderle, 1999; Dietsch, 2001; Petit and Petit, 2003), canopy insects (Perfecto and Rice, 1996), bats (Estrada et al., 1993; Numa et al., 2005; Pineda et al., 2005), and orchids (Williams-Linera et al., 1995). In contrast, the effects of forest conversion on species richness at the understorey and soil level are not as well assessed, and the available information is inconsistent. The species richness of leaf

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litter and twig-nesting ants found in a forest (43 species) drops by 23% when compared with a shaded coffee plantation nearby (Perfecto and Vandermeer, 2002; Armbrrecht and Perfecto, 2003). On the other hand, copronecrophagous carabid beetles (Pineda et al., 2005) and army ants (Roberts et al., 2000) are not affected by the conversion of forest into shaded coffee plantations. However, species of birds (Tejeda-Cruz and Sutherland, 2004) and frogs (Pineda and Halffter, 2004) that are specialized to exploit the forest understorey are missing from shaded coffee plantations, whereas arboreal species of these groups tend to be conserved.

In central Veracruz in Mexico, the mountain coffee region overlaps with the historical distribution of the tropical cloud forest (Williams-Linera et al., 2002). In central Veracruz this kind of forest covered the humid northeast watershed of the Eastern Mountainous Ridge (Sierra Madre Oriental) between 1000 meters above sea level (m asl) and 2400 m asl. It is considered one of the most diverse ecosystems in Mexico, for instance it hosts about 10% of the plant species recorded in the whole of Mexico but covers less than 1% of the territory (Rzedowski, 1978).

In addition, the tropical cloud forest in central Veracruz hosts a rich mycobiota and at the soil level, leaving aside macroscopic fruiting bodies, mycelial cord-forming fungi (mainly Basidiomycotina, Fig. 1) are one of the most conspicuous elements in the soil present year round. These fungi are abundant at the interface of the soil horizons L (leaf litter layer) and O (usually a top layer dominated by organic material, consisting of partially decomposed litter, such as leaves, needles, twigs, moss, and lichens) where discrete resource units (twigs, logs, and seeds) are interconnected by mycelial cords that vary from 0.5 to 5 mm in diameter.



Fig. 1. Mycelial cords in the soil of a tropical cloud forest interconnecting several discrete resources units, wood fragments (WF), oak seeds (S), and seed cups (C).

Mycelial cords are one of several life forms exhibited by fungal mycelia (Cooke and Rayner, 1984), other mycelial life forms are thick and dense mycelial mats, diffuse mycelial networks and rhizomorphs. Mycelial cords start as diffuse mycelial fans that extend from a discrete resource unit (seed, twig or log). The mycelial fan scouts the soil for additional woody resources. Once the scouting mycelium contacts and colonises a suitable resource there is a rearrangement of the mycelium with an accumulation of tightly packed parallel and undifferentiated hyphae between the discrete resource units thus forming a mycelial cord. In turn, mycelial cords form networks that interconnect nutrient-rich resources (woody resources) scattered over a relatively poor matrix (soil). These mycelial cord networks can extend up to a few meters exploiting several resource units (Boddy, 1993). When a mycelial cord is broken, the parts have the potential to develop independently (a kind of asexual reproduction), and it is difficult to determine initially whether two or more individuals occurring in close proximity were initially part of the same cord system. Therefore, I will refer to them as mycelial cord-forming units (MYCOFUs), rather than as individuals.

Mycelial cord-forming fungi do not form a monophyletic group, but they represent a functional group with a major role in ecosystems, they are major wood decomposers and can translocate (through the cords) large quantities of essential nutrients (for instance, nitrogen and phosphorous) over several meters. Additionally, mycelial cords can immobilize nutrients for long periods (several months) and by so doing they may serve as a buffer system against nutrient lixiviation (Boddy, 1993; Boddy and Watkinson, 1994; Boddy, 2000). In this study, I analyse the abundance, size and temporal dynamics of MYCOFUs in forest and shaded coffee plantations in central Veracruz and discuss the conservation value of shaded coffee plantations for local understorey and soil biodiversity. It is important to point out to non-mycologist readers that I deal exclusively with MYCOFUs leaving aside any other mycelial life form even if it may be developed by the same species of fungi that form mycelial cords.

