

Chapter 4

Soil Fungi and Macrofauna in the Neotropics

Yiqing Li and Grizelle González

4.1 Introduction

Decomposition is a critical ecosystem function that decomposes dead organic materials, removes wastes, recycles nutrients and renews soil fertility. In natural ecosystems most nitrogen (N) and phosphorous (P) required for plant growth are supplied through the decomposition of detritus, relying therefore on the activities of soil microbes and macrofauna. Decomposition is a consequence of interacting physical and chemical processes occurring inside and outside of living organisms in an ecosystem (Chapin III et al. 2002). The two major processes include fragmentation, breaking larger pieces of organic mater into smaller ones, and chemical alteration, the change of chemical elements of dead organic mater into others. Fragmentation is largely a consequence of feeding activity of soil macrofauna and chemical alteration is primarily associated with the activity of bacteria and fungi.

Land conversion from forests to pasture or agricultural land alters the below-ground ecosystem and decomposition process, and depletion of soil organic C (Doran and Zeiss 2000). Degradation processes such as losses in soil C, nutrient depletion and reduced water holding capacity often lead to considerable change in soil microbial community and macrofuana (Bever et al. 1996, Picone 2000, Thomas et al. 2004). In the Neotropics, land conversion from tropical forest to agricultural land and then to pasture is the most common kind of land use practices (Fearnside 1993, Thomlinson 1996, Cleveland et al. 2003). Studies of the dynamics of microbes and macrofauna following land conversion are thus particularly of importance for establishing effective strategies of post-agriculture recovery and forest ecosystem restoration because soil microbial community and soil macrofauna play a key role in successional pathways.

4.2 Fungi

Together with bacteria, fungi are the main initial decomposers of dead plant and animal materials and account for 80–95% of the total decomposer biomass and heterotrophic soil respiration (Macfadyen 1963, Coleman 1985, Chapin III et al. 2002).

Fungi alone constitute a major portion of the soil biomass, with fungal biomass carbon (C) equal to or exceeding root biomass C (Paul and Clark 1996). Their biomass in soils ranges from 1,000 to 15,000 kg/ha in the top 15 cm (Brady and Weil 2002).

Typically, fungi produce slender filaments or hyphae with a dense concentration of cytoplasm, either branched or un-branched, and commonly multinucleate. The hyphae constitute the soma, mycelium and thallus and contain more vacuoles when resources are scarce, which enables fungi to grow into new areas to explore for substrate. Fungi secrete enzymes capable of breaking down complex cell wall components, such as lignin, enabling them to penetrate the cuticle of dead leaves or the exterior of roots to gain access to more labile compounds that occur within the cell. Reproduction in fungi is sexual, asexual or both. Asexual spores are produced at hyphal tips in structures and sexual spores are produced following hyphal conjugations. In asexual reproduction, the offspring are genetically identical to the "parent" organism (clones). During sexual reproduction, a mixing of genetic material occurs so that the offspring exhibit traits of both parents. Many species can use both strategies at different times or different conditions, while others are apparently strictly sexual or strictly asexual. As heterotrophs, fungi depend on living or dead organic materials for their energy and C sources.

As major decomposers of organic materials in soil, fungi comprise an extremely diverse group of microorganisms. Thousands of species have been identified in soils, representing some 170 genera, and at least 1 million of fungal species in soils are waiting for discovery (Brady and Weil 2002). Two groups of fungi common to soils are the single-celled organisms called yeasts and the multicellular filamentous organisms, such as molds, mildews, smuts, and rusts. Generally, filamentous fungi are abundant in well-aerated environments, whereas yeasts inhabit in poor-aerated soils. Most filamentous fungi lack a capacity for anaerobic metabolism and therefore often absent from anaerobic soils. Mushrooms are the true reproductive structures of filamentous fungi. The aboveground fruiting structure of most mushrooms is only a small part of the total body. An extensive hyphae network of mushrooms permeates below ground. Mushroom fungi are important wood rots that attack standing and felled timber, stumps, slash and wooden structures, given appropriate moisture contents. Molds are microscopic and semi-macroscopic fungi that play a much more important role in soil organic matter decomposition than the mushroom fungi. The four most common genera of molds in soils are *Penicillium*, *Mucor*, *Fusarium* and *Aspergillus*.

In many terrestrial ecosystems, fungi are the most abundant decomposers which are more effective than bacteria. Fungi are better equipped for carrying out the decaying of the dead organic materials since their hyphae networks can penetrate new substrates and proliferate both within and between dead plant cells. Fungi also have an ability to transport nutrients through their hyphal networks to zones of exploitation. Fungi have enzyme systems capable of breaking down all types of plant compounds. All these advantages of fungi over bacteria made fungi dominant in most ecosystems. Up to 50% of the substances decomposed by fungi are used for fungal tissue, compared to around 20% for bacteria (Brady and Weil, 2002). Fungi continue to decompose various complex organic materials which bacteria and actinomycetes cannot decompose.

Fungi play a critical role in the mineralization of nutrients. Fungi, together with bacteria and other microbes, break down soluble and insoluble organic matter and convert it into inorganic forms which can be used by plants. The majority of N is contained in dead organic matter which depends upon the decomposition by microbes for the N availability of plants. Nitrogen fixation by microbes is another route through which plants obtain N. These microbes form nodules with the plant root where they gain carbohydrate from the plants and in turn they provide the plants with amino acids. Although bacteria play a key role in N fixation through symbiotic association with plants (legumes), the primary route by which N enters this soil is through the break down of legume leaf litter inputs that are enriched with N (Read and Perez-Moreno 2003, Bardgett 2005). The breaking down of these leaf litters are mainly completed by fungi. Phosphorous availability for plants is determined by geochemical process rather than biological process, soil microbes however are actively involved in the cycling of P (Sanders and Tinker 1971, Dodd et al. 1987, Jayachandran et al. 1992, Salas et al. 2003, Joner and Jakobsen 2005).