## 2. Methods

### 2.1. Study sites

This study was conducted in proximity to the cities of Xalapa and Coatepec, using a total of six field sites (Fig. 2). These field sites included two relatively conserved areas of tropical cloud forest (F1 and F2), and four shaded coffee agro-ecosystems (C1–C4). The forest sites were located on mild slopes facing northwest, with streams running along the base of the hill. Two of the coffee plantations were also located on mild slopes (C1

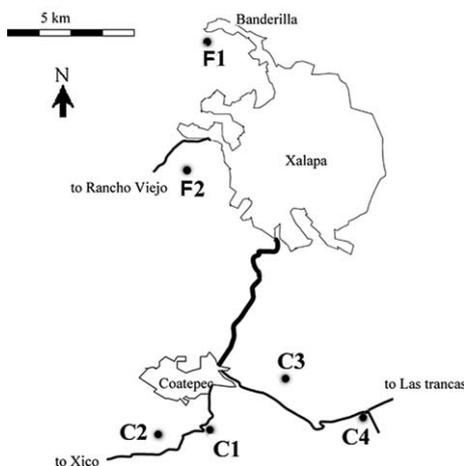


Fig. 2. Spatial distribution of forest sites (F1 and F2) and shaded coffee plantations (C1–C4).

and C3), whereas the other two plantations were located on flat ground (C2 and C4). All four plantations also included streams. In all cases, coffee plantations were constructed between 35 and 40 years ago and because they are rustic shaded coffee plantations there is little labouring other than berry picking; an activity reduced almost exclusively to selfconsumption in all four study sites as a consequence of the low income currently derived from this farming activity.

The dominant tree species in both forest sites included species of oaks (*Quercus*), sweet gum (*Liquidambar*), elm (*Ulmus*), summer sweet (*Clethra*), American hornbeam (*Carpinus carolineana*), jonote (*Heliocarpus*), and haya (*Platanus*). These trees support a diverse and abundant community of epiphytes (mosses, ferns, bromeliads, and orchids) and lianas. The forest sites covered an area of about 15 ha (F1, between 1520 and 1540 m asl), and 8 ha (F2, between 1400 and 1430 m asl) but secondary growth covered a large fraction of the F2 site.

The vegetation structure of the shaded coffee plantations was complex and similar to what Moguel and Toledo (1999) classified as traditional polyculture. The shade layer was composed of two strata: canopy trees (17–23 m) including elms, jonotes, oaks, matapalos (*Ficus*) and *Oreopanax*; whereas trees between 5 and 15 m in height included mainly cultivated species such as chalahuite and jinicuil (*Inga*), citrus, bananas, avocados, and guavas, among others. As in the forest sites, epiphytes were abundant in the coffee plantations. The coffee plantations covered an area of 6 ha (C1, between 1100 and 1180 m asl), 30 ha (C2, at 1140 m asl), 21 ha (C3 between 1180 and 1220 m asl), and 18 ha (C4, at 1040 m asl).

## 2.2. Design

In the field sites, F1 and C2–C4, I randomly set up 10 plots, each covering a surface area of 60 m<sup>2</sup> (15 m × 4 m);

in sites F2 and C1, I established six and five plots, respectively, since these sites were smaller than the other four sites. Every month from May 2002 to April 2003, I recorded and marked all MYCOFUs in each plot. To do this, all the loose leaf-litter was manually removed from the surface of each plot and all MYCOFUs were completely uncovered, even if it extended beyond the plot surface area. For each MYCOFU I recorded the length of mycelial cords, the number, kind and size of the resource units colonized. The length of mycelial cords was estimated based on the Buffon's needle theorem (Schroeder, 1974) using a lattice (wooden frame and thread) spaced every centimeter. I counted the intersections of mycelial cords with the lattice and used the formula, mycelial cord length =  $H\pi N/4$  (where  $H$ , lattice opening = 1 cm and  $N$  is number of intersections between mycelial cords and the lattice). Then, I marked each MYCOFU with a labelled-plastic shell buried at the centre of the cord system and covered it again with leaf litter.

In addition, I recorded, measured and identified all trees with a diameter at breast height (DBH) > 10 cm in each plot, and estimated the percent canopy cover at the centre of each plot with a spherical convex densitometer. To investigate the relation between the abundance of MYCOFUs and soil moisture content I collected tree soil samples (about 100 g) from each plot (bottom, middle and top sections of the plot) in the dry season (May) and I calculated the percent weight difference between wet samples and oven-dried soil samples (three days at 70 °C). To assess the availability of resources for MYCOFUs in each field site, I randomly set up five plots, each covering a surface area of 1 m<sup>2</sup>, in May 2002 (dry season), August 2002 (rainy season), and January 2003 (cold and windy season). All plots were independent, and I collected all wood litter (diameter > 1 cm) and large seeds (oak, *Inga*, etc.), which were then oven-dried for four days at 55 °C prior to weighing them.

## 2.3. Data analysis

I used a one-way ANOVA to compare the abundance of MYCOFUs per plot and the length of mycelial cords among study sites. The count data were transformed to normalize the residuals in the model. I added 0.5 to the observed values, and then I took the square root of the summed value (Zar, 1996). A two-way ANOVA test was used to compare the amount of available resources for MYCOFUs with the main factors being the study site (six levels) and season (three levels). I used a generalized linear model to explore the association between the observed number of MYCOFUs and, the abundance and species richness of trees with a DBH > 10 cm, basal area, percent canopy shade and soil moisture content. The count data, MYCOFUs, the number of trees and tree species richness were transformed as described

above, whereas for canopy cover and soil moisture content I used the angular transformation (arcsine of the square root of the observed proportion) and for the basal area I used the Neperian logarithm of the observed value. The model was fit with a normal error and identity link using GLMStat 5.7.7 (Beath, 2004).

To explore the temporal dynamics of mycelial cord systems, I developed life tables for one cohort (May 2002) in three sites. Since there were a reduced number of MYCOFUs in each coffee site, I pooled the data of the four coffee plantations to work out the life table and contrast it with that from the forest sites. I used a generalized linear model, as described, to address whether survivorship trends differed between sites.

### 3. Results

#### 3.1. Abundance of MYCOFUs

Overall, I observed a total of 418 MYCOFUs. Almost 60% (250 MYCOFUs) were observed in forest site F1, whereas forest site F2 hosted 27% (113) of the observed MYCOFUs. Coffee plantations only hosted 13% (55) of the recorded MYCOFUs. In accordance with this, I found a highly significant difference in the abundance of MYCOFUs in forest and coffee plantations ( $F=20.65$ ;  $df=5, 44$ ;  $P<0.001$ ). On average I found 25.8 ( $\pm 11.3$  standard deviation, SD) MYCOFUs per plot in forest site F1, and 19 ( $\pm 13.6$  SD) MYCOFUs per plot in forest site F2, whereas in coffee plantations the average number of MYCOFUs per plot ranged from one to three (Fig. 3(a)). In addition, for size taken as total length of mycelial cords in each MYCOFU, I found that the MYCOFUs in forest sites were significantly larger ( $F=6.14$ ;  $df=5, 412$ ;  $P<0.001$ ) than in coffee plantations (Fig. 3(b)). MYCOFUs were about 61% larger in forest site F1 than in forest site F2 and, on average, over twice the size of those found in coffee plantations. Overall, the average size of MYCOFUs was 16.8 cm and the average distance ( $\pm$ SD) to the nearest MYCOFU neighbour was  $3.98 \text{ m} \pm 3.6 \text{ m}$ .