4.3 Soil Macrofauna

Soil macrofauna play a very important role in improving structure, organic matter content and distribution patterns of nutrient elements. Soil macrofauna may affect soil function and processes in a variety of ways, and could be used as indicators of nutrient status of soils (Vanlauwe et al. 1997, Rao et al. 1998, Martius et al. 2001). Members of the macro-fauna group of soil animals include: arthropods (isopods, amphipods, millipedes, termites), annelidans (earthworms) and molluscs (slugs and snails). These animals are mostly responsible for the initial shredding of plant remains and its redistribution within decomposer habitats (Swift et al. 1979) as their body sizes are large enough to disrupt the structure of mineral and organic soil horizons through their feeding and burrowing activities (Anderson 1988). The macro-fauna have an important role in the maintenance of soil structural stability and fertility in many natural and human-modified habitats (Gillison et al. 2003). Not surprisingly then, the soil macro-fauna are considered important ecosystem "engineers"; particularly in tropical ecosystems where their bioturbation actions are major determinant of soil processes (Lavelle 1997), climatic conditions rarely limit their activities, and their feeding strategies produce biogenic structures that can determine the activities of microorganisms and other smaller invertebrates (Lavelle et al. 2001).

The function of soil decomposer organisms may be categorized by body size, or by various physiological aspects of trophic function (Swift et al. 1979). In terms of body size, soil fauna were traditionally subdivided on the basis of body length (Wallwork 1970). However, the use of meshed litterbags to separate the effects of particular groups of the fauna on litter decomposition led to the classification of soil fauna based on their body diameter classes (Swift et al. 1979). Thus, soil invertebrates can be classified by body width into micro- (< 100 μm), meso- (< 2 mm) and macro-fauna (> 2 mm). This latter classification being more of a functional

classification with respect to litter breakdown and decomposition processes (Fig. 4.1, Swift et al. 1979). These size categories are somewhat arbitrary because juveniles of some species may be classified differently as adults, and also ignores the range of trophic diversity of animals in the soil (Anderson 1988). Yet, body width rather than body length broadly defines the extent to which the feeding and burrowing activities of soil animals are constrained by, or modify, the structure of soil and litter habitats (Anderson 1988).

The size of an organism is also an important determinant of its distribution (Swift et al. 1979). It has been argued that micro-fauna species tend to have large geographic distribution patterns as a result of the size and ubiquity of the microsites they occupy, whereas the macro-fauna show a greater discontinuity in distribution (Fig. 4.2, Anderson 1977). The microorganisms and the micro-fauna may be widely dispersed by abiotic and biotic agents, whereas most of the larger saprotrophic animals are sedentary and rarely dispersed except by their locomotive efforts (Swift et al. 1979). The relative contribution of different functional groups of the soil fauna to soil / ecosystem processes is dependant on the confounding effects of their size, abundance, diversity and functionality (e.g., Hansen 1999, Heneghan et al. 1999, Imler 2000, González and Seastedt 2001) but also by the landscape in which they

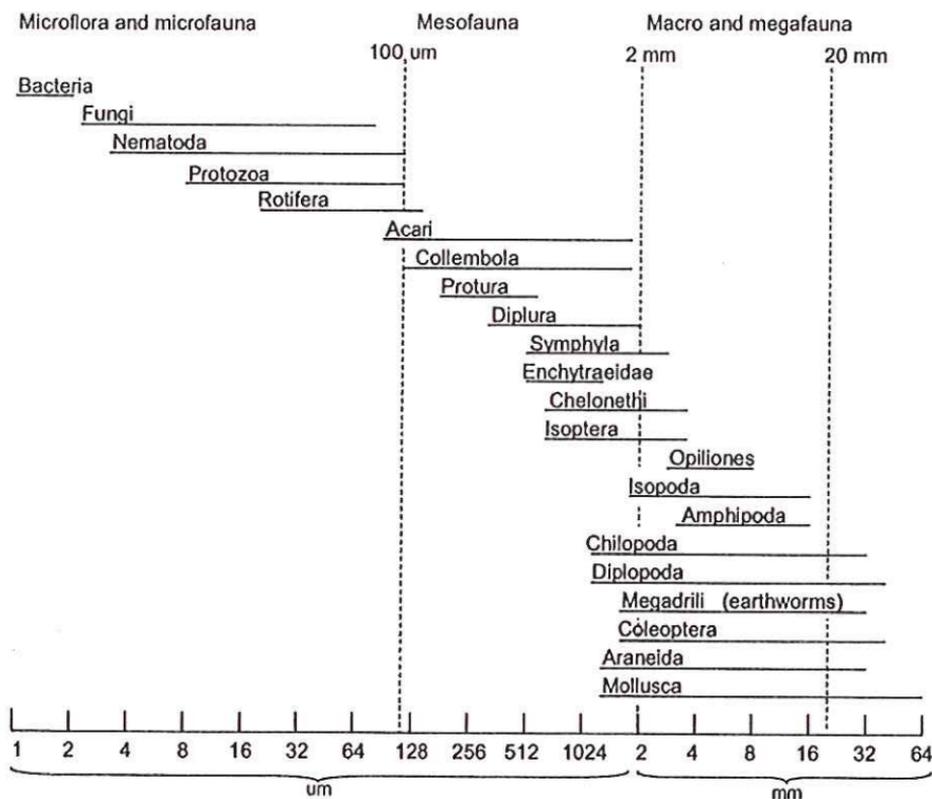


Fig. 4.1 Size classification of organisms in decomposer food webs by body width (from Swift et al. 1979)

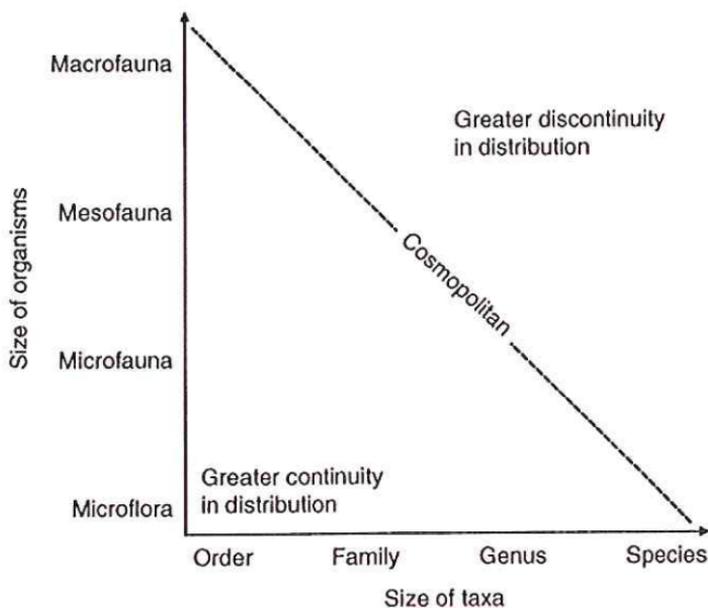


Fig. 4.2 Biogeographical distribution of soil animals in relation to body size and taxonomic level (modified from Anderson 1977)

occur (i.e., the degree of fragmentation, state of plant community succession and / or habitat alteration) as it can affect their distribution patterns.