Correlations (correlation coefficients from 0.65 to 0.97) between the number of trees, canopy cover and soil moisture content were high and positive whereas these factors were only weakly correlated with basal area and tree species richness (from 0.12 to 0.24). Following model simplification, I found that the two simplest and most parsimonious models include, separately, percent canopy cover ( $F=147.1$ ;  $df=1, 49$ ;  $P<0.001$ ;  $R^2=0.75$ ) and soil moisture content ( $F=122.7$ ;  $df=1, 49$ ;  $P<0.001$ ;  $R^2=0.73$ ) as explicative variables for the number of MYCOFUs per plot (Fig. 4). The number of trees had a significant effect in both models ( $P<0.05$ ) but it was entirely redundant with either canopy shade or soil moisture content and therefore it was removed from the

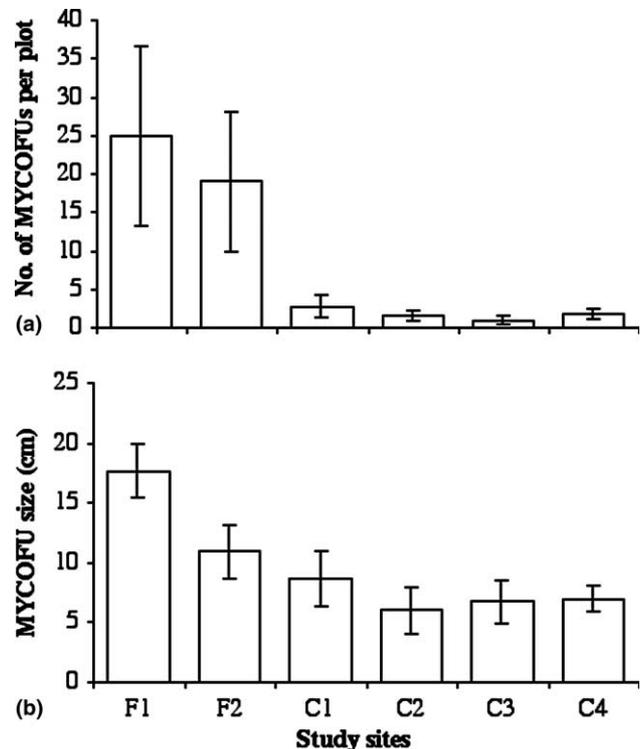


Fig. 3. (a) Abundance and (b) size of mycelial cord-forming units (MYCOFUs) in two sites of tropical cloud forest (F1 and F2) and four shaded coffee plantations (C1–C4). The plots showed average  $\pm 95\%$  confidence intervals.

models. None of the second-order interactions neither basal area and tree species richness had significant effects on the abundance of MYCOFUs.

In relation to the availability of resources, I found no significant differences among sites ( $F=1.1$ ;  $df=5, 72$ ;  $P=0.36$ ), but there was a significant seasonal variation ( $F=25.6$ ;  $df=2, 76$ ;  $P<0.001$ ). The dry mass of woody litter was lower in the dry season (mean  $\pm$ SD,  $358.5 \text{ g} \pm 149.7 \text{ g}$ ) than in the rainy ( $826.0 \text{ g} \pm 393.5 \text{ g}$ ), and cold and windy season ( $930.5 \text{ g} \pm 388.5 \text{ g}$ ). The interaction between the site and season did not have a significant effect ( $F=1.0$ ;  $df=10, 72$ ;  $P=0.45$ ).

#### 3.2. Temporal dynamic of MYCOFUs

Given the reduced number of MYCOFUs found in each coffee plantation, I pooled all data from coffee plantations in order to compare with the forest sites. For the temporal dynamic of MYCOFUs, I found overall five main cohorts (May, September, November, January, and April) (Fig. 5(a)). All of these five cohorts were numerous in Forest sites and in general had few units in coffee plantations. Furthermore, there were no newly formed MYCOFUs recorded in January and April in none of the coffee sites. The life table analysis was performed only for the cohort of May since it was the only cohort with enough MYCOFUs for both the forest sites