Conversely, soil organisms can have substantial ecosystem effects on natural and human-altered habitats. This is important to consider given that (1) more than 95% of the earth's land surface is affected by human activities, including agriculture and urbanization (Moguel and Toledo 1999) and (2) the majority of animals in terrestrial habitats are invertebrate members of the decomposer community (Hansen 2000). Thus, soil macro-fauna might be more prone than smaller invertebrates to show an even greater discontinuity in distribution and more patchy effect on ecosystem processes in the context of habitat alteration and as compared to their expected distribution given size. In addition, land use intensification and fragmentation in the Neotropics can significantly modify the relative contribution of native and exotic elements within the macro-fauna; further challenging the incorporation of soil organismal effects on ecosystem processes into sound management plans and practices.

Ecosystem engineers—like the macro-fauna—are less able to withstand high levels of natural and anthropogenic environmental constraints and lower order groups may become predominant with significant differences in the function of the ecosystem (Lavelle 1997). Consequently, modifications of soil fauna communities may lead to loss of diversity and soil functions (Lavelle 1997). In the following section of this chapter, we will discuss the effects that soil macro-fauna have on soils and ecosystem functioning under different post agricultural management practices; and highlight gaps in knowledge that might stimulate further studying of soil macro-fauna effects in the Neotropics.

4.4 Discussion

4.4.1 *Fungi*

4.4.1.1 General Patterns in Tropical Forests and Pastures

Since the Industrial Revolution, first temperate and then tropical land-use change has significantly affected biogeochemical and biophysical processes of various ecosystems at multiple scales. Typically, when tropical forests are cut down the land is converted for cattle ranching or agricultural use. Human alteration of natural forest ecosystems for pastures is an important component of tropical land use change, and has the potential to alter soil nutrient and C cycles (Buschbacher et al. 1988, Neill et al. 1997, Holl 1999, Nepstad et al. 1999, Post and Kwon 2000, Amundson 2001, Townsend et al. 2002, Myster 2004). The nature and extent of such changes of nutrient and C cycles vary widely across gradients in climate, soil type and management strategies (Spaans et al. 1989, Groffman et al. 2001). Although the changes of biogeochemical patterns following land conversion are becoming well documented, the major mechanisms driving the variation of such changes are still poorly understood. Most previous studies have focused on environmental or plant-driven factors over biogeochemical changes following deforestation. However, soil microbial community, one of the possible mechanical controls over the biogeochemical changes, has been less documented. Land conversion disrupts the structure and activity of soil microbial community (Borneman and Triplett 1997, Nüsslein and Tiedje 1999) and microbes in turn affect the biogeochemical variables. Fungi play a significant role in regulating populations of other soil organisms and ecosystem processes (Fitter and Garbaye 1994). Thus, it is essential to understanding the relationship between patterns and activities of microbial community and biogeochemical changes following land conversion in the tropical ecosystems.

A main component of the tropical soil microbial community is fungi. Fungi are primarily responsible for mineral nutrient recycling through decomposition of organic matter and the transfer of nutrients into plants by mycorrhizal fungi (Lodge 1993, Myster 2006). The conversion of forest to pasture causes significant changes to soil environment, leading to changes in fungi community (Nüsslein and Tiedje 1999, Cleveland et al. 2003). Studies suggested the shift in overall microbial composition could be up to 50%. The change of fungal diversity following land conversion is closely related to initial fungal species in different regions even with similar climates. For example, the Neotropics have a very high fungal diversity comparing to African and Asia in the tropics (Lodge and Cantrell 1995). In addition, microbial biomass C also declines when from forest to pasture. For example, in an oxisol pasture in Costa Rica, microbial biomass (main component being fungi) is 40–60% lower than values in the forest (Cleveland et al. 2003). The decrease in microbial biomass may not entirely driven by soil organic matter because the decrease of soil organic matter in oxisol pasture was around 20% lower in pasture than in forest. Generally, the impacts of land use change on soil fungi community is larger in

nutrient-poor sites and relatively modest in more fertile sites (Luizao et al. 1992, Henrot and Robertson 1994). Groffman (2001) found that land conversion did not decrease microbial biomass and activity in a relatively nutrient-rich tropical ecosystem. Fungal biomass and total biomass of all microorganisms contain significant fractions of labile nutrients in forest floor of tropical ecosystems. During the conversion from forest to pasture most of these microbial related labile nutrients are lost. Based on litter and basidiomycete nutrient concentration, 22% of litter P and 4% of K could have been immobilized in fungal biomass (Lodge 1993). Phosphorus immobilization by fungi in the Luquillo Experimental Forest is considerable because leaf decomposer fungi maintained P concentration (Lodge 1987). In pastures, the total amount of immobilized P in litter significantly decreased because of less fungal biomass in the pasture litters.