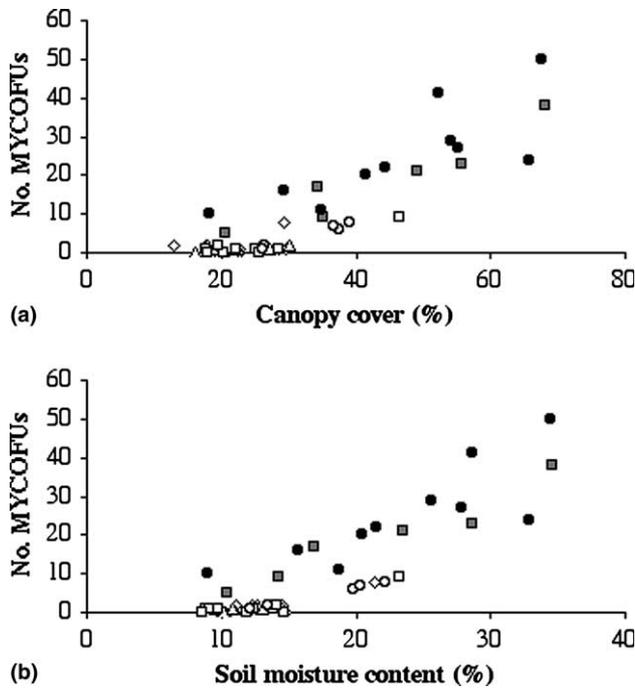


Fig. 4. Distribution patterns of abundance of mycelial cord-forming fungi (MYCOFUs) in relation to the transformed values of (a) percent canopy cover and (b) percent soil moisture content in two forest sites (F1, black circles and F2, grey squares) and four shaded coffee plantations (open figures, C1 (circles), C2 (triangles), C3 (squares), and C4 (diamonds)).

and coffee plantations. The life table analysis (Table 1) showed that the mean age ( $\pm$ SD) of MYCOFUs for forest site F1 was 4.5 months ( $\pm$ 2.5 months), and for forest site F2 it was 3.5 months ( $\pm$ 2.3 months), whereas for the coffee plantation it was 3.7 months ( $\pm$ 2.1 months).

The survivorship curve showed that MYCOFUs face an even mortality rate all through their life in forest sites as well as in coffee plantations (Fig. 5(b)). However, the linear model ( $F=27$ ;  $df=3, 23$ ;  $P<0.001$ ;  $R^2=0.93$ ) showed that the slope of the curves differed significantly

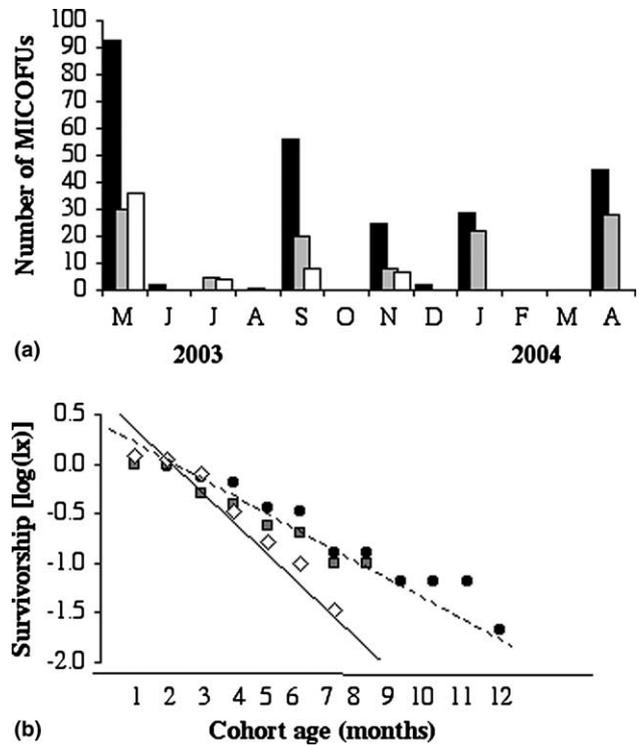


Fig. 5. Temporal dynamics of mycelial cord-forming fungi (MYCOFUs). (a) Monthly emergence of MYCOFUs and (b) survivorship curves of MYCOFUs in two forest sites, F1 (black bars and circles), F2 (grey bars and squares) and pooled data of four shaded coffee plantations (open bars and open diamonds). Lines in (b) represent the two regression lines found in the simplest model, solid line (coffee sites) and broken line (forest sites).