Mycorrhizal associations have been intensively studied over the past several decades and increased understanding of the important role of this symbiosis in the functioning and performance of plants in tropical ecosystems. Besides mycorrhizal fungi providing phosphorus from host plants and reciprocal C provision from host to fungus, additional effects of mycorrhizal fungi on the functioning of their host plants include increased disease resistance, improved water relations, alternation in other soil properties, and acquisition of soil nutrients. Mycorrhizal fungi are of particular importance in the tropical ecosystems because of their widely distribution with a higher proportion of total fungal biomass. In nutrient-poor soils of humid tropics, a number of late-successional woody species are obligately dependent on arbuscular mycorrhizae (Picone 2000). Previous studies have suggested that plant succession, restoration or reforestation could be inhibited by either the abundance or the diversity of arbuscular mycorrhizal fungi in old pastures or agricultural lands (Jenos 1988, van der Heijden et al. 1998). Because disturbances to the host plant community alter the mycorrhizal fungi community (Bever et al. 1996) and host plant diversity is much lower in pastures than in forests, mycorrhizal fungal diversity dramatically declines. Thus, unlike in forests, pastures are usually dominated by a few mycorrhizal species with each species produces more spores than the species in forests. Several hypotheses have been suggested to explain why most species of arbuscular mycorrhizal fungi produce more spores in pasture than in native forests (Picone 2000). For example, it is suggested by these hypotheses that higher fine root density and turnover rate, higher pH value, and more host specific sporulation in pasture favor producing more spores. Species richness of arbuscular mycorrhizal fungi also decreases in agroecosystems comparing to natural ecosystems. Frequently irrigated and fertilized agricultural lands reduce more arbuscular mycorrhizal fungi than un-intensive managed agricultural lands since high nutrient inputs diminish the soil colonization potential and the dependency of plants on mycorrhization (Höflich and Metz 1997). Phosphorous limitation to fungal processes has been demonstrated in forest ecosystems and such constraints are also present in the pastures. However, since conversion from forest to pasture dramatically reduces the abundance of spores and the diversity of arbuscular mycorrhizal fungi, forests tend to conserve limiting nutrients, such as P, more tightly than pastures because of the nutrient immobilization by fungi which maintain limiting nutrient concentration.

4.4.1.2 A Case Study: Fungal Biomass Dynamics Following Reforestation in Puerto Rico

Fungal biomass contains significant fractions of labile nutrients in the forest floors and surface soils of some tropical ecosystems (Yang and Insam 1991, Li et al. 2005). Nutrients can be immobilized and conserved by fungi and other microbes in their biomass during periods of high precipitation that cause leaching (Behera et al. 1991, Yang and Insam 1991). Therefore, fungal biomass and total biomass of all microorganisms are important indicators for the nutrient dynamics and availability. However, relatively few publications contain measurement of fungal or total microbial biomass in tropical primary forests and other forest ecosystems following reforestation, such secondary forests and plantations (Frankland et al. 1990, Korf 1997, Tufekcioglu et al. 2001, Myster and Schaefer 2003, Li et al. 2004). Secondary forests account for 40% of the total area of tropical forests and this percentage is still increasing throughout the tropics (Brown and Lugo 1990). The success of management of tropical forests in the future might well depend upon the adequacy of our ecological understanding of secondary forests (Cheng 1993). Tree plantations, covering 11 million ha of the tropics (Lanly 1982), are rapidly increasing in area in the tropics as a reforestation approach. Reforestation through plantation on abandoned and degraded agricultural lands in the tropics has been proposed as an effective C management approach (Montagnini and Porras 1998).

In this case study, total fungal biomass and active fungal biomass were measured in surface soil in subtropical wet forest zone at Guzmán site in Puerto Rico. Using a 20-year old pine plantation and a secondary forest originating from the same abandoned farmland in the wet tropics in Puerto Rico, we examined microbial biomass after 7-year litter exclusion, root exclusion, and both litter and root exclusion treatments in the plantation and the secondary forest. The study was conducted on two sites that were within 100 m of each other. One site was in a *Pinus caribaea* (Morelet)-dominated plantation and the other was in a secondary forest. Both sites were located in the Guzmán sector of the Luquillo Experimental Forest in northeastern Puerto Rico (18°18'N, 65°50'W). The plantation and the secondary forests originated from the same abandoned agricultural land with the same cropping system and management/disturbance history (Lugo 1992). The sites were characterized by a wet tropical climate with mean annual precipitation of 3,920 mm and mean annual air temperature of 22.3°C. The temperature was mild and stable with diurnal and seasonal temperature ranges of 3–4°C. Soils were classified as mixed isothermic tropohumult in both the plantation and the secondary forest. The sites were relatively flat with a slope of <5 degrees and an elevation of about 400 m above sea level.

The tree plantation was established on the abandoned cropland in 1976 as part of a reforestation program of the United States Forest Service (Lugo 1992). The secondary forest had naturally developed also on the same abandoned cropland since 1976. The plantation was dominated by *Pinus caribaea* (Morelet) with small trees and grass species underneath the canopy. When our study started in 1996, the average tree height was about 15 m and the average diameter at breast height (DBH) was 22 cm in the plantation. The secondary forest was characterized by a sparse

overstory and a dense understory with abundant shrubs and grasses comparing to the plantation but there were still a lot of spaces among the vegetations. The dominant canopy species in the secondary forest include *Myrcia splendens* (Sw.), *Miconia prasina* (Sw.) and *Casearia arborea* (L C Richard). The major understory species include *Casearia sylvestris* (Sw.), *Miconia mirabilis* (Aubl.) and *Tabebuia heterophylla* (DC.). Total microbial biomass was measured using a fumigation-incubation procedure (Jenkinson and Powlson 1975) in August 1996 and March 1997, which represented a wet and a dry season, respectively. Biomass of active and total fungi was estimated using the agar film techniques (Lodge and Ingham 1991). Biomass of active and total bacteria was obtained using fluorescein isothiocyanate techniques (Zou and Bashkin 1998).

In this study, we found total soil microbial biomass in the litter-and-root exclusion plots decreased the most among all the treatments in both forests. Specifically, total fungal biomass was reduced 84.6 and 87.5% and total bacterial biomass was reduced 62.1 and 56.9%, respectively, in the plantation and the secondary forest. We found that microbial biomass demonstrated considerable seasonal variation in both the plantation and the secondary forest. Total microbial biomass, in general, was greater in the wet season than in the dry season with exceptions for the root exclusion and the litter-and-root exclusion plots in the secondary forest. Total and active fungal biomass was significantly ($P \leq 0.05$) higher in the plantation than in the secondary forest in all treatments during both the wet and dry seasons (Figs 4.3 and 4.4). Total and active fungal biomass was significantly greater in the wet season than in the dry season in both forests.

Microbial biomass was also significantly different among different treatments. The litter exclusion and the litter-and-root exclusion significantly reduced total fungal, total bacterial, active fungal, active bacterial biomass except for the active bacteria in the secondary forest during the wet season. In most plots, the litter-and-root exclusion reduced microbial biomass the most in comparison with the control and the other treatments. While root exclusion significantly reduced total fungal biomass in both forests (Fig. 4.3 a, b). Root exclusion plots, in general, had the least reduction in fungal biomass among all the treatment plots.

We also measured soil CO₂ efflux in the same site in another study (Li et al. 2005) and found microbial activity in the plantation was more sensitive to the litter input than the secondary forest. Soil CO₂ efflux had higher correlation with total fungal biomass but lower correlation with total bacterial biomass in the plantation than in the secondary forest, suggesting that the fungal communities may dominate soil heterotrophic respiration in the plantation, while bacterial communities may take the control in the secondary forest. By separating the total fungal biomass into active and inactive components, we found that active fungal biomass demonstrated higher correlations with soil CO₂ efflux than their corresponding total fungal and bacterial biomass.

In conclusion, fungal biomass and total microbial biomass are important variables in the reforestation processes. Although the plantations and the secondary forests originated from the same abandoned farm lands but they have different proportions of fungal communities and therefore might have different nutrient cycle

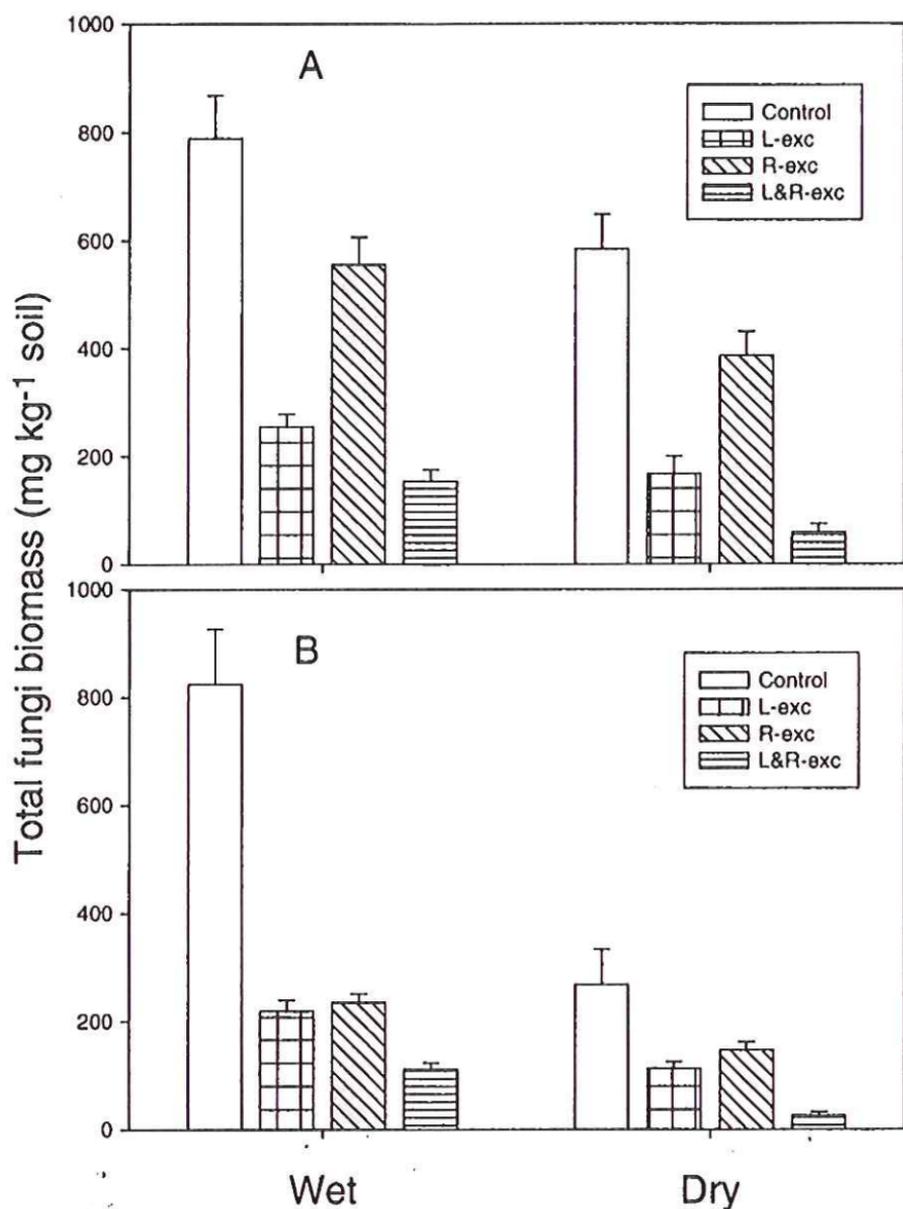


Fig. 4.3 Active fungal biomass (mg C kg^{-1} soil) in the plantation (A) and the secondary forest (B) and active bacterial biomass (mg C kg^{-1} soil) in the plantation (C) and the secondary forest (D) in the wet (August) and dry (March) seasons. Common letters on the bars indicate no significant difference between the treatments at 95% confidence level