between sites, i.e., that the interaction of age and site was highly significant ( $F=222$ ;  $df=2, 23$ ;  $P<0.001$ ); MYCOFUs' survivorship declined faster in coffee sites as cohort ages than in forest sites. The simplest model showed a difference between coffee sites and forest sites, but there was no significant difference between forest sites.

Table 1  
Summary of the life table for the forest sites and coffee plantations for the cohort of May 2003

X	Forest site 1				Forest site 2				Coffee plantations			
	$l_x$	$n q_x$	$n d_x$	$e_x$	$l_x$	$n q_x$	$n d_x$	$e_x$	$l_x$	$n q_x$	$n d_x$	$e_x$
1	1.000	0.043	0.043	3.995	1.000	0.033	0.033	3.000	1.200	0.083	0.100	2.611
2	0.957	0.236	0.226	3.152	0.967	0.483	0.467	2.086	1.100	0.273	0.300	1.803
3	0.731	0.118	0.086	2.971	0.500	0.200	0.100	2.567	0.800	0.583	0.467	1.292
4	0.645	0.450	0.290	2.300	0.400	0.417	0.167	2.083	0.333	0.500	0.167	1.400
5	0.355	0.061	0.022	2.773	0.233	0.143	0.033	2.214	0.167	0.400	0.067	1.300
6	0.333	0.613	0.204	1.919	0.200	0.500	0.100	1.500	0.100	0.667	0.067	0.833
7	0.129	0.000	0.000	3.167	0.100	0.000	0.000	1.500	0.033	1.000	0.033	0.500
8	0.129	0.500	0.065	2.167	0.100	1.000	0.100	0.500				
9	0.065	0.000	0.000	2.833								
10	0.065	0.000	0.000	1.833								
11	0.065	0.667	0.043	0.833								
12	0.022	1.000	0.022	0.50								

X, cohort age (months);  $l_x$ , survivorship rate;  $n q_x$ , proportion of deaths occurring from  $X_t$  to  $X_{t+1}$  ( $t$  = time interval, age);  $n d_x$ , proportion of the initial cohort size death at age  $x$ ;  $e_x$ , life expectancy.

#### 4. Discussion

Mycelial cord-forming fungi are found in a variety of habitats such as temperate deciduous and coniferous forests, sand dunes, tropical rainforests, and cloud forest (see Boddy, 1993). Nevertheless, I am unaware of any study reporting the abundance of mycelial cord-forming fungi (MYCOFUs) comparable to this study. In tropical ecosystems, my own observations (unpublished) indicate that MYCOFUs are far more abundant in cloud forests than in low land rainforests and coniferous forests. This is consistent with the observations made in temperate forests (Boddy, 1993) that cordforming fungi are more abundant in deciduous forests than in coniferous forests. Far less documented are the effects of forest conversion to other land uses on the abundance of mycelial cord forming fungi.

##### 4.1. MYCOFUs and conversion

I found that the conversion of tropical cloud forests to shaded coffee plantations severely impacts the abundance, cord length, and temporal dynamic of MYCOFUs. My data show that the percent canopy cover and soil moisture content account for a large proportion of the observed variation in the abundance of MYCOFUs, whereas tree species richness and the availability of resources does not.