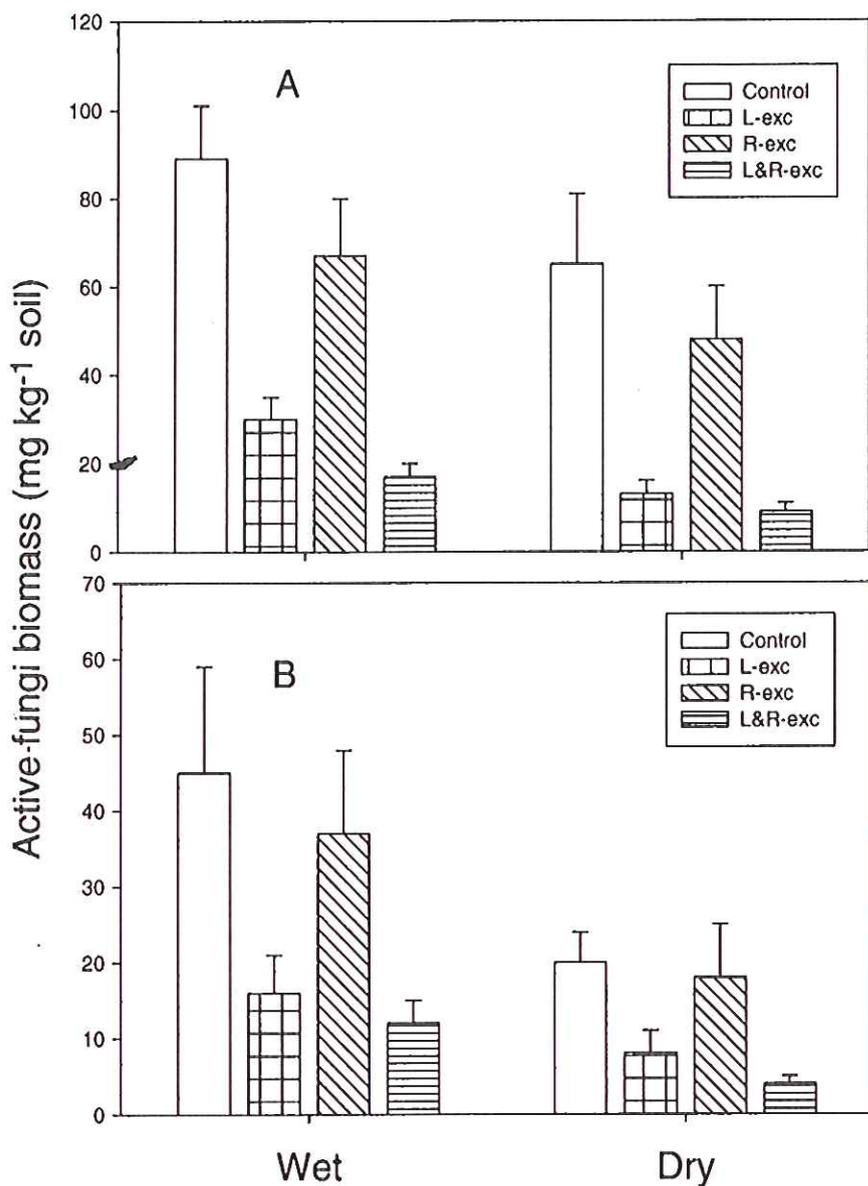


Fig. 4.4 Total fungal biomass (mg C kg⁻¹ soil) in the plantation (A) and the secondary forest (B) and total bacterial biomass (mg C kg⁻¹ soil) in the plantation (C) and the secondary forest (D) in the wet (August) and dry (March) seasons. Common letters on the bars indicate no significant difference between the treatments 95% confidence level

pathways. In addition, separation of active fungal biomass and total fungal biomass may enhance our understanding on the interactions between microbial communities and soil nutrient and organic C cycles.

4.4.2 Macrofauna

4.4.2.1 General Patterns of Macro-Fauna Composition Under Natural and Post-Agricultural Management Practices in the Neotropics

Earthworms, termites, ants, coleopterans, and myriapods constitute the largest component of the macro-fauna. Lavelle and Fragoso (1999) compared 12 communities from tropical rain forests, and estimated that earthworms and termites are the most important macro-fauna in these soils. Lavelle et al. (1994) analyzed the composition of 73 macro-invertebrate communities from 29 sites in the humid tropics and found termites, earthworms and litter arthropods (mostly millipedes and coleopterans) to account for the dominant proportion of the biomass. Further, Lavelle et al. (1997) argued that earthworms and termites are the most important engineers in terrestrial ecosystems based on the influence they exert on the diversity and activity of biota in subordinate trophic levels and the creation of organo-mineral structures that can affect soil physical and chemical properties. In general, earthworms are best represented in grasslands in humid areas as their abundance decreases towards humid forests and dry forests and grasslands (Lavelle et al. 1994). Termites are well adapted to dry environments where earthworms are not found (Menaut et al. 1985). Millipedes are important in litter dominated ecosystems; where their feeding activity is specialized on dead organic matter, or on saprophytic organism consumption (Bertrand and Lumaret 1992).

Disturbances linked to land use practices seem to severely affect the species richness and abundance of soil invertebrate communities world-wide (Lavelle et al. 1997). There are clear differences in soil macro-fauna between forested and grassland systems and other types of land use (Giller 1996). In the Neotropics, annual crops on sites where the natural vegetation has been cleared have depleted macro-invertebrate communities in terms of abundance and biomass (Lavelle et al. 1994); usually irrespective of the annual crop species but mostly associated to soil disturbance and the absence of a permanent soil cover (Barros et al. 2005). Termites seem thrived better than earthworms in annual crops and fallows and as compared to pastures, forests and agroforestry systems (e.g., Lavelle and Pashanasi 1989, Barros et al. 2002). Also for example, Lavelle and Pashanasi (1989) described the soil macrofauna communities of Yurimaguas (Peruvian Amazonia) and found the primary forest to have diverse and abundant fauna with a population density of 4,303 ind. m^{-2} and biomass of 53.9 g. m^{-2} —2 to 3 times higher than in similar environments in Mexico. Yet, clearing and cropping soon destroyed most of the fauna where half of the taxonomic units disappeared (see Table 4.1, Lavelle and Pashanasi 1989); where termites and ants become the dominant in terms of abundance. They also found pastures to have the highest biomass (83.3–159.2 g. m^{-2})

but the lowest population densities (922–2,347 ind. m⁻²) and taxonomic richness (20–27) due to the dominant development of populations of *Pontoscolex corethrurus* (Oligochaeta: Glossoscolecidae) which represent 82.3–95% of the biomass (also see Chapter 5 on more information in earthworm dominance in pastures). Further, secondary forests had a soil invertebrate community with population densities on the same order (4,032 ind. m⁻²) of the primary forest but biomass and taxonomic units were lower in the secondary forest as compared to the latter (see Table 4.1).

4.4.3 Crop Systems

Leaving soils to “rest” or “fallow” is a traditional management practice throughout the tropics for restoration of soil fertility during cropping (Sánchez 1995). Successful restoration of soil fertility normally requires a long fallow period for sufficient regeneration of the native vegetation and establishment of tree species (Young 1997). In this context, Thomas et al. (2004) studied the biodiversity of soil macrofauna along a chronosequence of abandoned rice paddy fields and plots without agricultural disturbance in Northern Argentina. They found that species diversity varied strongly along the chronosequence; it was highest in the natural grassland, lowest in the 2 years- fallow and increased progressively through the chronosequence, but was still lower in the fallow after 15 years of abandonment as compared to the natural grassland. Yet while working on Andean agroecosystems in Colombia, Barrios et al. (2005) found that improved fallows (as an alternative to the natural regeneration of the native flora) could help regenerate soil fertility in degraded volcanic-ash soils via changes in the soil macrofauna diversity. Similarly, in the

Table 4.1 Taxonomic richness, mean abundance and biomass of macroinvertebrates in different types of land-use at Yurimaguas, Peru. Modified from Lavelle and Pashanasi, 1989

Type of land use	Taxonomic units (no.)	Density (ind. m ⁻²) ± SE	Biomass (g. m ⁻²) ± SE
Forests			
Primary forest	41	4,304 ± 933	53.9 ± 8.54
Secondary forest (15 years)	27	4,099 ± 1,828	24.1 ± 5.85
Crops (1st crop)			
High input maize	20	730 ± 221	3.1 ± 1.04
Low input rice	24	3,683 ± 1,059	8.5 ± 2.75
Cassava	18	1,197 ± 283	7.6 ± 3.26
Pastures			
Improved (<i>Bracharia-Desmodium</i>)	27	922 ± 81	159.2 ± 16.4
Moist	23	1,768 ± 308	121.1 ± 20.8
Dry	20	2,347 ± 453	82.3 ± 15.5
Fallows			
6-mo. <i>Centrosema</i> after pasture	22	1,546 ± 253	111.9 ± 13.2
6-mo. Kudzu after high input crop	23	2,214 ± 969	15.5 ± 6.2
Peach-palm + Kudzu cover	32	1,858 ± 380	93.9 ± 25.2

above mentioned study from the Peruvian Amazonia, Lavelle and Pashanasi (1989) found that recent fallows (6 mo.) of Kudzu (*Leguminosea*) and *Centropema* retained characteristics of the system from which they were originally started; continued with low taxonomic richness but then showed increases in the density of the macrofaunal population. Hence, they argued these fallows were on a slight development towards the original forest situation (Lavelle and Pashanasi 1989). Meanwhile, they found the association of palm-trees and Kudzu cover had macro-faunal elements of the primary forest and new species introduced after disturbance and the land was cleared. Thus, it seems that invertebrate communities are best conserved when the derived system has a structure similar to that of the original system, such as pastures planted in savanna areas and tree-based systems in forested areas (Decaëns et al. 1994, 2004, Fragoso et al. 1997, Barros 1999 and as presented by Barros et al. 2002; see Fig. 4.5). In Western Brazilian Amazonia (Barros et al. 2005) found that macrofauna communities in agroforestry systems were similar to the undisturbed

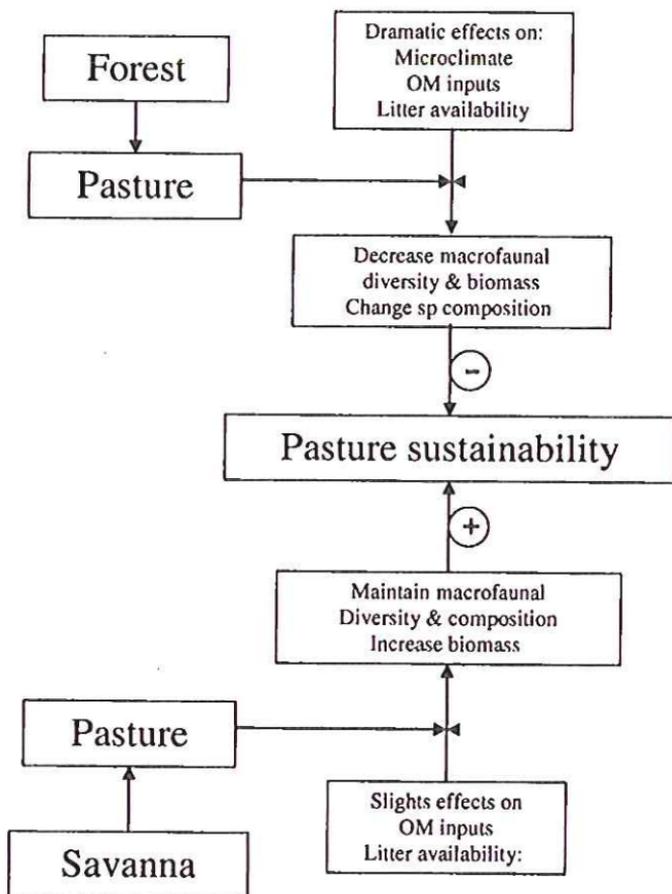


Fig. 4.5 A model of the response of macroinvertebrate communities to pasture establishment and the potential effects on agro-ecosystem sustainability (modified from Decaëns et al. 2004)

lowland rain forest, in spite of higher densities of social insects in the former. Yet in terms of abundance, they showed that land use practices (pastures, fallows, agroforestry and annual crop) were able to sustain sizeable macro-faunal communities similar to those of a disturbed forest.

4.4.4 Agroforestry

In general, pastures have been found to enhance earthworm abundance but reduce the overall macro-fauna diversity, whereas tree-based systems seem to be the best for conserving diversity and sustaining high levels of abundance (Mboukou-Kimbatsa et al. 1998, Barros et al. 2002). Alteration of the land use history plays a major role in determining the abundance and community structure of earthworms and the establishment of exotic earthworms in areas previously inhabited by worms (González et al. 2006). For example, in the tropics, conversion of forest to pastures has been associated to significant decreases in soil macro-invertebrate diversity (Lavelle and Pashanasi 1989) and the dominance of a few exotic earthworm species that can persist along different stages of plant succession after disturbance (e.g., Zou and González 1997, Sánchez-de León et al. 2003). Yet, considering the vast area under pastures and the different edapho-climatic and management parameters in the Neotropics, it is not surprising that the results on biological, physical and chemical properties may sometimes appear contradictory (Brossard et al. 2004). For example, Brown et al. (2004) studied soil macro-faunal communities in native and introduced pastures in Southeastern Mexico and suggested that if nutrient-poor savannas are converted to native pastures, these can maintain higher soil macrofauna populations and earthworm diversity than introduced pastures. Yet, Jiménez et al. (1998) studied earthworm communities in native savannas and man-made pastures of the Eastern Plains of Colombia and found a positive response of earthworm communities (higher density and biomass) to improved pastures; which is a type of land use being increasingly adopted in most Neotropical savannas. Further, Benito et al. (2004) compared macro-fauna communities from the native vegetation of a Brazilian Cerrado with renewed pastures and showed that renewed pastures had less diversity, population density and biomass of macro-fauna than the deforested Cerrado.