Alternatively, given the spatial distribution of study sites, it is plausible that the observed differences in the abundance of MYCOFUs are simply a consequence of the differences in altitude between the sites. Site F1 with the highest abundance of MYCOFUs is high in the mountain (above 1500 m asl) whereas site F2 is located at a lower altitude (about 1400 m asl) and coffee plantations are further down in the mountain (from 1040 to 1220 m asl). In addition, autocorrelation may be significant since coffee plantations are relatively concentrated in a small area (about 25 km<sup>2</sup>) whereas forest sites are relatively far away (about 15 km in straight line) from the coffee plantations (see Fig. 1). Similar limitations are faced by many studies that contrast coffee plantations and conserved forest sites, since plantations tend to be in and around wide valleys whereas conserved forest remnants usually are in steep ground (see Tejeda-Cruz and Sutherland, 2004). Even so, there are some indications that forest conversion rather than changes in altitude, may be the underlying factor for the low abundance of MYCOFUs in coffee plantations.

First is the fact that historically the whole area considered in this study was covered by tropical cloud forest which used to be distributed from 1000 m asl (or even lower altitude in protected glens) to 2400 m asl (Rzedowski, 1978). Second, the historical records of weather stations in the region show roughly the same weather regime (average monthly rain and average monthly mean tem-

perature) occurring around coffee and forest sites F1–F2 and C1–C4 (see García, 1973). Third, canopy shade and soil moisture content in forest sites and coffee plantations largely explained the abundance of MYCOFUs. Plots in forest sites with low canopy cover had a low abundance of MYCOFUs. Conversely, plots in coffee plantations with relatively high percent of canopy cover and soil moisture content had a high abundance of MYCOFUs similar to that found in some plots in forest sites. Additionally, there are no differences in the available mass of wood litter between forest sites and coffee plantations and the mean age of MYCOFUs in coffee sites is similar that that observed for MYCOFUs in forest sites F2. This evidence suggest that shaded coffee plantations have the potential to sustain a high abundance of MYCOFUs, however, their abundance is limited by the overall low canopy cover and consequently low soil moisture content of these sites. This is in agreement with Perfecto and Vandermeer (1996), who found that microclimatic changes in coffee plantations compare to nearby forest sites have indirect effects on ant diversity.

Microclimatic changes, however, are only one of several factors that could influence the size and abundance of MYCOFUs; other factors not estimated in this study are soil and leaf litter chemistry, the diversity of wood litter and the intensity of human activities. The abundance of MYCOFUs in forest sites could be overestimated since I have no way to distinguish whether two MYCOFUs in close proximity represent the same genotype. However, since the average size of MYCOFUs was 16.8 cm and the average distance to the nearest neighbour was almost four meters, it seems that fragmentation of MYCOFUs was not a recurrent event. On the other hand, human activities in coffee plantations could reduce the size and abundance of MYCOFUs. However, I have no evidence that suggests such effects, but even if that were the case, increased human activities have to be considered as part of the changes associated with forest conversion into shaded coffee plantations.

As indicated earlier, in this study, I deal with a functional group of mycelial cord-forming fungi, and it was not an objective to resolve the number of species of cord-forming fungi involved. Nevertheless, it is worth to point out that there is a strong seasonal pattern of occurrence of MYCOFUs in all six sites. In general, there are five main pulses in which new MYCOFUs were first recorded: April, May, September, November and January. Whether each of these pulses of emergence of MYCOFUs represents phenological stages of the same or different species of fungi has to be solved by molecular methods. Nevertheless, data suggest that a similar set of strategies (genotypes and/or species) is present in the two forest sites although there are marked differences in abundance. In contrast, some of these strategies (January and April) are missing from coffee plantations and the abundance of MYCOFUs is low in all cases compared to forest sites.

Bearing in mind that cord-forming fungi are major wood decomposers (Boddy, 1993), it could be hypothesize that decomposition of wood litter will proceed at a lower rate in coffee plantations than in forest sites. This may explain the fact that I did not find significant differences in the mass of woody resources between forest sites and coffee plantations. However, most importantly for ecosystem functioning may be the immobilization of mineral nutrients in the biomass of MYCOFUs which has been hypothesized as a buffer against mineral nutrient loss from the system (Boddy, 1993) a function that could be strongly diminished in shaded coffee plantations. All these are aspects directly linked to the conservation of biological diversity in the soil of the coffee growing area and deserve further investigation.

#### 4.2. Conservation of understorey and soil biodiversity

My findings are consistent with a growing body of information showing that the forest understorey and soil biodiversity, e.g., ants (Armbrecht and Perfecto, 2003), birds (Tejeda-Cruz and Sutherland, 2004), frogs (Pineda and Halfpeter, 2004; Pineda et al., 2005), cord-forming fungi (this study), and, obviously, understorey plant species, are not being adequately conserved in shaded coffee plantations. However, those taxa or guilds exploiting arboreal strata tend to be less disadvantaged, e.g., birds (e.g., Aguilar-Ortiz, 1982; Corredor, 1989; Greenberg et al., 1997; Wunderle and Latta, 1998; Petit et al., 1999; Wunderle, 1999; Dietsch, 2001; Petit and Petit, 2003), canopy insects (see Perfecto and Rice, 1996), bats (Estrada et al., 1993; Estrada and Coates-Estrada, 2002; Numa et al., 2005; Pineda et al., 2005), and orchids (Williams-Linera et al., 1995). Such a pattern is not surprising since in the construction of a shaded coffee plantation the understorey of the forest is radically simplified, as coffee bushes replace many different species of plants. In contrast, a large proportion of trees tend to be conserved (López-Gómez, 2004).

Whether this pattern will hold for fungi other than MYCOFUs is still to be uncovered. Mycorrhizal fungi deserved attention on this line of thinking since in the tropical cloud forest two guilds of mycorrhizal fungi coexist. Ectomycorrhizal fungi are associated with some of the large tree species in the forest such as *Quercus*, *Carpinus*, *Liquidambar*, and *Fagus* that tend to be conserved in shaded coffee plantations. On the other hand, arbuscular mycorrhizal fungi are predominantly associated to understorey plant species (for instance *Piper*, *Eugenia*, *Hoffmania*, *Palicourea*, *Psychotria*, *Miconia*, etc.) most of which are replaced by coffee bushes in the construction of shaded coffee plantations. This fact would suggest that arbuscular mycorrhizal fungi are not adequately conserved in shaded coffee plantations. However, given that coffee bushes associate themselves with arbuscular mycorrhizal fungi, a detailed study is needed

to address the conservation value of shaded coffee plantations for mycorrhizal symbiotic mutualisms.

## 5. Conclusions

The evidence presented in this study showed that MYCOFUs are not adequately being conserved in shaded coffee plantations. At least part of the genetic diversity (genotypes and/or species) found in forest-sites seems to be missing in coffee plantations and in general there is a low abundance of MYCOFUs in the agroecosystem. This reduction could have two significant effects at the ecosystem level. MYCOFUs are major wood decomposers and therefore their low abundance and reduced size in coffee plantations is expected to reduce the overall rate of wood decomposition. Furthermore, lixiviation in shaded coffee plantations may be high, since MYCOFUs immobilized large amounts of mineral nutrients and serve as buffer against mineral nutrient loss from the system (Boddy, 1993). Additionally, changes in the dynamics of these processes could directly affect other components of soil such as species richness of wood-inhabiting arthropods and the spatial and temporal distribution of fine-roots (see Guevara and Romero, 2004).

In general, the accumulating evidence suggests that understorey and soil biodiversity are not adequately conserved in shaded coffee agro-ecosystems. This has important implications for conservation strategies in shaded coffee-producing regions. There should be no doubt that shaded coffee plantations are valuable refuges for part of the local biodiversity in coffee-producing regions. Nevertheless, it seems that forest fragments may be the only alternative to conserve the biodiversity of the understorey and the forest soil. Therefore, further investigation is necessary to address the effects of size, shape, and spatial arrangement of forest fragments in shaded-coffee producing regions on the biodiversity of the understorey and soil strata.

## Acknowledgements

The Department of Soil Biology (INECOL) and CONACYT-J63326V supported this project. Iliana Romero and Luis Alfredo Pineda assisted in the collection of field data. Comments from three anonymous reviewers helped to improve the content and presentation of the manuscript. Evodia Silva-Rivera proofread the manuscript.

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