With the vast amount of abandoned tropical land due to non-sustainable farming practices, tropical tree plantations become an effective means in restoring soil productivity and preserving ecosystem biodiversity (Zou and González 2001). Tree planting accelerates the process of tree invasions and establishment (Myster 1993) in abandoned agricultural fields and it has been shown to mitigate barriers to secondary succession by re-establishing nutrient dynamics and improving the microclimate for plant understory species (Hagger et al. 1997, Binkley and Resh 1998). Forest management practices can influence earthworm communities through changing physical and chemical properties of soil, net primary productivity, or plant litter chemistry (Fig. 4.6, González et al. 1996, Zou and González 2001). Yet the response of the macro-faunal community to the forest management practices might differ depending among the various groups of fauna given their functionality. For

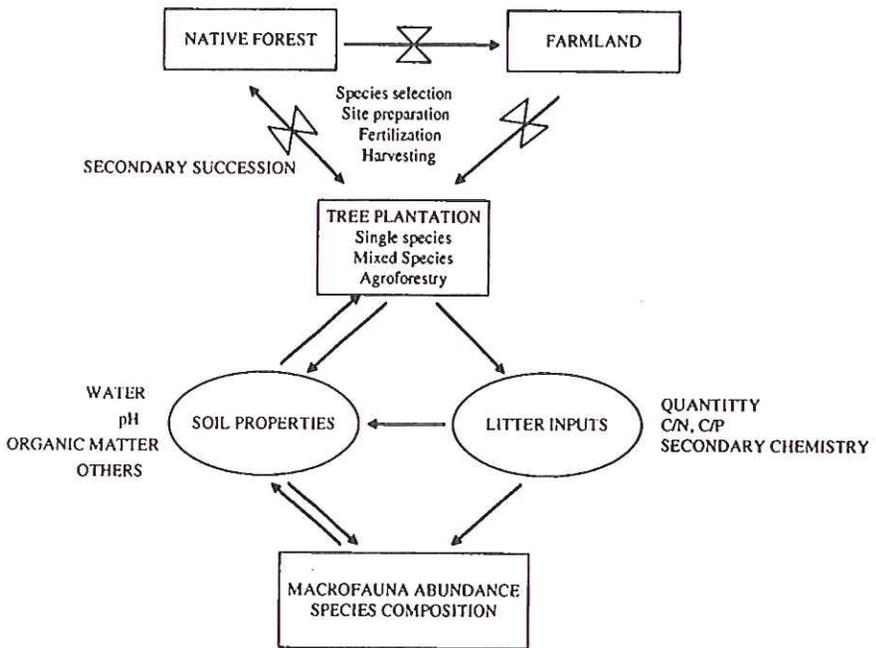


Fig. 4.6 Forest management practices (species selection, site preparation, fertilization and harvesting) that affect earthworm abundance and community structure in tropical tree plantations. Native forest refers to forests that are not disturbed by human activities. Farmland includes crop fields and pastures (modified from González et al. 1996)

example, Warren and Zou (2002) studied soil macro-fauna and litter inputs in three tropical plantations started from a disturbed site in Puerto Rico, and found that earthworm biomass did not differ among plantation treatments. However, they found the millipede biomass and abundance were significantly higher in *Leucaena* than in *Casuarina* and *Eucalyptus* plantations. Further, the millipede biomass was highly correlated to the N concentration and the C/N ratio in the incompletely decomposed organic layer (O_i). Warren and Zou (2002) suggested that in this study, millipedes may be influenced by litter chemistry at fairly small spatial scales, and earthworms are probably more affected by higher order controls such as soil physical conditions.

In the Neotropics and the world in general, soil fauna are important to consider if we are to sustain and maintain, functioning and healthy soils. As forests are converted to pastures, the effects of heavy machinery and trampling by cattle as a result from techniques used for deforestation and pasture management can have widespread and long lasting effects on the reduced abundance and diversity of macro-faunal communities in the newly created pastures (Chauvel et al. 1999); further instigating a cascade of deleterious effects which are linked to ecosystem health (see Chapter 5 for detailed examples on the effects of exotic earthworms on ecosystem processes). Land use alteration in the tropics has historically been dominated by a shift from forest to agriculture, but there are also trends towards increasing urbanization and reforestation. The role of exotic earthworms (the dominant group

in tropical pastures) includes influence on current pasture ecosystems, their potential invasion into surrounding forests and consequent ecosystem effects, their influence on regenerating secondary forests in abandoned pasture, and their overall effects on tropical biodiversity. Many of these potential effects are yet unstudied and unknown (González et al. 2006).

In conclusion, the study of fungi and macrofauna, the major players in the decomposition processes of ecosystem functioning, is of particular importance since knowing the relationship between patterns and activities of fungal and macrofauna communities and biogeochemical changes following land conversion could greatly improve our understanding of the post-agricultural recovery mechanisms. In this chapter, we discussed general patterns of fungi and macrofauna in forests, pastures and agroforestry systems. In general, fungal and total microbial biomass significantly reduced following the conversion from forests to pastures or agricultural lands. In the case study of fungal biomass dynamics following reforestation in Puerto Rico, we found the plantations and the secondary forests have different proportions of fungal communities although they were developed originally from the same abandoned farm lands and therefore might have different nutrient cycle pathways. Soil macrofauna play a very important role in improving structure, organic matter content and distribution patterns of nutrient elements. Soil macrofauna may affect soil function and processes in a variety of ways, and could be used as indicators of nutrient status of soils. In general, earthworms are best represented in grasslands in humid areas as their abundance decreases towards humid forests and dry forests and grasslands. Termites are well adapted to dry environments where earthworms are not found. Millipedes are important in litter dominated ecosystems where their feeding activity is specialized on dead organic matter, or on saprophytic organism consumption. Fungal and macrofauna communities might be the most important variables controlling the biogeochemical changes following land conversion. However, most previous studies have focused on environmental or plant-driven factors over these biogeochemical changes. Future studies on post-agricultural recovery mechanisms need to pay more attention to the forms of trophic interactions among the functional groups, such as fungi and macrofauna, in soil.

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